GENERAL INFORMATION

MEMBERSHIP.—Any person or member of any group engaged in scientific work or interested in the promotion of science is eligible for membership in The Texas Academy of Science. For more information, please access the Academy’s home page at:

http://www.utty1.edu/~tas/taswhat.htm

Dues for regular members are $30.00 annually; supporting members, $60.00; sustaining members, $100.00; patron members, $150.00; associate (student) members, $15.00; family members, $35.00; affiliate members, $5.00; emeritus members, $10.00; corporate members, $250.00 annually. Library subscription rate is $50.00 annually.

The Texas Journal of Science is a quarterly publication of The Texas Academy of Science and is sent to most members and all subscribers. Payment of dues, changes of address and inquiries regarding missing or back issues should be sent to:

Dr. Brad C. Henry
Department of Biology
The University of Texas-Pan American
Edinburg, Texas 78539
E-mail: bradhenry@panam.edu

AFFILIATED ORGANIZATIONS
American Association for the Advancement of Science,
Texas Council of Elementary Science
Texas Section, American Association of Physics Teachers
Texas Section, Mathematical Association of America
Texas Section, National Association of Geology Teachers
Texas Society of Mammalogists

The Texas Journal of Science (ISSN 0040-4403) is published quarterly at Lubbock, Texas, U.S.A. Periodicals postage paid at San Angelo, Texas and additional mailing offices. POSTMASTER: Send address changes, and returned copies to The Texas Journal of Science, Box 43151, Lubbock, Texas 79409-3151, U.S.A. The known office of publication for The Texas Journal of Science and The Texas Academy of Science is P. O. Box 10986, ASU Station, San Angelo, Texas 76909, U.S.A.; Dr. Michael J. Carlo, Treasurer.
CONTENTS

A Late Pleistocene (Sangamonian) Vertebrate Fauna from Eastern Texas.
By John D. Pinsof and Joan Echols ........................................... 3

The Fort Polk Miocene Terrestrial Microvertebrate Sites
Compared to those from East Texas.
By Judith A. Schiebout .................................................. 23

Assigning Numbers to the Nodes on a Ring: The First Step to improved
Performance of a Ring Network.
By A. Kazmierczak .................................................. 33

Field Ecology and Population Estimates of the Veined Tree Frog
(Phrynohyas venulosa) in the Eastern Chaco of Argentina.
By A. Alberto Yanosky, C. Mercolli and James R. Dixon ............... 41

Aggressive Behaviors of Lizards of the Parthenogenetic
Chemidophorus laredoensis Complex (Sauria: Teiidae) in Southern Texas.
By Mark A. Paulissen ................................................. 49

Distributional Records of Small Mammals from the Texas Panhandle.
By Kristie Jo Roberts, Franklin D. Yancey, II and Clyde Jones ........ 57

Annual Fruit Production of Pricklypear (Opuntia engelmannii) and
Mesquite (Prosopis glandulosa) in Southern Texas.
By Lamar A. Windberg ................................................. 65

General Notes

Petroleum Utilizing Bacillus spp. from Soil at Oil Springs, Texas.
By J. Dickson Ferguson III, Stephen L. Beekman
and Thomas G. Benoit ............................................. 73

New Records of the Eastern Cottontail (Sylvilagus floridanus)
and Black-tailed Jackrabbit (Lepus californicus) in México.
By Fernando A. Cervantes, Consuelo Lorenzo and
Mark D. Engstrom .................................................. 75

Radiocarbon-dated Bison from Taos County, Northern New Mexico.
By Spencer G. Lucas, Michael O'Neill and Gary S. Morgan ............. 78

Range Extension of the Freshwater Mussel Potamilus purpuratus
(Bivalvia: Unionidae) in Texas.
By Robert G. Howells .................................................. 79

By R. Kathryn Vaughan ................................................. 83

Instructions to Authors .................................................. 85
THE TEXAS JOURNAL OF SCIENCE
EDITORIAL STAFF

Manuscript Editor:
Jack D. McCullough, Stephen F. Austin State University

Managing Editor:
Ned E. Strenth, Angelo State University

Associate General Editor:
Michael J. Carlo, Angelo State University

Associate Editor for Botany:
Robert I. Lonard, The University of Texas-Pan American

Associate Editor for Chemistry:
John R. Villarreal, The University of Texas-Pan American

Associate Editor for Geology:
M. John Kocurko, Midwestern State University

Associate Editor for Mathematics and Statistics:
E. Donice McCune, Stephen F. Austin State University

Associate Editor for Physics:
Charles W. Myles, Texas Tech University

Manuscripts intended for publication in the Journal should be submitted in TRIPLICATE to:
Dr. Jack D. McCullough
TJS Manuscript Editor
Department of Biology - Box 13003
Stephen F. Austin State University
Nacogdoches, Texas 75962

Scholarly papers in any field of science, technology, or science education will be considered for publication in The Texas Journal of Science. Instructions to authors are published one or more times each year in the Journal on a space-available basis, and also are available from the Manuscript Editor at the above address.

The Texas Journal of Science is published quarterly in February, May, August and November for $30 per year (regular membership) by THE TEXAS ACADEMY OF SCIENCE. Periodical postage rates (ISSN 0040-4403) paid at Lubbock, Texas. Postmaster: Send address changes, and returned copies to The Texas Journal of Science, PrinTech, Box 43151, Lubbock, Texas 79409-3151, U.S.A.
A LATE PLEISTOCENE (SANGAMONIAN) VERTEBRATE FAUNA FROM EASTERN TEXAS

John D. Pinsof and *Joan Echols
Department of Natural Sciences, Daemen College, Amherst, New York 14226,
Geology Division, Buffalo Museum of Science, Buffalo, New York 14211 and
*Department of Earth Sciences, East Texas State University
Commerce, Texas 75429

Abstract.—The Iron Bridge local fauna is the seventh assemblage of fossil vertebrates of Sangamonian age thus far recognized in Texas. These fossils were collected over 30 years ago from an area now inundated by Lake Tawakoni in Rains County in northeast Texas. A minimum of 13 vertebrate taxa are present in the assemblage including one piscine, two reptilian, and 10 mammalian species. Most notable in the collection is a nearly complete cranium of the extinct Shuler’s pronghorn antelope Tetrameryx shuleri. Taphonomic analysis suggests that the fossil assemblage accumulated within an active meandering stream via attritional means. An environmental reconstruction based upon the inferred ecologic and dietary preferences of the taxa reveals three presumably contemporaneous habitats: a permanent stream, grassland, and parkland.

Diverse assemblages of Tertiary fossil vertebrates have been recovered from Texas. Pleistocene deposits have similarly produced numerous and rich assemblages of fossil vertebrates (e.g., Hay 1924; Lundelius 1967; Graham 1987). Among these Pleistocene deposits are six assignable (see Pinsof 1996) to the last interglacial interval, the Sangamonian: the Moore Pit (Slaughter 1966), Pitts Bridge (Hay 1924), Ingleside (Lundelius 1972), Trinidad (Slaughter et al. 1962), Clear Creek (Slaughter & Ritchie 1963), and Easley Ranch (Dalquest 1962) localities. More recently Lundelius (pers. comm.) has promoted a younger age for the Ingleside locality. A heretofore undescribed group of Sangamonian fossils, the Iron Bridge local fauna, is here presented and described. Aspects of the Iron Bridge local fauna have been mentioned by Slaughter et al. (1962), Lundelius (1972), and Preston (1979), but these authors did not elaborate on the faunal constituents.

METHODS AND MATERIALS

Collection of the Iron Bridge fossils occurred intermittently from March, 1959 through October, 1960 during construction of the Iron Bridge Dam on the Sabine River. Upon initial discovery by construction workers of a partial mastodont (Mammuth?) skeleton, Hazel A. Peterson of East Texas State University, her colleagues, and students launched an effort to recover as many bones as possible before completion of the
dam and subsequent flooding of the site. Collecting efforts centered upon excavation of larger bones; no sieving of matrix was performed. Due to a series of unfortunate circumstances, beginning with inadequate time to properly unearth the specimens, a small percentage of the Iron Bridge collection was subjected to breakage, inadequate preparation, or loss. While successful in repairing and stabilizing some specimens, others remain fragmented beyond repair or have disintegrated beyond identification. Thus, several skeletal elements and taxa mentioned in the initial reports by Peterson (1961; 1962) are not documented in the present inventory. As the inaccessibility of the fossil locality precludes further collecting, the materials reported here constitute the existing Iron Bridge local fauna.

The Iron Bridge fossils are curated at the Department of Earth Sciences, East Texas State University (ET) except for a small collection of mussel shells which are housed at the Shuler Museum of Paleontology, Southern Methodist University (SMP-SMU), and two Camelops jaws housed at the Vertebrate Paleontology Lab, the University of Texas at Austin (TMM). Several of the Iron Bridge fossils were directly compared to material in the collection of the Shuler Museum of Paleontology and the Royal Ontario Museum, Toronto (ROM) for confirmation of taxonomic identity. Abbreviations used herein include: L = left, R = right, AP = anteroposterior, and TR = transverse. Dental abbreviations include: I = incisor, C = canine, P = premolar, and M = molar.

**PROVENIENCE AND AGE**

The Iron Bridge Dam, the namesake of the fossil assemblage, interrupts the flow of the Sabine River in northwestern Rains County, thereby creating Lake Tawakoni. This lake occupies parts of southeastern Hunt, northeastern Van Zandt, and northwestern Rains Counties, Texas. The fossil locality (ET Locality 60), which is presently inundated by Lake Tawakoni, is approximately 2 km NNE of the dam spillway and 8 km SSW of the town of Point, or approximately 32° 49’ 30" N by 95° 54’ 45" W (Figure 1).

Pleistocene sediments in the Lake Tawakoni area overlie bedrock of Paleocene Midway Group (Wills Point and Kincaid Formations) and consist of, in ascending order, gravels, sands, and clays for a total thickness of about 9 m (Peterson 1962). The gravel clasts range from 5 to 110 mm in diameter and are supported within a ferruginous matrix of fine sand and clay. These basal gravels dip as much as 45 degrees to the west and have a sharp contact (presumably representing a diastem)
The Iron Bridge local fauna is inferred to be Sangamonian in age from four lines of evidence. First, there are similarities in lithology and stratification between the Iron Bridge sediments and the Hill-Shuler (T2 terrace) fossiliferous beds in nearby Dallas and Denton Counties. Slaughter et al. (1962:56) emphasized these similarities by stating that a "paleontologic correlation exists between [the Iron Bridge] terrace fill and the T-2 deposits on the Trinity River at Dallas. Allowing for the difference in upstream drainage, lithologic similarities are notable."
Given that the radiocarbon age dates of the Hill-Shuler beds are in excess of 37,000 years before present (Slaughter et al. 1962), this age is taken to be the minimum age of the Iron Bridge sediments. Second, the presence of *Bison* suggests an age no older than the Illinoian glacial event. Assuming the Iron Bridge bison to be *B. latifrons* (see below), a Sangamonian (or younger) age is appropriate, as this species achieved its greatest distribution during that interglacial (McDonald 1981). Third, two Iron Bridge faunal taxa, *Alligator* and *Holmesina*, are cold-intolerant and, especially in the case of the latter, are not believed to have been able to survive even mild winters. Fossils of *Holmesina*, a Neotropical immigrant, are known mainly from Texas, Oklahoma, Louisiana, and Florida (James 1957; Kurten & Anderson 1980). The most northern occurrence of *Holmesina* is at Kanopolis, Kansas, which is regarded as an interglacial assemblage (Hibbard et al. 1978). Finally, the faunal constituents of the Iron Bridge and the aforementioned Sangamonian local faunas in Texas are so similar, especially to species, that they appear to represent samplings of one fauna. With these four points taken together, the Sangamonian interglacial seems a reasonable age for the Iron Bridge fossil assemblage. It is acknowledged, however, that refinements in the criteria (e.g., chronological and ecological) for distinguishing between Sangamonian interglacial and early Wisconsinan interstadial deposits may necessitate a younger age assignment of the Iron Bridge local fauna.

**SYSTEMATIC PALEONTOLOGY**

Class Osteichthyes  
Order Semionotiformes  
Family Lepisosteidae  
*Lepisosteus* sp. indet.

*Material examined.*—Partial jaw and isolated scales (ET 5457).

*Remarks.*—A minimum of one individual is represented. The jaw fragment, which is 44.7 mm long, bears a single tooth 5.8 mm in height. The Iron Bridge *Lepisosteus* jaw compares well with that of a modern gar in the Shuler Museum of Paleontology. Several dozen thick, rhombohedral scales characteristic of this genus have also been recovered. Some of the Iron Bridge scales are identical to those from the Hill-Shuler localities (Uyeno & Miller 1962).
Class Reptilia  
Order Crocodilia  
Family Crocodylidae  
*Alligator mississippiensis* (cf. Daudin 1803)

*Material examined.*—Partial skeleton (ET 5352).

*Remarks.*—The American alligator is represented at Iron Bridge by an incomplete cranium and most elements of the axial and appendicular skeleton. The width of the lateral edges of the orbits measured from the dorsal side is 40 mm, the maximum width of the skull (at the posterior end) is 100 mm, and the length of the tail about 330 mm (Peterson 1961). The relatively small size of the skeleton suggests it is a juvenile.

The specimen was found in an articulated state with the limbs flexed and the tail curled around the body. No conclusions can be made from the alligator’s body position, as it may have died while hibernating during a prolonged cold period, or while aestivating during a prolonged drought. Preston (1979) reviewed the Pleistocene record of *A. mississippiensis* from Texas and found, with few exception, that it closely coincided with the range of the living forms.

*Order Testudines*

*Testudines indet.*

*Material examined.*—Eight shell fragments (ET 5351).

*Remarks.*—Eight shell fragments are preserved in the fauna. The relatively great size of the largest specimen, having a maximum length and thickness of 80.1 and 16.4 mm, respectively, suggests it may belong to the extinct tortoise *Geochelone*. The remaining specimens are too fragmentary for specific identification.

*Class Mammalia*

*Order Edentata*

*Family Dasypodidae*

*Holmesina septentrionalis* (cf. Leidy 1889)

*Material examined.*—Osteoderm (ET 5343).

*Remarks.*—*Holmesina septentrionalis*, the correct name of the northern pamphere (Edmund 1987), is known from over 70 middle to late Pleistocene localities in the southern and southeastern United States and from three localities in Mexico (Anderson 1984; Edmund 1987). The specimen is a hexagonal immovable osteoderm (see Hulbert and Morgan...
1993: Fig. 8.3E), with maximum diameter and thickness of 37.8 mm and 8.2 mm, respectively. Comparison of the Iron Bridge specimen to a pampathere osteoderm (SMP-SMU 60841) from Delta County, Texas, did not reveal any significant differences in overall morphology and diameter, except that the former is slightly thinner than the latter.

Order Perissodactyla  
Family Equidae  
*Equus scotti* Gidley 1900  
(Figure 2)

*Material examined.*—Cranial, dental, and postcranial elements (ET 5359 through ET 5397).

*Remarks.*—In terms of numbers of curated specimens, horses are the most abundant in the assemblage, representing at least three individuals. Beyond their close comparison in morphology to modern *Equus*, most of the fossil material, especially the postcranials, are unremarkable.

The diagnostic features of the Iron Bridge horses are found chiefly in two specimens: ET 5359, a nearly complete cranium; and ET 5360, a partial left dentary (Figure 2). The cranium, which lacks only the nasals and basicranium, is compressed dorsoventrally and slightly toward the
right. The basicranial length (basal length: occipital notch to posterior I/) of ET 5359 is 513 mm. All teeth are preserved, including both canines and the right P1/, which is located immediately medial to the anterior end of P2/. The existence of a left P1/ is evidenced by its alveolus and an interdental wear facet on the anteromedial side of the left P2/. The left M3/ had just erupted and shows minimum wear. The salient feature of the dentary (ET 5360) is the deep ectoflexid penetration of the metaconid-metastylid isthmus on all three molars, the so-called "zebrine" style of lower molars (see MacFadden 1992: Fig. 5.22).

Referral of the Iron Bridge horses to E. scotti is based upon characters described in the most recent revision of the genus by Winans (1985; 1989). According to her classification, E. scotti is defined by four traits: (1) basicranial length greater than 500 mm, (2) stout metapodials, (3) ectoflexid penetration on M/1 and M/2 but less frequently on M/3, and (4) P1/ frequently retained and, if present, located medial to P2/. As noted above, these traits, except metapodial size, are evident in the Iron Bridge material. While exceeding 500 mm, the basicranial length of ET 5359 is not as great as the type specimen of E. scotti from Briscoe County, Texas (549 mm; Johnston 1937). Although ET 5359 and 5360 derive from different individuals, their composite features support an identification of E. scotti. No other features in the assemblage (e.g., noticeably different enamel plication patterns of cheek teeth) contradict this identification.

Family Tapiridae
Tapirus sp. indet.

Material examined.—Partial tooth (ET 5347).

Remarks.—The specimen consists of enamel from the posterior loph of an upper right molar. It shows no significant difference in size or morphology from a Tapirus M3/ (ROM 31075) collected from the Florida Pleistocene. Specific identification of the Iron Bridge tapir is not possible based upon the available material.

Order Artiodactyla
Family Camelidae
Camelops sp. indet.
(Figure 3)

Material examined.—Dental and postcranial elements (ET 5414 through ET 5432); mandible (TMM 40436-1); R. dentary (TMM 40436-2).
Figure 3. Occlusal views of Camelops sp. indet., from the Iron Bridge local fauna. A. TMM 40436-1, left cheek teeth. B. TMM 40436-1, right cheek teeth. C. TMM 40436-2, right cheek teeth. All scale bars = 1 cm.

Remarks.—The Iron Bridge camel material is not significantly different in morphology from that of Camelops described by Webb (1965); however, measurements of the two jaws (Table 1), especially those of TMM 40436-1, are slightly smaller than those reported by that author. The partial skeleton (ET 5417) consists of a cervical and a thoracic vertebra, two teeth, a pisiform, and portions of a scapula and two metapodials. Typical of camelids, the cervical vertebra is elongated and narrow. ET 5431, a heavily worn and slightly damaged right M/1 or M/2, has two lobes. The maximum transverse width across the anterior lobe of this tooth is 10.6 mm; the width across the posterior lobe is 17.3
Table 1. Measurements of selected skeletal elements of *Camelops* sp. indet. from the Iron Bridge local fauna. Measurements follow those of Webb (1965: Tables 6 and 10).

<table>
<thead>
<tr>
<th>DENTARY</th>
<th>TMM 40436-1 Left</th>
<th>TMM 40436-2 Right</th>
</tr>
</thead>
<tbody>
<tr>
<td>Parameter Measured</td>
<td>32.3 mm</td>
<td>34.2 mm</td>
</tr>
<tr>
<td>Depth below C</td>
<td>47.0 mm</td>
<td>—</td>
</tr>
<tr>
<td>Depth below anterior part P/4</td>
<td>68.9 mm</td>
<td>65.2 mm</td>
</tr>
<tr>
<td>Length: P/4 to M/3</td>
<td>126.0 mm</td>
<td>131.4 mm</td>
</tr>
<tr>
<td>Length: M/1 to M/3</td>
<td>106.7 mm</td>
<td>110.2 mm</td>
</tr>
<tr>
<td>P/4: AP</td>
<td>23.3 mm</td>
<td>24.3 mm</td>
</tr>
<tr>
<td>P/4: TR</td>
<td>13.0 mm</td>
<td>13.9 mm</td>
</tr>
<tr>
<td>M/1: AP</td>
<td>26.6 mm</td>
<td>26.5 mm</td>
</tr>
<tr>
<td>M/1: TR</td>
<td>20.7 mm</td>
<td>21.4 mm</td>
</tr>
<tr>
<td>M/2: AP</td>
<td>34.1 mm</td>
<td>36.1 mm</td>
</tr>
<tr>
<td>M/2: TR</td>
<td>20.3 mm</td>
<td>20.1 mm</td>
</tr>
<tr>
<td>M/3: AP</td>
<td>51.5 mm</td>
<td>51.5 mm</td>
</tr>
<tr>
<td>M/3: TR</td>
<td>19.8 mm</td>
<td>19.7 mm</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>PROXIMAL PHALANX</th>
<th>ET 5414</th>
<th>ET 5428</th>
</tr>
</thead>
<tbody>
<tr>
<td>AP: proximal end</td>
<td>34.9 mm</td>
<td>—</td>
</tr>
<tr>
<td>TR: proximal end</td>
<td>42.5 mm</td>
<td>—</td>
</tr>
<tr>
<td>AP: distal end</td>
<td>—</td>
<td>28.3 mm</td>
</tr>
<tr>
<td>TR: distal end</td>
<td>—</td>
<td>37.5 mm</td>
</tr>
</tbody>
</table>

mm. Measurements of the proximal phalanges ET 5414 and 5428 (Table 1) fall within the lower range of *Camelops* forelimb proximal phalanges (Webb 1965: Table 10).

Family Cervidae

*Odocoileus* sp. indet.

*Material examined.*—Atlas (ET 5345); basicranium (ET 5346); R. M/1 (ET 5348); R. frontal (ET 5349); L. frontal (ET 5350).

*Remarks.*—At least one individual is represented at Iron Bridge by four cranial fragments and one cervical vertebra. Both frontals are incomplete, each bearing an antler pedicle and a small portion of the orbit. The minimum and maximum diameters of the most complete pedicle on ET 5350 are 23.6 and 26.4 mm, respectively. The basicranium includes both occipital condyles, a complete foramen magnum, and the sphenoid. The atlas lacks some of the left and most of the right wing. Characteristic of *Odocoileus*, the atlas has a deep and broad fossa surrounding the transverse foramen and lacks a process at the ventral lip
of the anterior condyle. The lower molar is 13.1 mm in length and 8.6 mm wide across the posterior cusp.

Family Antilocapridae  
Capromeryx sp. indet.

Material examined.— Partial R. dentary (ET 5353); M/3 (ET 5354); upper molar (ET 5355); lower molar (ET 5356).

Remarks.— A small antilocaprid is represented by an incomplete right dentary and three isolated molars. The alveolus for P/2 is preserved on the dentary as well as P/3 (AP = 5.5 mm; TR = 2.9 mm), P/4 (AP = 5.7 mm; TR = 3.7 mm), and a damaged M/1. ET 5354 measures 15.3 mm AP and 5.3 mm TR. Measurements of ET 5355 and 5356 are 9.7 and 9.2 mm AP and 4.1 and 6.8 mm TR, respectively.

The diminutive size of the teeth rules out all Pleistocene artiodactyls except Capromeryx (cf. Kurten & Anderson 1980). This genus, which has been recovered from dozens of Pleistocene sites in the southern United States and Mexico, contains four species. Measurements of the Iron Bridge cheek teeth are comparable to those of C. furcifer given by Hibbard & Taylor (1960). Because Miller (1971) cautioned against
basing species identifications on isolated antilocaprid teeth, referral of the Iron Bridge \textit{Capromeryx} remains at the generic level.

\textit{Tetrameryx shuleri} Lull 1921

(Figure 4)

\textit{Material examined}.— Associated cranial and postcranial material (ET 5342); partial cranium (ET 5357).

\textit{Remarks}.— Two specimens of Shuler’s pronghorn have been recovered from Iron Bridge: ET 5342, consisting of a cranium, partial left dentary, a partial left metacarpal, and a medial phalanx; and ET 5357, a fragmentary cranium including eight isolated cheek teeth. \textit{Tetrameryx shuleri} is known from two other Sangamonian deposits, the Moore Pit and Pitts Bridge local faunas, both of which are located in Texas (Pinsof 1996).

As the cranium of ET 5342 (Figure 4) is more complete than the holotype (Lull 1921), it deserves thorough description and mensuration (Table 2). The cranium was crushed prior to collection in October, 1959, but it was subsequently reconstructed by Gideon T. James. Those portions not preserved include most of the rostrum, both orbital rims, the left parietal region, most of the occipital crest, virtually all of the ventral surface posterior to the maxillae, and the distal ends of the posterior horn cores. Lull’s (1921) description of the holotype cranium (SMP-SMU 60004) refers to two longitudinal ridges on the dorsal surface separated by a deep median depression which itself bears a longitudinal ridge. While the Iron Bridge cranium possesses the ridged median depression, damage to the frontal bones precludes recognition of the paired ridges. All of the cheek teeth on ET 5342 are well preserved. The Iron Bridge cranium shares the following dental traits with the holotype: hypsodonty, lack of cingula, prominent parastyles and mesostyles on the molars with an especially strong mesostyle on M3/, and a progressive increase in tooth size from P2/ to M3/. The Iron Bridge M3/’s differ from those of the holotype specimen by exhibiting a robust heel on their posterolabial side. This heel is also not present on the M3/’s of ET 5357, suggesting variability in this feature. The two smaller anterior and two larger posterior horn cores are identical to those of the holotype specimen. Where preserved, the horn cores of ET 5342 display subrounded cross-sections, especially at their bases, and a shallow longitudinal sulcus that courses anteriorly on the lateral surface of all four horn cores. A transverse ridge connecting the bases of the two posterior horn cores is present on both ET 5342 and the holotype specimen.
Table 2. Measurements of selected skeletal elements of *Tetrameryx shuleri* from the Iron Bridge local fauna, and of the holotype (SMP-SMU 60004).

<table>
<thead>
<tr>
<th>Parameter Measured</th>
<th>ET 5352</th>
<th>ET 5357</th>
<th>SMP-SMU 60004</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>HORN CORES</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>AP diameter base of left posterior horn core</td>
<td>33.3 mm</td>
<td>32.3 mm</td>
<td>33.0 mm</td>
</tr>
<tr>
<td>TR diameter base of left posterior horn core</td>
<td>20.6 mm</td>
<td>22.0 mm</td>
<td>21.4 mm</td>
</tr>
<tr>
<td>AP diameter base of right posterior horn core</td>
<td>36.5 mm</td>
<td>35.7 mm</td>
<td>32.8 mm</td>
</tr>
<tr>
<td>TR diameter base of right posterior horn core</td>
<td>21.5 mm</td>
<td></td>
<td>20.5 mm</td>
</tr>
<tr>
<td>AP diameter base of left anterior horn core</td>
<td>27.5 mm</td>
<td>34.8 mm</td>
<td>28.4 mm</td>
</tr>
<tr>
<td>TR diameter base of left anterior horn core</td>
<td>19.0 mm</td>
<td>20.8 mm</td>
<td>19.0 mm</td>
</tr>
<tr>
<td>AP diameter base of right anterior horn core</td>
<td>28.6 mm</td>
<td>33.2 mm</td>
<td>28.4 mm</td>
</tr>
<tr>
<td>TR diameter base of right anterior horn core</td>
<td>18.6 mm</td>
<td>22.1 mm</td>
<td>18.7 mm</td>
</tr>
<tr>
<td>Minimum breadth base of horn cores on left side</td>
<td>63.7 mm</td>
<td>65.5 mm</td>
<td>60.2 mm</td>
</tr>
<tr>
<td>Minimum breadth base of horn cores on right side</td>
<td>64.3 mm</td>
<td></td>
<td>64.0 mm</td>
</tr>
<tr>
<td>Crotch to tip length of anterior left horn core</td>
<td>74.0 mm</td>
<td></td>
<td>85+ mm</td>
</tr>
<tr>
<td>Crotch to tip length of anterior right horn core</td>
<td>77.0 mm</td>
<td></td>
<td>94.0 mm</td>
</tr>
<tr>
<td><strong>DENTITION</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Length: P2/ - M3/ (left)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Length: P2/ - M3/ (right)</td>
<td>77.0 mm</td>
<td></td>
<td>76.0+ mm</td>
</tr>
<tr>
<td>Length: P2/ - P4/ (left)</td>
<td>75.1 mm</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Length: P2/ - P4/ (right)</td>
<td>24.1 mm</td>
<td></td>
<td>25.0+ mm</td>
</tr>
<tr>
<td>Length: M1/ - M3/ (left)</td>
<td>24.4 mm</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Length: M1/ - M3/ (right)</td>
<td>52.7 mm</td>
<td>52.0+ mm</td>
<td></td>
</tr>
<tr>
<td>Length: M1/ - M3/ (right)</td>
<td>51.6 mm</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>ET 5352</strong></td>
<td></td>
<td></td>
<td>SMP-SMU 60004</td>
</tr>
<tr>
<td>Left</td>
<td>Right</td>
<td>ET 5357</td>
<td>Left</td>
</tr>
<tr>
<td>M1/ : AP</td>
<td>12.2 mm</td>
<td>13.1 mm</td>
<td>13.5 mm</td>
</tr>
<tr>
<td>M1/ : TR</td>
<td>10.8 mm</td>
<td>10.3 mm</td>
<td>11.3 mm</td>
</tr>
<tr>
<td>M2/ : AP</td>
<td>16.5 mm</td>
<td>16.2 mm</td>
<td>17.2 mm</td>
</tr>
<tr>
<td>M2/ : TR</td>
<td>13.0 mm</td>
<td>12.0 mm</td>
<td>12.5 mm</td>
</tr>
<tr>
<td>M3/ : AP</td>
<td>22.3 mm</td>
<td>22.4 mm</td>
<td>20.8 mm</td>
</tr>
<tr>
<td>M3/ : TR</td>
<td>13.9 mm</td>
<td>11.6 mm</td>
<td>12.4 mm</td>
</tr>
</tbody>
</table>

* = from Lull (1921)

Three additional specimens were curated with the ET 5342 cranium with the presumption that they all belong to the same individual. The left dentary consists of a partial M/3 embedded in a short section of horizontal ramus. The transverse width of the molar is 6.3 mm. The proximal end of the metacarpal measures 17.5 mm AP and 25.8 mm TR. There is a shallow U-shaped groove on its posterior surface. The medial phalanx, 25.5 mm in total length, is slightly damaged at its
Table 3. Measurements of selected skeletal elements of *Bison* sp. cf. *B. latifrons* from the Iron Bridge local fauna. Mensuration of the cranium was performed by Bob Slaughter in 1960 from the jacketed specimen *in situ*. Measurements of *Bison* dentaries follow those of von den Driesch (1976).

### CRANIUM

<table>
<thead>
<tr>
<th>Measurement</th>
<th>ET 5435</th>
</tr>
</thead>
<tbody>
<tr>
<td>Spread of horn cores: tip to tip</td>
<td>1954.0 mm</td>
</tr>
<tr>
<td>Greatest spread on outside curvature</td>
<td>2060.0 mm</td>
</tr>
<tr>
<td>Horn core length: inner curvature, burr to tip</td>
<td>987.0 mm</td>
</tr>
<tr>
<td>Horn core length: outer curvature, burr to tip</td>
<td>1230.0 mm</td>
</tr>
<tr>
<td>Straight line distance, tip to base of burr</td>
<td>965.0 mm</td>
</tr>
</tbody>
</table>

### DENTARY

<table>
<thead>
<tr>
<th>Measurement</th>
<th>ET 5435</th>
</tr>
</thead>
<tbody>
<tr>
<td>Length from the angle: gonion caudale-infradentale</td>
<td>465.0 mm</td>
</tr>
<tr>
<td>Length from the condyle: aboral border of the condyle process-infradentale</td>
<td>493.0 mm</td>
</tr>
<tr>
<td>Length: gonion caudale - aboral border of the alveolus of M/3</td>
<td>148.0 mm</td>
</tr>
<tr>
<td>Length of the horizontal ramus: aboral border of the alveolus of M/3 - infradentale</td>
<td>323.0 mm</td>
</tr>
<tr>
<td>Length: gonion caudale - oral border of the alveolus of P/2</td>
<td>342.0 mm</td>
</tr>
<tr>
<td>Length of cheek tooth row, measured along the alveoli on the buccal side</td>
<td>195.0 mm</td>
</tr>
<tr>
<td>Length of M/3, measured near the biting surface</td>
<td>55.1 mm</td>
</tr>
<tr>
<td>Breadth of M/3, measured near the biting surface</td>
<td>18.7 mm</td>
</tr>
<tr>
<td>Aboral height of the vertical ramus: gonion ventrale - highest point of the condyle process</td>
<td>183.0 mm</td>
</tr>
<tr>
<td>Middle height of the vertical ramus: gonion ventrale - deepest point of the mandibular notch</td>
<td>170.0 mm</td>
</tr>
<tr>
<td>Oral height of the vertical ramus: gonion ventrale - coronion</td>
<td>222.0 mm</td>
</tr>
</tbody>
</table>

proximal end. The distal end of the phalanx is 12.5 mm AP and 10.9 mm TR.

ET 5357 consists of a fragmented cranium including four horn cores, a basicranium, both P3/’s, and all upper molars as isolated teeth. Measurements of the horn cores and molars of ET 5357 are given in Table 2.

**Family Bovidae**

*Bison* sp. cf. *B. latifrons* (cf. Harlan 1825)

*Material examined.*—Partial skeleton (ET 5434); partial skeleton (ET 5435); partial skeleton (ET 5436); partial L. dentary (ET 5458).

*Remarks.*—The remains of at least three crania with associated postcraniumal elements are present in the collection. As recounted by Peterson
(1961; 1962), the manner in which these specimens were found and collected resulted in the destruction of at least one pair of horn cores and other bone. ET 5434, which was collected in April 1959, consists of a partial cranium lacking both horn cores but retaining all 12 cheek teeth, a cervical vertebra, four centra of thoracic vertebrae, two ribs, a proximal left femur, a proximal right humerus, a right scapula, and a partial mandible with right P/3-M/1 and left M/1-M/3. ET 5435 was collected in April 1960 several meters away from ET 5434. After these horn cores were field jacketed but prior to their removal from the earth, the cranium was vandalized, resulting in its loss except for two upper molars. Further excavation at the same site in June revealed a left dentary with P/3-M/3, two thoracic vertebrae, and at least 12 ribs. ET 5436, also collected in April 1960, consists of a partial cranium with only minor portions of the horn cores preserved, and one thoracic vertebra. The single dentary (ET 5458), which retains badly damaged second and third molars, is too fragmentary for mensuration.

The extremely large measurements (taken from the jacketed specimen *in situ*) of the ET 5435 cranium (Table 3) fall only within the range of male *B. latifrons* (cf. McDonald 1981). Observations of the *in situ* ET 5434 cranium (Peterson 1961) suggest that its horn cores were roughly equal in size to those of ET 5435. Whereas the horn cores of ET 5436 were destroyed by a bulldozer, they are reported to have been slightly smaller than those of the other *Bison* crania. Because these horn cores were destroyed and the measurements of the others can not be confirmed, the large Iron Bridge bison are tentatively referred to *B. latifrons*. Measurements of the ET 5435 mandible (Table 3) are approximately 10% smaller than those of *B. latifrons* mandibles from American Falls, Idaho (Pinsof 1992).

*Bison* sp. indet.

*Material examined.*—Dental and postcranial elements (ET 5437 through ET 5456).

Remarks.—Three species of *Bison* (*B. alaskensis*, *B. antiquus*, and *B. latifrons*) have been identified from Sangamonian deposits in Texas (Pinsof 1996). Lacking associations with horn cores, the most diagnostic portion of the bison skeleton (McDonald 1981), it is nearly impossible to assign the isolated elements recovered from Iron Bridge to species.
Order Proboscidea
Family Mammutidae
*Mammut americanum* (cf. Kerr 1791)

*Material examined.*—Cheek tooth fragment (ET 5403); cheek tooth fragment (ET 5404); cheek tooth fragment (ET 5405); cheek tooth fragment (ET 5406); cheek tooth fragment (ET 5407); partial R. M/3 (ET 5408); partial cheek tooth (ET 5409); dentary fragment (ET 5410).

*Remarks.*—Dental remains of the American mastodont are recognized by their relatively thick enamel (6.2 mm on ET 5403), smooth occlusal surface, and the absence of additional enamel plications characteristic of gomphotheres. ET 5410 consists of a small portion of mandible bearing a smooth and conical alveolus. ET 5408, the most complete tooth, consists of the three most posterior lophids (trito-, tetra-, and pentalophid) of a right M/3. Cusps on the tritolophid have sustained light wear; progressively decreasing amounts of wear are evident on more posterior cusps. The maximum width across the tritolophid is 97.1 mm, a value within the observed range of the Ingleside mastodonts (Lundelius 1972: Table 23). The remaining dental specimens are too fragmentary for assignment to specific teeth.

Family Elephantidae
*Mammuthus* sp. cf. *M. imperator* (cf. Leidy 1858)

*Material examined.*—R. M/2 (ET 5399); partial cheek tooth (ET 5400); tooth plate (ET 5401); tooth plate (ET 5402); deciduous P/4 (ET 5433).

*Remarks.*—Only two specimens, ET 5433 and 5399, are sufficiently preserved for mensuration. The former is a deciduous fourth premolar having the anterior four plates preserved. Its maximum height is 43.9 mm, its maximum width is 31.5 mm, and its enamel thickness is 0.8 mm. The latter tooth, a right M/2, is 90.1 mm wide, has a lamellar frequency (*sensu* Maglio 1973) of four, and has an enamel thickness of 2.5 mm. The plates are angled approximately 45 degrees down from the occlusal surface, and the transverse enamel ridges on the occlusal surface are more crescent shaped than linear. ET 5400 consists of five plates, all damaged at the occlusal surface, from the middle of a molar tooth.
Specific identification of the Iron Bridge elephants is more problematic than their obvious generic identity. *Mammuthus primigenius*, the woolly mammoth, may be excluded based upon morphologic dissimilarity of its teeth to those from Iron Bridge, its more northern distribution, and inferred tundra habitat (Harington & Ashworth 1986). The imperial and Columbian mammoths, however, inhabited Texas during the late Pleistocene and are common fossil finds (Agenbroad 1984). Provisional referral to *M. imperator* is suggested by the relatively low lamellar frequency and the relatively thick interplate dentine and plate enamel on ET 5399, although these dental features may also reflect a less progressive *M. columbi*.

**Taphonomy**

Fossil specimens were collected from the entire suite of Pleistocene sediments exposed during dam excavation. Only a few isolated tooth fragments from the basal gravels exhibit surface abrasion. Specimens from the basal gravels are stained orange-brown from the iron within the matrix, and those from the upper clays have limey concretions associated with them. Examples of columnar, sawtooth, and perpendicular bone breaks (Shipman 1981: Fig. 5.2) are evident in the assemblage, but are not in sufficient numbers to be statistically important. The majority of fossils, except a partial alligator skeleton (ET 5352) and Peterson’s original mastodont skeleton (present location unknown), were disarticulated finds. The general lack of surface abrasion and the total lack of carnivore gnaw markings on the bones suggests little or no predepositional erosion and/or rapid burial. Thus, a carcass (or any portion thereof) experiencing rapid burial could yield the few examples of associated skeletal remains seen in the local fauna.

The geologic and taphonomic features of the deposit correspond to the general parameters of the channel-lag taphonomic mode, one of two end-member models of taphonomic behavior within fluvial systems devised by Behrensmeyer (1988). Briefly, the channel-lag mode particularizes recurring patterns of an attritional bone assemblage transported within an active channel containing coarse clastics. Components of the Iron Bridge deposit supporting the channel-lag mode include the presence of basal channel gravel, heterogeneous sediment size, and a preponderance of disarticulated skeletons, broken bones, and large skeletal elements. The channel-lag mode is usually coincident with low gradient, active meandering streams with low sediment loads (Behrensmeyer 1988), an
interpretation concordant with the fining-upward sequence, the lithology of the Iron Bridge sediments, and with drainage patterns of the Gulf Coastal Plain during stands of high sea level (Walker & Coleman 1987). Within the constraints of the model and what is known of the deposit, it is reasonable to infer that the Iron Bridge fossils accumulated within meander channels that were gradually filling with clastic material.

**Environmental Interpretations**

Several difficulties arise when reconstructing the paleoenvironment of the Iron Bridge area. First, there is scant geologic data associated with individual specimens, so that nothing is known pertaining to specific depositional environment(s) of each bone. The absence of recorded vertical (stratigraphic) data during excavation of the fossil material impedes efforts to establish a chronology of ecologic changes at the site (see Shipman 1981). Relevant data on the ecologic changes over time are often deduced from the vertical distribution of a fossil assemblage (Shipman 1981). Further, small mammalian taxa, which are quite specific in habitat choice, are not represented in the fossil assemblage. Therefore, the known or inferred habitat and dietary preferences of the taphocoenose animals must be used to reconstruct the physical environment.

Three physical habitats, presumably representing contemporaneous settings, are suggested by the Iron Bridge taxa. The first habitat, necessitated by the presence of *Lepisosteus*, is a body of freshwater such as a perennial stream. This stream and its associated riparian habitats would have been suitable for *Alligator*. The two remaining habitats, a grassland and a parkland, are inferred, but their relative areal extent is not known. As used herein, the term grassland refers to areas in which grasses dominate and trees or shrubs are rare or absent; the term parkland refers to predominately wooded areas with incomplete canopies but having complete ground cover. *Equus, Camelops, Capromeryx, Tetrameryx*, and *Mammuthus*, all animals known or presumed to be chiefly grazers, most likely inhabited the grassland. Hibbard et al. (1978) suggested that *Holmesina* inhabited well-drained grassy uplands. The presumed parkland inhabitants include *Tapirus, Mammut*, and, according to McDonald (1981), *Bison latifrons*. *Mammut* is often reconstructed as a browser in open spruce-dominated forests; however, stomach contents of a mastodont from Licking County, Ohio consisted largely of nonconiferous flora (Lepper et al. 1991), suggesting a mixture
of browsing and grazing strategies. *Odocoileus* most likely frequented both grassland and parkland habitats on an opportunistic basis, much like their modern counterparts.

**ACKNOWLEDGMENTS**

We thank Bob Slaughter and Hazel Peterson for their assistance during the research phase of this project. Louis Jacobs (Shuler Museum of Paleontology), Kevin Seymour (Royal Ontario Museum), and Howard Savage (University of Toronto) graciously allowed one of us (JDP) access to their respective osteological collections. Brenda Young, Richard Laub, and Ernest Lundelius, Jr. provided critical comments on initial drafts the manuscript.

**LITERATURE CITED**


von den Driesch, A. 1976. A guide to the measurement of animal bones from

JDP at: mammut@aol.com
THE FORT POLK MIocene TERRESTRIAL MICROVERTEBRATE SITES COMPARED TO THOSE FROM EAST TEXAS

Judith A. Schiebout
Louisiana State University, Museum of Natural Science
Baton Rouge, Louisiana 70803

Abstract.—The small mammal faunas of four Miocene sites from western Louisiana are compared with two sites of similar age from east Texas. All sites are Barstovian and the three most abundant categories of small mammals are the geomyoid, cricetid and heteromyid rodents. Each site differs significantly from the others in the distribution of the most abundant small mammals. These relative differences are probably related to forest/grass cover and soil wetness. Taphonomic factors and mode of fossil recovery are also partially responsible for observed differences, and slight differences in age are considered likely. At the Fort Polk sites, squirrels, beavers, lagomorphs, bats, shrews and hedgehogs total less than 10% of the fauna.

Paleontological research on the Fort Polk Military Reservation (Fig. 1) since 1993 has resulted in the first Miocene terrestrial mammal fauna from Louisiana (Schiebout 1994; 1996). The fossiliferous beds, from the Castor Creek Member of the Fleming Formation, are fluvial overbank deposits including fossil soils (Jones et al. 1995). The best concentrations of small vertebrates (Fig. 2) are recovered from conglomerates formed by concentration of coarse material, including soil-formed nodules (Schiebout 1994). Remains of eight orders of land mammals, including insectivores, chiropterans, a lagomorph, a large carnivore, rodents, horses, a prosynthetocerine, and a gomphothere, have been recovered. Lower vertebrate fossils include fish, alligator, gavial, turtle, snake, and lizard remains. Before the discovery of the Fort Polk Miocene site, there was only a single report of a Miocene terrestrial vertebrate from Louisiana. This find, reported by Arata (1966), consisted of the tips of the lower tusks of a gomphothere (Mammalia: Proboscidea). Arata (1966) estimated that the specimen was from Miocene beds at Fort Polk, but precise stratigraphic and locality data were not available. It could have come from the Castor Creek Member.

The Fort Polk Miocene fauna is early late Barstovian in age, probably between 13 and 11.5 million years ago (Schiebout et al. 1996). At that time, the Fort Polk area was coastal, environmentally different from the long-studied Miocene fossil localities of the Great Plains, for example, Norden Bridge site, Valentine Formation in Nebraska (Voorhies 1990).
The two Texas sites at which bulk screening was conducted are the sites most likely to be comparable in fauna. The two Texas sites, Trinity River and Town Bluff in east Texas (Fig. 1), are currently placed in the Burkeville Local Fauna and considered Barstovian (Prothero & Manning 1987).

**METHODS & MATERIALS**

Laboratory treatment of the Fort Polk Miocene conglomerates involves soaking chunks in approximately 10% acetic acid to partially dissolve and break up the rock, which releases a residue including the fossils. A laboratory area and procedures for bulk acid dissolution have been developed at LSU especially to process material from the Fort Polk Miocene. Calcium carbonate is the main mineral in the nodules and in the cement holding the rock together. It is dissolved in weak acetic acid, while teeth and bones are composed of apatite and are not dissolved. Bulk dissolution takes place in hazardous waste overbarrels. Productivity in preliminary results at one of the most productive Fort Polk Miocene sites (Stonehenge) is 0.2 mammal specimen(s) per pound and 429 mammal specimens per ton.
RESULTS AND DISCUSSION

There are five localities in the Castor Creek Member of the Fleming Formation at Fort Polk where the fossil-bearing conglomerate is exposed. All yield fossils which are Barstovian in age. The exposures are usually in creek beds or gullies, although the site at which Miocene vertebrates were first discovered in 1993, named Discovery site (DISC), is a manmade outcrop. In most places, the exposed conglomerate is a near horizontal, tabular ledge, between 10-25 cm thick, and about 1 to 1.5 m wide, with some trough cross-bedding present (Jones et al. 1995). The conglomerate is usually overlain and underlain by a massive gray clay, often with common CaCO₃ nodules.

The most striking generalization about the Fort Polk Miocene fauna is that many of the animal remains recovered in screening, from catfish to rodents, are very small representatives of their taxa. Certainly there are biases produced by the deposition and the mode of recovery of the specimens. The most likely explanation would be that the Fort Polk small mammals are smaller than those at most other sites because of sorting in the original deposition and because of the use of fine screens.
in their recovery. The catfish spines, for example, are smaller than most material used for comparison, and it is difficult to conjecture a single ecological cause for small cricetid rodents and small catfish. Larger bone fragments have been recovered in the screens, however, indicating that the lack of larger rodents cannot be entirely explained by depositional sorting and processing biases. If a beaver the size of Eucastor tortus from Nebraska (Xu 1995) were present, the odds of its teeth being within the range of material concentrated in the fossiliferous conglomerates of Fort Polk are high, and it should have been recovered during this study. Likewise, although many of the Fort Polk Miocene small animals, such as the tiny heteromyids, would pass through the
window screen used in some prior bulk screening at other Miocene sites, material such as the Fort Polk Miocene small beaver tooth should have been found. The possibility that much smaller kinds of mammals would be universally available if similar screening techniques were used at other sites is intriguing, but the more likely scenario is that there is also an environmental component to the explanation. The Castor Creek Gulf coastal environments may have been more finely divided into microhabitats than Great Plains wooded or savanna environments, and may have offered less overall food or perhaps more concentrated food sources available to small forms. Black (1963) commented that forest dwelling forms tend to be rare as fossils, and many of the Fort Polk animals are probably forest types.

Intersite variation at Fort Polk is approached herein solely by comparison of the faunas recovered by laboratory processing and screening. The lack of appreciable surface exposure of the claystones from which the Discovery site large fauna appear to be weathering, at the other Fort Polk Miocene microvertebrate sites (TVOR, Gully, Stonehenge), rules out their yielding comparable large material. For further description of the sites, see Jones et al. (1995). In addition to comparing the Fort Polk Miocene sites to each other (Fig. 3), they can be compared to the two Texas Coastal Plain sites from which good faunas of small animals are available (Dorsey 1977). The Texas sites (Town Bluff site and Trinity River site), shown in Figure 4, have the most abundant faunas from a Southern Methodist University program, which Dorsey (1977) reported as having screened 150 tons. The amount
Table 1. Statistical comparison of rodent distributions (Figures 3 and 4) at Fort Polk and Texas sites. All Chi square values are significant at the 0.001 level. Results were obtained by use of the StatView II Program.

<table>
<thead>
<tr>
<th></th>
<th>DISC</th>
<th>TVOR</th>
<th>STONEHENGE</th>
<th>GULLY</th>
<th>TRINITY RIVER</th>
<th>TOWN BLUFF</th>
</tr>
</thead>
<tbody>
<tr>
<td>DISC</td>
<td>248.1</td>
<td>25.7</td>
<td>161.5</td>
<td>51.3</td>
<td>112.6</td>
<td></td>
</tr>
<tr>
<td>TVOR</td>
<td>1435.7</td>
<td>12206.3</td>
<td>423.6</td>
<td>317.5</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Stonehenge</td>
<td>881.6</td>
<td>63.4</td>
<td>83.9</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Gully</td>
<td></td>
<td>104.2</td>
<td>168.6</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Town Rr.</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>62.8</td>
</tr>
</tbody>
</table>

screened from Fort Polk for roughly similar amounts of rodents is about 1.5 tons.

Modern heteromyid rodents prefer open areas, and cricetid rodents prefer wooded areas (Dorsey 1977). This type of information may be used to infer the extent of forest cover of individual Fort Polk sites. At three Fort Polk sites, cricetids outnumber heteromyids (Fig. 3), a situation suggesting more forest cover and fewer open areas, and at the fourth site the situation is reversed. Trinity River site has more cricetids than heteromyids and Town Bluff has more heteromyids than cricetids.

The presumed ecology of geomyoids at both Fort Polk and the two Texas sites is less certain, because they may not be closely comparable to modern geomyoids. Dorsey (1977) referred the Texas geomyoids to *Texomys* and *Jimomys*. The Louisiana specimens are tentatively referred to *Texomys*. Korth (1994) called *Texomys* and *Jimomys* "problematical taxa". At DISC, TVOR, and Trinity River sites, geomyoids are first in abundance, cricetids second, and heteromyids third. At Gully site on Fort Polk, geomyoids are first in abundance, with heteromyids second, and cricetids third. At Town Bluff site in Texas, heteromyids are slightly more abundant than geomyoids, with cricetids third. Stonehenge is the only site of the six to have cricetids most abundant, with geomyoids ranking second, and heteromyids third.

All of these sites exhibit statistically significant differences in rodent distribution (Table 1). All probably included specimens from both wooded and open areas, probably averaging mixed environments, in addition to time averaging, the result of the mode of burial and
recovery. The Texas sites were sandy (Jacobs, pers. comm.), probably deposited in fluvial channels, and much larger amounts of material were reported screened at the Texas sites. These differences suggest that the percentage differences between Texas and Fort Polk sites, which are roughly equivalent in rodent taxa, should not be overemphasized. Possibly, Stonehenge was the most heavily wooded of the Fort Polk sites, DISC, TVOR, and Trinity River had a more mixed environment, and Town Bluff was the most open, but still had a significant wooded component. It appears that the geomyoids thrived in a variety of coastal areas in the middle Miocene.

An animal present at Fort Polk, but absent at the Texas sites, despite the larger amounts screened, is a lagomorph. A single lagomorph tooth, identified by Dawson (pers. comm.) as cf. Hypolagus, has been recovered from the Stonehenge site. Slaughter (1981) has commented on the absence of Miocene rabbits in the Gulf Coast. It now appears that this lack does not include Louisiana.

In addition to analysis of the animals present in the Fort Polk Miocene sites and consideration of variation between sites, it is interesting to consider some of the animals that might be expected to be present at these sites, but which are absent. Of course, in the case of vertebrate fossils, absence of specimens can indicate that the animals were not preserved or have not yet been found. For large members of the fauna, the chance that more kinds remain to be found is good. Their remains are scarce and scattered in occurrence, exactly what might be expected from normal attrition without much effect of concentrating agents. Four genera of rhinoceroses are known from the Texas coastal plain, including two dwarf species (Prothero & Sereno 1982), so the appearance of an unmistakable rhinoceros specimen in the Fort Polk Miocene had been expected. Rare, small fragments of teeth with enamel thicker than that of the horse or prosynthetocerine, but smaller than that of the gomphothere, currently document some type of rhinoceros at Fort Polk. Also, among the missing are small ruminants and the many large rodents reported from other sites similar in age. In some cases, Fort Polk Miocene small fragmentary specimens indicate the presence of forms which cannot yet be identified on the available material. An example is LSUMG 3599, a small artiodactyl right premolar, which differs from AMNH 95489, Blastomeryx from the Trinity River site in Texas, in lacking a distinctive posterolabial heel. Further specimens are needed for more precise identification, but LSUMG 3599 indicates the presence
of a Blastomyx-sized small artiodactyl in the Fort Polk assemblage. Holman (1977) reported four salamanders, four anurans, and nine snakes from the Miocene of the Texas Gulf Coast. Some of these taxa may be present in the Louisiana Barstovian.

Differences between the Texas and Louisiana sites can be partly a result of age differences as well as differences in paleoenvironment, taphonomy, and collecting methods. The Texas sites fit into a long-studied sequence of Texas Miocene vertebrate local faunas (Wilson 1956; Fig. 5) as part of the Burkeville Local Fauna. The Louisiana sites show closest affinity to the overlying Cold Spring Local Fauna (Schiebout et al. 1996). The correlation of the Fort Polk fossils with the Cold Spring Local Fauna is made mainly on the presence of a similar prosynthetocerine, *Prosynthetoceras francisi*. The Synthetoceratinae have been recently revised by Patton & Taylor (1971). The Trinity River site yields *P. trinitensis*, considered by Patton & Taylor (1971) to be an incursion of Great Plains stock into the Gulf Coastal region and not closely related to the common Burkeville *P. texanus*, forerunner of *P. francisi*. If the correlation of the Louisiana sites with those at Cold Spring on the basis of *P. francisi*, a large animal, is correct, then there are no Texas micromammal sites of comparable age to those from
Louisiana. The similarities between Texas and Louisiana collections of micromammals may or may not span the entire Burkeville and Cold Spring intervals. As additional large taxa are recovered from Fort Polk, the biostratigraphic importance of the prosynthetocerine may weigh less heavily, and the Louisiana sites be linked more closely to the Burkeville Local Fauna. The number of Fort Polk specimens and taxa being recovered is increasing steadily. These finds are expected to refine correlation and paleoecological comparison to Texas Miocene sites and others.

ACKNOWLEDGMENTS

I wish to thank individuals at Fort Polk, especially Director of Public Works, Lieutenant Colonel Rory A. Salimbene, and his environmental staff, including Dr. Charles Stagg, James Grafton, Bob Hays and James Hennigan, for their help and cooperation which made this research possible. I appreciate being allowed to study specimens in the collections of the Shuler Museum of Paleontology, Southern Methodist University, and in the Frick Collection of AMNH. Louis Jacobs of Southern Methodist University, Margaret Stevens of Lamar University, and Mary Dawson of the Carnegie Museum of Natural History were among many colleagues providing helpful discussions. Timothy Dalbey, Louis Jacobs, Ruth Hubert, Brett Dooley and two anonymous reviewers provided helpful comments on the manuscript.

Work is currently supported by U. S. Army FORSCOM, on a contract administered and managed by Timothy S. Dalbey, Fort Worth District, U. S. Army Corps of Engineers, issued under Contract No. DACW64-94-D-0008, Delivery Order No. 006, entitled "Paleofaunal Field Survey, Collection, Processing, and Documentation at Two Locations on Fort Polk, Louisiana" to Prewitt and Associates, Inc. Parts of the discussion comparing Texas and Fort Polk Miocene sites were presented in a report of the same title to the U. S. Army Corps of Engineers, submitted for review in August, 1995. Support has also been provided by the LSU Museum of Natural Science.

LITERATURE CITED


JAS at: naschi@lsuvm.sncc.lsu.edu
ASSIGNING NUMBERS TO THE NODES ON A RING:
THE FIRST STEP TO IMPROVED
PERFORMANCE OF A RING NETWORK

A. Kazmierczak
Department of Computer Science, University of Texas at Tyler
Tyler, Texas 75799

Abstract.—Recent research into computer communication networks has focused on improving performance of token ring networks. Many protocols openly depend on the nodes of the ring being numbered in increasing order, each node knowing its own number and the relative positions of all other nodes in the network. It has always been assumed a means exists to order the nodes and determine their relative positions. This paper provides that means.

Recent research into computer communications networks has focused on improving network performance. One idea proposed for a token ring network is to reuse the information field of a packet to send "hidden" information to another node. If the destination, or another node, has information to send to another node, it can reuse the information field of the packet already delivered (Zhu & Denton 1992; Xu & Herzog 1988).

Several networks have been proposed or implemented which use dual counter-rotating rings. Both rings are used to send packets, a node uses the ring on which the destination is closest (Bondavalli & Strigini 1991; Cidon & Ofek 1990; Yih et al. 1993; Schaffa et al. 1993).

Several proposals to improve the throughput of a token ring network rely on having multiple tokens on the ring (Kamal 1990), or partitioning the ring into multiple segments (Ho & Mukherjee 1990). These protocols, and many more (Song & Yang 1993; Wee & Kamal 1992; Dobosiewicz et al. 1990), require the nodes of the ring to be numbered sequentially and to know the relative positions of all other nodes. It is necessary to sequentially number the nodes because the simplistic approach of following the logical ordering is totally inadequate. The logical ordering provides no information about the relative positions of nodes.

This paper presents the means to sequentially number the nodes on the ring and to make relative position information available to all nodes. The technique used has been termed "leader election in a ring" (LeLann 1977; Chang & Roberts 1979; Hirschberg & Sinclair 1980; Dolev et al.
1982; Peterson 1982; Frederickson & Lynch 1984; Frederickson & Lynch 1987) in the area of distributed algorithms. Hereafter, it is referred to as leader election.

This paper contains section addressing the following major topics: some results of leader election in distributed algorithms, numbering the nodes in the ring and disseminating the relative position information, special LAN configurations, an approximate performance analysis, and conclusions.

**Leader Election in a Ring**

A leader election algorithm finds the distinguished node with the smallest (or largest) identifier, where each node has a unique identifier in an ordered set of identifiers. This identifier could be a name assigned to the node or the node address used to address packets to the node. The node address is usually a number programmed into the communication card installed in the node. In addition, the other nodes in the ring are informed of the identifier selected.

The problems of leader election in a ring have been vigorously investigated by researchers in the area of distributed algorithms. Many algorithms have been proposed which run from very straightforward (LeLann 1977; Chang & Roberts 1979; Hirschberg & Sinclair 1980) to complex (Dolev et al. 1982; Peterson 1982; Frederickson & Lynch 1984; Frederickson & Lynch 1987). The more complex algorithms were designed to reduce the number of messages needed to elect a leader.

Chang & Roberts (1979) describe a very simple distributed algorithm where a node can receive from the left and send to the right. Any one node or number of nodes can start the algorithm. Unlike LANs, distributed algorithm nodes can send a message without permission of a token. However, as shown in the next section, this algorithm works for a token ring LAN.

Assume the smallest identifier is sought. The algorithm starts by a node sending its identifier to the right. The node receiving the message compares the received identifier with its own and passes the smaller identifier to the right. Thus, the smallest identifier circulates completely around the ring and is received by the node having that identifier and all nodes know the smallest identifier. Chang and Roberts prove the correctness of the algorithm.
Table 1. Sequence of node numbering of formal algorithm.

```
Begin
  execute leader election algorithm
  node 1 sends broadcast packet
  upon return of broadcast packet send free token to neighbor
repeat
  for each successive node
  begin
    upon receiving broadcast packet, store node info
    upon receiving free token
    begin
      increment last number received
      assign this number to self
      send broadcast packet
      upon packet return send token to neighbor
    end
  end
until node 1 receives free token
node 1 terminates algorithm
End
```

**NUMBERING THE NODES ON A RING**

Sequential number assignment to the nodes on a token ring LAN requires two phases. Phase one consists of one execution of the leader election algorithm described in the last section. Phase two assigns numbers to nodes sequentially, starting at the node numbered 1. The following two sections describe these phases informally.

**Finding node number 1.**—Finding the node to number 1 requires execution of the leader election algorithm described above with only a minor modification. In the case of a token ring, only one node can transmit at one time, so only one node can start the algorithm. The node starts the algorithm by sending a broadcast packet, a packet received by all nodes, containing its identifier and notifying all nodes that leader election is taking place. As this packet traverses the ring, each node compares the received identifier with its own and passes the smaller identifier.

This phase of the algorithm terminates when a node receives a packet containing its own identifier. The node then assigns itself the number 1.

**Numbering the nodes.**—Phase two, assigning sequential numbers to the nodes, is straight-forward. The node numbered 1 sends a broadcast packet with its identifier and assigned number so all other nodes know it is numbered 1. When the packet returns, node 1 sends the free token to the next node on the ring.
Figure 1. An eight node ring.

The node receiving the free token is next to assign itself a number. It assigns itself \( i + 1 \), where \( i \) is the number transmitted in the last broadcast packet. This node then sends a broadcast packet containing its identifier and assigned number so all other nodes learn its relative position. When the packet returns, the node sends the free token to the next node.

This process is repeated until all nodes have assigned themselves a number and broadcast their identifier and assigned number. The process terminates when node 1 receives the free token.

As each node receives the broadcast packet containing the identifier-assigned number pair, it builds a table containing node identifiers-assigned number pairs. This table provides relative position information. At the termination of phase two, all nodes are numbered in sequential order and know the identifier and assigned number for every other node on the ring. Henceforth, whenever a node has information to send, it can check this table to determine the relative position of intended destination.

Table 1 is a more formal description of the node numbering algorithm written in a very high level English like language.

**Correctness**

*Theorem 3.1.*—The node numbering algorithm correctly sequentially numbers the nodes in a ring.

*Proof.*—Phase one is an application of an existing algorithm and has already been proven correct.

Phase two is initiated by node 1 sending a broadcast packet giving its
identifier and assigned number. All nodes copy this information. Node 1 then sends the free token to its neighbor. This node increments the number last received and assigns the number to itself, number 2, before sending a broadcast packet. Node 2 then sends the free token to its neighbor. This process is repeated for each node until the free token reaches node 1.

Since each node increments the number last received before assigning the number to itself, and the numbering begins and ends with node 1, the nodes are numbered sequentially and the algorithm is correct.

**Examples**

*Node numbering.*—Figure 1 shows a simple eight node ring network. For this example a single character is used to denote a nodes identifier. As is clear from the figure, a nodes identifier carries no information of the order of the nodes or their relative positions.

Assuming the direction of transmission is clockwise, Figure 2 shows the same eight node ring after execution of the node numbering algorithm. Phase one of the algorithm chose the smallest node identifier, A, as the leader so node A is assigned number 1. The rest of the nodes are then numbered sequentially in a clockwise rotation by phase two of the algorithm.

*Transmitting hidden information.*—This section describes how the protocol of Zhu and Denton (Zhu & Denton 1992) works and how it depends on the correct sequential numbering of nodes on the ring.

Figure 3 shows one packet transmission scheme. In this case, node Y sends a packet to node E, indicated by the solid line. The packet is
transmitted unused to node M, indicated by the dashed line. Node M uses the packet to send to send a hidden packet to node I, indicated by the solid line. The packet is then transmitted unused to node Y, indicated by the dashed line, where the node is removed from the ring. The packet can be used for node M to node I transmission only because node I is encountered before node Y.

Figure 4 shows another packet transmission scheme. In this case, node Y sends a packet to node C, indicated by the solid line. The packet is transmitted unused to node I, indicated by the dashed line. Assume that node I has information to send to node Q. The unused packet cannot be used for this transmission because node Y will be encountered first and node Y, as the source of the original packet, will remove the packet. Thus the packet must be transmitted unused from node I to node Y, indicated by the dashed line.

Special LAN configurations.—The above two phase algorithm for numbering the nodes on a ring is designed for topological rings in which nodes are indistinguishable and no node is required to perform any special processing. This is not always the case since two other situations exist. First, one node might perform some special function, like the monitor node of an IEEE 802.5 ring. Also, the network may not be a topological ring but a topological star.

In both cases, the algorithm needs to execute phase two only. In the first case, the monitor node declares itself leader and initiates phase two. In the other, the central node assigns the numbers since it has knowledge of all other nodes on the network.

In any case, on a ring with all nodes equal or topologies with special nodes, the nodes are numbered in sequential order around the ring.
Approximate performance analysis. — The following notations and terminology are adopted:

- \( r \) - time to transmit a packet
- \( p \) - mean time for a packet to propagate between nodes
- \( t \) - mean time for a token to propagate between nodes
- \( N \) - number of nodes on the ring
- \( T_L \) - time for leader election
- \( T_N \) - time for node numbering
- \( T \) - total time for algorithm

Referring to Figure 1, the worst case scenario is if node Y starts the algorithm. In this case, phase 1 will require the free token to work its way completely around the ring once. This will take time:

\[
T_L = 2N(Np + r + t)
\]

Phase two requires the free token to work its way completely around the ring once. During this time each node will send one broadcast packet. Phase two then takes time:

\[
T_N = N(Np + r + t)
\]

Thus the total time taken by the entire node numbering algorithm is:

\[
T = T_L + T_N = 3N(Np + r + t)
\]

CONCLUSIONS

This paper has provided a technique to sequentially assign numbers to nodes in a token ring network. The technique provides the means necessary for many protocols to operate correctly based on the fact the protocols require nodes to be numbered sequentially.
If the ring is stable, that is, if nodes are rarely added or removed from the ring, this algorithm needs to be executed only once, when the ring is initialized. The cost of initialization is well worth the price since now the performance gains of the protocols can be realized.

LITERATURE CITED


AK at: akazmier@mail.uttyl.edu
FIELD ECOLOGY AND POPULATION ESTIMATES OF THE VEINED TREE FROG (*PHRYNOHYAS VENULOSA*) IN THE EASTERN CHACO OF ARGENTINA

A. Alberto Yanosky, C. Mercolli and *James R. Dixon

Fundacion Moises Bertoni, Rodriguez de Francia 770, Asuncion, Paraguay and
*Department of Wildlife and Fisheries Sciences, Texas A&M University
College Station, Texas 77843 USA

Abstract.—Breeding times for the veined frog, *Phrynohyas venulosa* (Salientia: Hylidae) from northeastern Argentina, are associated with a daily rainfall of 60 mm or more. Population dynamics, based upon capture and recapture data, suggest a mode of 800-1080 individuals per hectare. A description of reproductive behavior is given and developmental times of 30-32 days are presented. At least four color pattern variations exist in this population. Hibernation occurs in tree cavities.

Resumen.—Las épocas de cría para la rana venosa, *Phrynohyas venulosa* (Salientia: Hylidae), del noreste de la Argentina, están asociadas con una precipitación diaria de 60 mm o más. La dinámica de la población, basada en los datos de captura y recaptura, sugieren un modo de 800-1080 individuos por hectárea. Se da una descripción de conducta reproductiva y se presentan tiempos de desarrollo de 30-32 días. Existen por lo menos cuatro variaciones de configuraciones de color en esta población. La invernación ocurre en los huecos de árboles.

*Phrynohyas* is one of four genera in the family Hylidae having paired lateral vocal sacs. Four species of this genus are currently recognized according to size, structural features, coloration and cranial osteology (Duellman 1971). *Phrynohyas venulosa* is the most widespread species, occurring in tropical lowlands from northern México to northeastern Argentina (Cei 1980; Lutz 1973). The southernmost populations of the species, are found in the Chaco territories of northern Argentina, Paraguay and neighboring Brazil (Cei 1980). Body size reduction and the presence of a normal dorsal pattern have been reported for Paraguayan specimens; e.g., snout-vent length of 64.2 to 86 mm for males and 68 to 89.1 mm for females (Duellman 1971). Some aspects of the ecology and behavior of *P. venulosa* in Panama and southern Mexico have been reported by Zweifel (1964) and Pyburn (1967), and summarized by Cei (1980). Though no information is available for the species from the subtropical environment of Argentina, Cei suggests Argentine populations would display little difference in ecology or behavior from more northern populations. Additional information on Argentine populations of this widespread frog was not available as of 1986 (Cei 1987).
Phrynohyas venulosa is of large size, highly polymorphic in color pattern (McDiarmid 1968), broadly distributed but uncommon, with venomous properties of skin secretions (Lutz 1973). It deposits eggs on the water surface with rapid development (Duellman 1986). Zweifel (1964) suggests that rapid egg development is an adaptation to poorly oxygenated waters.

The occurrence of Phrynohyas venulosa in Formosa, northeastern Argentina was assumed by Cei (1980) and Gallardo (1987), and its presence confirmed by Yanosky et al. (1993). This species is relatively common at El Bagual. Ecological data were obtained and are herein given for the southernmost limit of its distribution.

**MATERIALS AND METHODS**

The study area, El Bagual Ecological Reserve, is strategically located between Río Pilcomayo National Park on the north, Formosa Nature Reserve on the east and Chaco National Park on the south. The reserve contains 3,600 hectares with a modestly equipped biological station. Since 1987, surveys were designed to generate a database on biodiversity of the fauna and flora for the Formosan Humid Chaco Region, a poorly known area within Argentina.

From November 1993 through October 1994, an average of five evenings per week were spent searching for individuals of Phrynohyas with flashlights. Special search efforts were made on rainy nights and successive nights thereafter. The time and place of chorusing males were noted. Specimens were captured using rubber gloves to avoid skin secretions, placed in plastic bags, and returned to the laboratory for obtaining weight and length measurements, and later released. Measurements consisted of snout-vent length taken with calipers (± 0.1 mm), and body weight with pesola scales (± 0.1 g). Sex was determined by the everted lateral black vocal sacs and conspicuous corneous nuptial pads on the first finger. Specimens were toe-clipped using a non-repetitive method that allowed identification upon recapture. The dorsal pattern was illustrated for each specimen, iris coloration and pattern noted. Occasionally, trees were felled and efforts were made to locate Phrynohyas in tree hollows. Statistix 4 was used for statistical analysis and tests employed are cited in the text. Measurements on body size were log₂ transformed for linearity, and statistical significance was 0.05.
RESULTS

Morphometrics.—The relationships of snout-vent length (SVL) to body weights of 70 individuals of Phrynohyas venulosa is shown in Fig. 1. Log transformed data (Fig. 2) resulted in a simple regression line best represented by the equation Log$_2$ SVL = 4.66 + 0.32 Log$_2$ Weight ($r^2 = 0.92$; $P = 0$). Twenty-eight males measured were 80.39 ± 8.98 mm SVL (64.2-95) and 33.02 ± 11.66 g weight (15-64). Log transformed length and weight was best represented by the equation Log$_2$ SVL = 5.01 + 0.264 Log$_2$ weight ($r^2 = 0.68$; $P = 0$). Twenty-nine females averaged 76.82 ± 11.837 mm SVL (60.1-110) and 34.6 ± 16.72 g (12-75) with an homogeneous distribution of sizes within this range. Log transformed variables were best represented by the equation Log$_2$ SVL = 4.84 + 0.28 Log$_2$ weight ($r^2 = 0.74$; $P = 0$). The data showed that sexes were not significantly different in SVL ($t = 1.09$; dF = 28; $P = 0.2871$), or in body weight ($t = 0.51$; dF = 28; $P = 0.6118$).

Metamorphic size is not known for this species. Of 17 small specimens, two were 19.6 and 19.9 mm SVL and 0.55 and 0.65 g in body
weight, respectively. They were captured on 14 and 17 December 1994 in high forest drift fences installed for other types of herpetological studies. The data suggest rapid development from tadpole to froglet (30-32 days) for this species, given that the first breeding opportunity was 12 November.

Population estimates.—Prior and post winter observed captures/recaptures (39/7, 21/7, respectively) and expected (9.1 and 4.83), resulted in an insignificant difference ($X^2 = 1.45; df = 1; 0.1 < P < 0.25$) in capture/recapture data for estimates of population size.

Petersen’s method of population size estimates resulted in a mean density of 69.48, SD = ± 52.49 *Phrynohyas*, for the study area over the seven months the species were captured and released. Schnabel’s method gave an estimate of 91.28 ± 7.54 specimens, with a 95% interval of confidence of 84-99. The regression method gave a similar estimate of 91.13 with an interval of 80-107. Bailey’s method gave an estimate of 127.68 ± 34.06 with an interval of 94-162 specimens for the study area. Although Peterson’s method showed the lowest estimated
density, conservatively, both Schnabel and Regression's estimates yield similar densities. Based upon the two latter estimates, the 0.1 ha study area would support a density of 80 to 107 Phrynohyas. This assumption suggests that a total biomass of 2.35 to 3.15 kg for this species, based on 60 individuals captured at the site with an average weight of 29.41 g. Extrapolating for total habitat within the reserve, a density of 800 to 1070 Phrynohyas per hectare was estimated.

Reproduction.—On 21 October 1994, a 160 mm rainfall filled a 2 by 10 m artificial pond. Ten males (8 captured) called from tree branches 1.5 - 2 m above water, another male called thirty meters northeast, and two others called 50 meters northwest of the pond. These three males were calling from tree branches with no standing water nearby. The next day seven males called from water; these males moved around the pond with all legs extended and the black lateral vocal sacs inflated. They "danced" about in the water and frequently touched one another. Similar observations were made on three other specimens, (two males, one female) in a 3m² pond 50 m north of the primary pond. They were "dancing" in clear water with tall grasses. Males gave release calls when amplexed by other males. Tape recordings of male-male vocalizations were taken at the time of amplexus.

Cei (1980) reported that vocal sacs resemble white balloons on either side of the head. Our observations indicate the vocal sacs are grayish black while inflated and black, deflated.

Occasionally, while handling a female, eggs were expelled; they contained one black and one light-green colored pole.

Cei (1980) reported that heavy rains were necessary to initiate breeding in this species. The timing of chorusing males was closely correlated with daily rainfall throughout the study period. Phrynohyas were heard on 15 occasions (Nov. 12-14, 24, 1993; Feb. 5, 8-9, 13-14, 17; Sept. 26, 29, and Oct. 1, 9, 12-13, 1994). More than 60 mm of rainfall was necessary to elicit male vocalization. Though rains of 60 mm + occurred in winter, they did not elicit male vocalization. Smaller rains (28, 33, 19 mm) at the beginning of spring elicited choruses. Pyburn (1967) suggested that P. venulosa breeds only once a year, usually following the first heavy rain of the activity season.

Hibernation.—Hibernation takes place in natural tree cavities. Felled trees were examined on two occasions. In each case two Phrynohyas were found together within vegetable fibers of the cavity. A protective
cover was not found on individuals as reported for wintering specimens by Vellard (1948). However, the data confirm that hibernation takes place in association with at least two individuals.

**Dorsal patterns.**—Dorsal patterns were recorded on 20 live specimens in the study area. Six individual specimen dorsal patterns were altered after the individuals were preserved. McDiarmid (1968) noted the taxonomic dilemma of recognizing color patterns in *P. venulosa* as diagnostic characters. He documented pattern variation in five widely distributed populations and synonomized five species into one wide-ranging species, *P. venulosa*. In general, all of the argentine specimens are brown or tan dorsally with darker markings and pigment. There is a considerable variation in dorsal color pattern which can be grouped into five categories:

1. **Normal** (*n* = 8, 40%). Large middorsal dark blotch from the occiput extending posteriorly where it widens at the rump. Middorsally the blotch extends down the sides to occupy all the dorsolateral portion. Duellman (1971) called this pattern number "4".

2. **Three Spots** (*n* = 5, 25%). The blotch in the normal pattern is divided into three smaller blotches, the anterior one subquadrangular, and the other two on the posterior half of the body. One recaptured specimen had changed the position of one blotch.

3. **Two Spots** (*n* = 2, 10%). The normal pattern blotch is divided into two spots, the postoccipital, and another smaller or larger in the posterior half of the dorsum. One recaptured specimen changed the position of the second blotch.

4. **Central Clearing** (*n* = 4, 20%). Identical to the normal pattern (1), but the posterior half of the dorsal body contains an unpigmented area in the center of the blotch. One recaptured specimen had changed to a three-spot pattern.

5. **Spotted** (*n* = 1, 5%). Dorsal pattern consisting of irregularly scattered small dark spots. Duellman (1971) described this type as pattern class 2.

**Iris pattern and color.**—The pattern and color of the iris was reported to be an invariable character, of golden color and composed of four radiating black lines (Lutz 1973; Duellman 1971). In the present series,
the iris color was gold or tawny, with sparse black pigment. It also had four black lines, that gave rise to four petal-like spots separated by black intervals, which comprised the pupil. Observed variations of this pattern were recorded: (1) the black lines and/or the dorsal vertical black line may be absent. (2) the width of the black lines are variable, and in most cases, they are the horizontal lines.

CONCLUSIONS

The most important information provided by this study is (1) information provided by the first complete annual study of an Argentine population of *Phrynohyas venulosa* and (2) population size estimates. Information is provided on variation in dorsal patterns and documented that these patterns may change though time in marked individuals. Southern latitude specimens are known to have more patterns than reported by Duellman (1971). Size reduction in southern populations of no more than 90 mm for Paraguayan specimens (Duellman 1971) may be localized, given the 110 mm SVL female reported herein from about 100 km west of Paraguay, maximum size for Maracaibo Basin (112.5 mm) and Ecuador (110.2 mm). In all cases, argentine females seem slightly larger than males, but the differences were not statistically significant in the sample of 70 specimens.

*Phrynohyas* is a difficult species to work with alive. Gloves are necessary and must be discarded after handling each specimen because of the sticky fast-dry secretions. Under laboratory conditions, irritant vapors affected the eyes and lips of the investigators while working with *Phrynohyas* for only a few minutes.

ACKNOWLEDGMENTS

D. and T. Yanosky helped during evening surveys while checking for *Phrynohyas*. M. Dixon also provided support during the study, and Alparamis S.A., El Bagual ecological Reserve Pty. provided logistic and financial support.

LITERATURE CITED


JRD at: jrdixon@tamu.edu
AGGRESSIVE BEHAVIORS OF LIZARDS OF THE PARTHENOGENETIC CNEMIDOPHORUS LAREDOENSIS COMPLEX (SAURIA: TEIIDAE) IN SOUTHERN TEXAS

Mark A. Paulissen

Department of Biological and Environmental Sciences
McNeese State University, Lake Charles, Louisiana 70609

Abstract.—The Cnemidophorus laredoensis complex consists of two separate parthenogenetic species, known as LAR-A and LAR-B, that coexist in southern Texas. Observations of free-roaming lizards in Bentsen-Rio Grande State Park demonstrate that both LAR-A and LAR-B behave aggressively toward conspecifics as well as toward each other. Seven different aggressive behaviors were observed. These were Supplant, Trail, Straddle, Chase, Face-Off, Arched Back Display and Straddle-Bite. The data suggest that LAR-B is behaviorally dominant to LAR-A and that both species may defend their burrows from intruders.

The lizard genus Cnemidophorus includes a number of all-female, obligately parthenogenetic species (Wright 1993). The Cnemidophorus laredoensis complex consists of two, independently derived, diploid parthenogens that commonly coexist in sandy, disturbed habitats in the Rio Grande Valley of southern Texas and northern México (Walker 1987a; 1987b; Abuhteba 1990). These two parthenogens are provisionally designated LAR-A and LAR-B following Walker (1986). LAR-A is the form originally described by McKinney et al. (1973) as C. laredoensis and is commonly known as the Laredo Striped Whiptail. LAR-B was discovered in 1984 (Walker 1987b) and has not been given a Linnaean name; refer to Wright (1993) for a discussion of nomenclatural issues. Both LAR-A and LAR-B are small (snout-to-vent length 65-75 mm) striped forms. They are easily distinguishable in the field by differences in their mid-dorsal stripes; single and vivid yellow-green in LAR-A, double and dull tan in LAR-B (Walker 1987b). Their diet consists of small arthropods, especially termites which lizards find by searching through leaf litter and clumps of dead vegetation where termite workers may be concentrated (Paulissen et al. 1988). Both LAR-A and LAR-B dig burrows which they use as overnight retreats and as refuges from hot or rainy weather (Walker et al. 1986).

The ecology of LAR-A and LAR-B has been the subject of much recent study (Paulissen et al. 1988; Paulissen 1994). In contrast, the behavior of LAR-A and LAR-B has received little attention. Since members of parthenogenetic species of Cnemidophorus are known to behave aggres-
sively toward each other (Crews et al. 1983; Leuck 1985; 1993; Mitchell 1991), it is likely that both LAR-A and LAR-B females do so as well. However, apart from reports of pseudocopulation (Paulissen & Walker 1989; Paulissen 1995) and interspecific copulation between parthenogenetic LAR-A females and males of the bisexual species C. gularis (cf. Walker et al. 1991; Paulissen 1995), there is no published information on behavioral interactions among parthenogenetic females of the C. laredoensis complex. The purpose of this report is to describe aggressive behaviors exhibited by LAR-A and LAR-B females in nature and to discuss the potential significance of these behaviors.

METHODS AND MATERIALS

This study was conducted during May and June 1993, 1994 and 1995 in Bentsen-Rio Grande State Park near Mission, Hidalgo County, Texas. Lizards were abundant along a 1.8 km dirt hiking trail that runs through a relict subtropical forest surrounded by cultivated fields and intermingled with bunchgrass, weeds, and cactus (Paulissen 1994; Walker et al. 1996). When the park was first surveyed for lizards in 1984, LAR-B outnumbered LAR-A by greater than a 4:1 ratio and there were no other species of Cnemidophorus present. However, by the time of this study, the relative population sizes had changed so that LAR-A outnumbered LAR-B by about 4:1 and the bisexual species C. gularis was present in small numbers (Walker et al. 1996).

Casual observations were made of lizard behavioral interactions during the course of other data collection activities in 1993. In 1994 and 1995, more formal observations of lizard behavior were undertaken by observing individual animals and recording their behaviors by use of a pocket tape recorder. Lizard behavior was not disturbed as long as a distance of at least 5 m was maintained between the lizard and the observer. Each case in which the focal lizard came within 0.5 m of another lizard and what interactions, if any, occurred was noted. A total of 76 lizards were observed for at least 10 minutes each for a total of approximately 19 hours of observations. All observations were made between 0830 and 1830 CDT on warm, sunny or partly cloudy days during May and June 1993-1995.

RESULTS

From 1993 through 1995, 35 observations in which an LAR-A or LAR-B female came within 0.5 m of another parthenogen that could be
Table 1. Summary of behavioral interactions observed between parthenogenetic lizards in the field from 1993 through 1995. $n =$ the number of recorded observations as two lizards approached within 0.5m of each other. Line two lists the number of times in which a behavioral interaction occurred. The remaining lines list the number of cases in which each of seven different aggressive behaviors was observed. More than one of the seven behaviors typically occurred during a behavioral interaction.

<table>
<thead>
<tr>
<th>INTERACTING LIZARDS</th>
<th>LAR-A/LAR-A ($n=19$)</th>
<th>LAR-B/LAR-B ($n=1$)</th>
<th>LAR-A/LAR-B ($n=13$)</th>
<th>Total ($n=33$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>No Interaction Occurred</td>
<td>8</td>
<td>0</td>
<td>5</td>
<td>13</td>
</tr>
<tr>
<td>Interaction Occurred</td>
<td>11</td>
<td>1</td>
<td>8</td>
<td>20</td>
</tr>
<tr>
<td>Supplant</td>
<td>2</td>
<td>0</td>
<td>1</td>
<td>3</td>
</tr>
<tr>
<td>Trail</td>
<td>4</td>
<td>0</td>
<td>3</td>
<td>7</td>
</tr>
<tr>
<td>Straddle</td>
<td>3</td>
<td>0</td>
<td>2</td>
<td>5</td>
</tr>
<tr>
<td>Chase</td>
<td>6</td>
<td>1</td>
<td>4</td>
<td>11</td>
</tr>
<tr>
<td>Face-Off</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>Arched Back Display</td>
<td>5</td>
<td>1</td>
<td>1</td>
<td>7</td>
</tr>
<tr>
<td>Straddle-Bite</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>1</td>
</tr>
</tbody>
</table>

positively identified were recorded. Two of these cases were pseudo-copulations and were excluded from analysis in this paper (see Paulissen 1995). Some type of behavioral interaction occurred in 20 of the remaining 33 cases; in the other 13 cases, the two lizards simply ignored each other. The behavioral interactions involved one or both lizards exhibiting at least one of the following seven behaviors: supplant, trail, straddle, chase, face-off, arched back display or straddle-bite (Table 1). The majority of aggressive behaviors observed were between either two LAR-A females or between an LAR-A female and an LAR-B female, probably reflecting the much greater abundance of LAR-A in the park. Each of the aggressive behaviors exhibited by lizards are described below.

Supplanting.—One lizard is stationary when a second lizard approaches it. The first lizard darts away and the second lizard stops in the vacated spot. In the two cases in which one LAR-A female supplanted another LAR-A female, the larger of the two lizards supplanted the smaller. In the single case in which an LAR-B female supplanted an LAR-A female, the two lizards were about the same size.

Trailing.—As one lizard walks along the ground, a second lizard follows one or two body lengths behind. The trailing lizard moves at a walk, i.e. does not run after or chase the lizard in front of it. The trailing lizard precisely follows the path of the other lizard. For example, if the lizard in front takes a circuitous route through vegetation or along open ground, the trailing lizard follows the same route rather
than veering off to intercept the lizard ahead. In three of the seven cases in which trailing occurred, the trailing lizard broke off the pursuit after three to five seconds, then moved away to continue foraging. In the other four cases, trailing was followed by more intense interactions (see below).

**Straddling.**—One lizard climbs onto the tail or back of another lizard. The lizard being straddled usually responds by trying to jerk forward, presumably to pull away from the straddling lizard. If this isn’t successful, the straddling lizard "rides" the other lizard for 10-50 cm. Straddling was usually associated with either trailing or chasing; however, it may also have a role in pseudosexual behavior (see Discussion).

**Chasing.**—One lizard runs swiftly in the direction of another lizard that has moved too close (within 0.5 m). The attacking lizard may have its mouth open and attempt to bite the intruder or may perform an arched back display. The intruder generally dashes away from its attacker (sometimes running several meters) though in one case (the single interaction between two LAR-B females), the intruder held its ground and a brief face-off ensued. In seven of the 11 cases in which a chase occurred, the aggressor lizard was digging or lying near the entrance of a burrow. In one other case, the aggressor was feeding on a concentration of termites in a small patch of leaf litter by the side of the trail.

**Face-off.**—This behavior was among the rarest observed. Two lizards stand side-by-side facing in opposite directions so that the nose of each lizard is a few cm away from the tip of the tail of its opponent. The two lizards then rapidly circle each other as if each lizard was trying to catch the tail of the other. In the case in which two LAR-B faced off, the lizards performed arched back displays at each other as they moved (the interaction lasted only one to two seconds and the lizards moved less than 10 cm). In the case in which an LAR-A and an LAR-B interacted, the LAR-B came up to the LAR-A on the trail and first tried to straddle it; then the lizards circled each other for about three seconds. The LAR-B then moved away but was trailed and straddled by the LAR-A. The two lizards tumbled around briefly before the LAR-B broke free and moved slowly away.

**Arched back display.**—In this display, the aggressor lifts its belly off the ground by stiffly extending all four legs, arches its back so its nose is pointed down, and violently wriggles its tail. The aggressor may
perform this display while walking stiffly toward its opponent or while standing parallel to its opponent during a face-off. The duration of this display is typically about one second after which the aggressor chases after and/or tries to straddle the other lizard. Usually, the lizard toward which the arched back display is directed flees. However, in one case (an interaction between two LAR-A females), one lizard was chased away from its burrow by an aggressor performing an arched back display; but in a few seconds, this lizard turned around, walked back to the burrow, and performed an arched back display itself, chasing away the former aggressor. In three of the seven cases in which the arched back display was observed, the lizard performing the display was lying over or next to the entrance of a burrow. In one additional case, the aggressor lizard was feeding on termites in a patch of leaf litter.

**Straddle-bite.**—This behavior was observed only once; a small LAR-A walked up to a burrow in which a larger LAR-A female was digging. When the large LAR-A came out of its burrow, it chased the smaller lizard, jumped onto its back, and grabbed the back of the smaller lizard’s neck with the jaws. The small LAR-A tried to struggle away but the large LAR-A maintained its grip and rode the small lizard for a distance of about 0.5 m. Eventually, the small LAR-A escaped and fled; the large LAR-A resumed digging in its burrow.

**DISCUSSION**

The observation that both LAR-A and LAR-B females display aggressive behaviors toward conspecifics in nature reinforces studies conducted using large outdoor enclosures that demonstrated parthenogenetic *Cnemidophorus* lizards exhibit intraspecific aggression (Leuck 1985; 1993). Such studies also suggest parthenogenetic species are less aggressive toward conspecifics than bisexual species (Leuck 1985). At present, it is impossible to determine if LAR-A and LAR-B are less aggressive than bisexual congeners because there are too few data on intraspecific aggression in the bisexual species *C. gularis* in Bentsen-Rio Grande State Park.

Two of the behaviors described in this study, face-off and arched back display, have not been reported in parthenogenetic whiptail lizards, but have been observed in males of bisexual species of other species of teiid lizards. For example, Anderson & Vitt (1990) noted that male *Cnemidophorus tigris* often face-off head to tail when they compete for females and Censky (1995) reported that male *Ameiva plei* sometimes perform an "arched dance display" as part of their aggressive inter-
actions during the breeding season. Female specimens of Ameiva plei also perform this display on rare occasions (Censky, pers. comm.). The genetic mechanisms that lead to the capacity of parthenogenetic females to express typically male behaviors, such as face-off and arched back display or pseudocopulation, are unknown.

It is surprising that LAR-B females behave aggressively toward LAR-A females and vice versa. Aggressive interactions occurred in eight of the 13 cases in which an LAR-A female and an LAR-B female came within 0.5 m of each other (Table 1). In seven of these eight cases, the LAR-B was the aggressor and caused the LAR-A to retreat; in the eighth case, the LAR-B was initially the aggressor and was chased away only after a face-off (see the description of "Face-Off" in Results). These observations suggest LAR-B may be behaviorally dominant to LAR-A in Bentsen-Rio Grande State Park.

Neither parthenogen exhibited territorial behavior but there is evidence that, at least sometimes, they defend their burrows from conspecifics. There were eight cases in which a parthenogen came within 0.5 m of another parthenogen that was digging or lying next to a burrow. In seven of these cases, the parthenogen at the burrow chased the intruder (and in three of these seven cases also performed an arched back display). In the eighth case, an LAR-B simply stopped digging at a burrow entrance to intently watch an LAR-A walk by; but about 20 seconds later, the LAR-B chased the LAR-A when the latter passed close to the burrow again. These observations contrast with results reported by Leuck (1982; 1985) for the parthenogenetic species C. tesselatus. She found that parthenogens housed in large outdoor enclosures did not defend cover objects under which they had constructed burrows and that individuals often shared cover objects. In these studies however, the cover objects (concrete blocks, rocks, boards) were large enough to accommodate several lizards and burrows were easy to dig (Leuck 1985). In Bentsen-Rio Grande State Park, burrows are very difficult for lizards to dig because the ground is hard due to a high clay content. Furthermore, burrows are probably the only refuges available in the Park because there are no rocks and few logs under which lizards can retreat. Therefore, it may be beneficial for a lizard to employ aggressive behaviors to defend a burrow from other lizards.

The behaviors described in this report appear to be forms of aggression that cause one lizard to retreat from the immediate vicinity of another. However, some of these behaviors may serve other purposes in other contexts; this is especially true of straddling. When straddling
occurs at the end of a chase, it is clearly an aggressive behavior (especially if the aggressor also bites the lizard it is straddling). When straddling occurs after a bout of trailing, it is probably an aggressive behavior in most cases since the lizard that is trailed and straddled typically reacts by fleeing. However, on 13 May 1996, a large LAR-A female was observed trailing a second LAR-A female for several meters; eventually the trailing LAR-A caught up with and straddled the other lizard and proceeded to pseudocopulate. The "female-like" lizard of this pseudocopulating pair (the lizard that was trailed) made no effort to escape the "male-like" lizard (the lizard that trailed and straddled). Since LAR-A females do accept pseudocopulations from conspecifics (Paulissen 1995), bouts of trailing and straddling that lead to pseudocopulation can be considered to be a form of courtship rather than aggression. It is not known if there are subtle differences between "aggressive" straddling and "courtship" straddling. It is possible that a parthenogenetic female that trails and straddles a conspecific is simply trying to solicit a pseudocopulation from a prospective "mate"; if the prospective mate is receptive, she allows pseudocopulation to commence; if she is unreceptive, she flees from the trailing/straddling lizard. If this proposal is correct, then the combination of trailing and straddling is actually a form of courtship that only appears to be aggressive in cases in which the trailed and straddled female is unreceptive. However, since it is impossible to gauge the receptiveness of a lizard independent of its behavior in the field, and since straddling is clearly an aggressive behavior in other contexts (e.g., after a chase, straddle-bite), it would be premature to conclude that trailing and straddling is always a courtship behavior. Additional work on the subtleties of these behaviors is needed to sort out these possibilities.

ACKNOWLEDGMENTS

I wish to thank the staff of Bentsen-Rio Grande State Park and the Texas Parks and Wildlife Department for permission to conduct this study (permit 3-95). I am also grateful to Mrs. Betty Boothe for providing lodging during part of this study. Financial support was provided by the F. C. and L. C. Miller Endowed Professorship in Science awarded to the author.

LITERATURE CITED


MAP at: mpauliss@mcneese.edu
DISTRIBUTIONAL RECORDS OF SMALL MAMMALS FROM THE TEXAS PANHANDLE

Kristie Jo Roberts, Franklin D. Yancey, II and Clyde Jones
The Museum and Department of Biological Sciences
Texas Tech University, Lubbock, Texas 79409-3191

Abstract.—Distributional notes based upon small mammals collectioned in the Panhandle of Texas are presented. These include two bats (Plecotus and Tadarida), one armadillo (Dasypus), one pocket gopher (Geomys), six mice (Perognathus, Chaetodipus, Reithrodon-tomys, Peromyscus, Baiomys, and Onychomys) and one rat (Sigmodon).

Small mammal research, supported by the Texas Parks and Wildlife Department, was conducted in order to determine the distribution and status of small mammals inhabiting Caprock Canyons State Park (CCSP). This field study resulted in the collection of 11 species of mammals previously undocumented from certain counties as reported by Jones et al. (1988), Schmidly (1991) and Davis & Schmidly (1994).

MATERIALS AND METHODS

Between December 1995 and July 1996, small mammals were collected in CCSP. This area includes 56,180 km² of park land, as well as a 100 km railtrail recently donated by the Fort Worth and Denver Railroad Line. The park includes parts of the High Plains and the Rolling Plains, as well as the corresponding transitional zone. Sherman live traps baited with rolled oats were set to catch rodents. The traps were set approximately one hour before sundown and retrieved approximately one hour after sunrise. Trap lines consisted of 40 traps set at 8 to 10 meter intervals. Bats were collected by hand and mammals found dead were salvaged. Notes were kept on habitat associations and sympatry of mammals. After animals were collected and identified, voucher specimens (standard museum skin and skull) were prepared. Tissues (heart, kidney, liver, and muscle) were collected from most specimens. Voucher specimens are deposited with the holdings of the Museum of Texas Tech University (TTU). All localities are represented by Universe Transverse Mercator (UTM) coordinates obtained from a hand-held global positioning device. Caprock Canyons State Park Headquarters, which is 3 miles north of
Quitaque, Briscoe County, Texas, can be used as a reference point. The UTM coordinates for this site are 14 310684E 3809910N. Scientific and vernacular names of the mammals reported follow those of Jones & Jones (1992).

RESULTS AND DISCUSSION

Plecotus townsendii (Cooper)

In Texas, Townsend’s big-eared bat is known to occur on the High Plains, Rolling Plains, Edwards Plateau, and Trans-Pecos region (Schmidly 1991). However, throughout its range in Texas, records of this bat are scattered. This account represents the first record of *Plecotus townsendii* from Briscoe County. One male specimen (testes 8 by 4 mm), roosting singly, was collected from a gypsum cave in Caprock Canyons State Park on 18 July 1996.

*Material examined.*—Briscoe County: CCSP, UTM Coordinates: 14 310118E 3812533N, one specimen (TTU 70812).

Tadarida brasiliensis (Saussure)

The Brazilian free-tailed bat is reported to be the most common bat in Texas (Schmidly, 1991), although it is less common in the Panhandle than in the southern and eastern portions of the state (Davis & Schmidly 1994). This report documents the first record of *Tadarida brasiliensis* from Floyd County. Several specimens of this bat were collected in an abandoned railroad tunnel along the railtrail.

Adult females in this collection yield the following reproductive information: 26 June 1996, two pregnant, each with one fetus, measuring 28 and 31 mm in crown-rump length, and one with no evident reproductive activity; 17 July 1996, one with no evident reproductive activity. Adult males in this collection yield the following reproductive information: 26 June 1996, six males with testes 3 by 2 to 4 by 2 mm; 17 July 1996, three males with no reproductive information available.

*Material examined.*—Floyd County: CCSP, UTM Coordinates: 14
Dasypus novemcinctus (Linnaeus)

The nine-banded armadillo is known from throughout most of Texas, except for the far western Trans-Pecos region (Davis & Schmidly 1994). However, there are few records of this species from the Panhandle. A specimen of this species found dead on the road in Hall County represents a new county record. No reproductive information is available.

Material examined.—Hall County: UTM Coordinates: 14 330685E 3813228N, one specimen (TTU 70811).

Geomys bursarius (Shaw)

The occurrence of the plains pocket gopher is well documented throughout much of the Texas Panhandle (Davis & Schmidly 1994). However, a specimen of Geomys bursarius from Floyd County represents a new county record. These pocket gophers were collected in their preferred habitat of loose sandy soils (Goetze & Jones 1992). Other small mammals collected in the same area include Chaetodipus hispidus and Peromyscus leucopus. Both specimens which were obtained on 15 December 1995 and 18 January 1996, were females that showed no evidence of reproductive activity.

Material examined.—Floyd County: CCSP, UTM Coordinates: 14 303948E 3790491N, one specimen (TTU 69129); CCSP, UTM Coordinates: 14 304554E 3791098N, one specimen (TTU 68805).

Perognathus flavus (Baird)

The silky pocket mouse has been reported to inhabit the western two-thirds of Texas (Jones & Jones 1992). A single specimen was taken from Floyd County and represents a new county record. The specimen was collected in short grasslands composed mostly of the following grasses: Schizachyrium scoparium, Sporobolus cryptandrus, Calamovilfa gigantea, Aristida sp., Bouteloua sp. and Eragrostis sp. Mesquite trees were also a minor component of the plant community. Other small
mammals collected with *P. flavus* include *Reithrodontomys megalotis*, *Peromyscus leucopus*, and *Baiomys taylori*. The male specimen (testes 6 by 4 mm) was collected on 29 March 1996.

**Material examined.**—Floyd County: CCSP, UTM Coordinates: 14 307003E 3797530N, one specimen (TTU 69405).

*Chaetodipus hispidus* (Baird)

The hispid pocket mouse is found throughout the state of Texas, except for the extreme southeastern section (Davis & Schmidly 1994). It is well documented throughout much of the Panhandle (Jones et al. 1988; Davis & Schmidly 1994). However, prior to this report, it was not known from Floyd and Hall counties. These pocket mice were collected in grassland areas with short to tall grasses, such as *Bouteloua gracilis*, *Stipa leucotricha*, *Hilaria belangeri*, *Tridens muticus*, *Aristida* sp., *Bothriochloa barbinodis*, *Schizachyrium scoparium*, and *Sorghastrum nutans*. Other small mammals collected with *C. hispidus* include *Peromyscus maniculatus*, *Peromyscus leucopus*, *Baiomys taylori*, *Neotoma micropus*, and *Sigmodon hispidus*.

Females in the collection yield the following reproductive information: 15 December 1995, one with no evident reproductive activity; 18 January 1996, two with no evident reproductive activity; 5 April 1996, one with no evident reproductive activity; 4 May 1996, one with no evident reproductive activity; 27 June 1996, two with no evident reproductive activity, one with no reproductive information available. Males in the collection yield the following reproductive information: 15 December 1995, one with testes 8 by 4 mm; 18 January 1996, one with testes 15 by 8 mm; 27 June 1996, one with testes 8 by 3 mm.

**Material examined.**—Floyd County: CCSP, UTM Coordinates: 14 304261E 3792048N, one specimen (TTU 69622); CCSP, UTM Coordinates: 14 304554E 3791098N, two specimens (TTU 68806-68807); CCSP, UTM Coordinates: 14 305151E 3793305N, three specimens (TTU 69130-69132); Hall County: CCSP, UTM Coordinates: 14 345566E 3820296N, one specimen (TTU 70849); CCSP, UTM Coordinates: 14 347057E 3820539N, one specimen (TTU 70848); CCSP, UTM Coordinates: 14 352731E 3821611N, two specimens (TTU 70847; TTU 70850).
Reithrodontomys montanus (Baird)

The plains harvest mouse ranges throughout the Panhandle of Texas (Davis & Schmidly 1994), however this is the first report of the species from Floyd County. This mouse was collected in grasslands with medium to tall grasses including Andropogon gerardii, Panicum virgatum, Tripsacum dactyloides, Sorghastrum nutans, and Sporobolus airoides. Other small mammals collected with R. montanus include Chaetodipus hispidus and Baiomys taylori. A single female specimen was collected on 4 May 1996 and was carrying 3 embryos (crown-rump length of 2 mm).

Material examined.—Floyd County: CCSP, UTM Coordinates: 14 304261E 3792048N, one specimen (TTU 69625).

Peromyscus maniculatus (Wagner)

The deer mouse ranges throughout all of Texas (Davis & Schmidly 1994), but previously was unreported from Floyd County. This species commonly was collected in prairie grassland habitats with a variety of short to tall grasses. Grasses found in the area include Bouteloua gracilis, Stipa leucotricha, Hilaria belangeri, Tridens muticus, Aristida sp., Bothriochloa barbinodis, Schizachyrium scoparium, and Sorghastrum nutans. Small shrubs and mesquite trees also were present at these sites. Other small mammals collected with P. maniculatus include Chaetodipus hispidus and Peromyscus leucopus.

Females in the collection yield the following reproductive information: 15 February 1996, one lactating, one with 3 embryos (crown-rump length of 10 mm). Males in the collection yield the following reproductive information: 18 January 1996, one with testes 2 by 1, one with testes 12 by 6; 15 February, two with testes 9 by 5, one with testes 10 by 6 mm.

Material examined.—Floyd County: CCSP, UTM Coordinates: 14 291349E 3790467N, five specimens (TTU 69384-69388); CCSP, UTM Coordinates: 14 305151E 3793305N, two specimens (TTU 69138-69139).
Baiomys taylori (Thomas)

The northern pygmy mouse is found throughout the southern portion of the Panhandle, as well as Central and South Texas (Davis & Schmidly 1994). However, this is the first report of the species from Briscoe County. The documentation of this mouse from Briscoe County supports the contention of Choate et al. (1990) that these mice may be moving both northward and westward in the state. This species was found in areas of dense vegetation on the Rolling Plains similar to that listed for Peromyscus maniculatus. Other small mammals collected with B. taylori include Chaetodipus hispidus and Peromyscus maniculatus.

Both specimens collected were males. One male, collected on 22 June 1996, had testes of 4 by 2, whereas the other male, collected on 25 June 1996, had testes of 5 by 3 mm.

Material examined.—Briscoe County: CCSP, UTM Coordinates: 14 310626E 3810517N, one specimen (TTU 70877); CCSP, UTM Coordinates: 14 311150E 3809408N, one specimen (TTU 70878).

Onychomys leucogaster (Wied)

The northern grasshopper mouse is widespread in the northern portion of the Panhandle, where it is common to abundant (Jones et al. 1988). However, this is the first report of the species from Briscoe County. Specimens were collected in grassland areas with medium to tall grasses, as well as some small shrubs. The grasses found in the area include Schizachyrium scoparium, Sporobolus cryptandrus, Calamovilfa gigantea, Aristida sp., Bouteloua sp., and Eragrostis sp. Other small mammals collected with O. leucogaster include Reithrodontomys megalotis and Peromyscus maniculatus. Both specimens were males collected on 1 February 1996 (testes 18 by 11, 10 by 6 mm).

Material examined.—Briscoe County: CCSP, UTM Coordinates: 14 309371E 3802661N, one specimen (TTU 69202); CCSP, UTM Coordinates: 14 310211E 3804323N, one specimen (TTU 69203).

Sigmodon hispidus (Say & Ord)

The hispid cotton rat has a statewide distribution (Davis & Schmidly 1994), but previously was unreported from Hall County. This species
was collected in tall Johnson grass associated with small shrubs and mesquite. Additional grasses include *Andropogon gerardii*, *Panicum virgatum*, *Tripsacum dactyloides*, *Sorghastrum nutans* and *Sporobolus airoides*. Other small mammals collected with *S. hispidus* include *Chaetodipus hispidus*, *Peromyscus leucopus*, *Peromyscus maniculatus*, *Baiomys taylori*, and *Neotoma micropus*.

Females in the collection yield the following reproductive information: 29 February 1996, one with 3 embryos (crown-rump length 9 mm); 27 June 1996, one with 4 embryos (crown-rump length 27 mm), one with embryos crown-rump length of 22 mm, one with five embryos (crown-rump length 40 mm). Males in the collection yield the following reproductive information: 29 February 1996, two males (testes 20 by 10, 15 by 9 mm); 27 June 1996, seven males (testes 15 by 6, 17 by 6, 19 by 7, 20 by 8, 10 by 3, 9 by 4, and 13 by 5 mm).

**Material examined.**—Hall County: CCSP, UTM Coordinates: 14 321822E 3808037N, three specimens (TTU 69390-69392); CCSP, UTM Coordinates: 14 345566E 3820296N, ten specimens (TTU 70884-70893); CCSP UTM Coordinates: 14 347057E 3820539N, four specimens (TTU 70880-70883).

**ACKNOWLEDGMENTS**

Mammals were collected on the Caprock Canyons State Park in accordance with scientific collecting permits issued by the Texas Parks and Wildlife Department (permit numbers SPR-0790-189, 25-95). Financial assistance was provided by the Natural Resources Program (David H. Riskind, Director) of the Texas Parks and Wildlife Department. Logistic support was provided by personnel of Caprock Canyons State Park (Geoffrey Hulse, Superintendent). Assistance in the field was provided by Mary Ann Abbey, Richard Manning, and Leslie Skibinski. We thank two anonymous reviewers for their comments on this manuscript.

**LITERATURE CITED**


KJR, FDY or CJ at: reprints@packrat.musm.ttu.edu
ANNUAL FRUIT PRODUCTION OF PRICKLYPEAR (OPUNTIA ENGELMANNII) AND MESQUITE (PROSOPIS GLANDULOSA) IN SOUTHERN TEXAS

Lamar A. Windberg
U. S. Department of Agriculture, Animal Health and Plant Inspection Service
Denver Wildlife Research Center, Utah State University
Logan, Utah 84322-5295

Abstract.—Fruit production by Texas pricklypear (Opuntia engelmannii) and mesquite (Prosopis glandulosa) was estimated from 1979 to 1988 in Webb County, Texas. The annual percentages of fruiting pricklypear and mesquite plants were variable and positively correlated. There were no detectable relationships between the percent of plants bearing fruit, mean numbers of fruit per plant, and the Fruit Productivity Index and rainfall during five phenological periods for either pricklypear or mesquite. However, less fruit production during two to three years of relatively high rainfall in the pre-flower and flowering period (January-April) suggests that both species may divert physiologic resources from reproduction to vegetative growth under conditions of excess soil moisture.

Texas pricklypear (Opuntia engelmannii) and mesquite (Prosopis glandulosa) are predominant shrubs in the Rio Grande Plains of southern Texas (Archer et al. 1988). Fruit of both species is utilized heavily by a wide variety of wildlife in the region (Everitt & Drawe 1993). The value of their fruit as a food source for wildlife may be most important during periods of low rainfall. Droughts occur frequently in southern Texas as the climate is characterized by extreme variability in rainfall (Norwine 1978).

Desert shrubs are adapted to produce greater vegetative growth in response to increased precipitation. However, the plants must balance their resource allocation between vegetative gains and reproductive output for survival (Bowers 1996). The mechanism that controls plant response in terms of vegetative growth versus flower bud production has not been identified (Inglese et al. 1995). In pricklypear and mesquite, reproduction is partially related to vegetative growth in the prior year. Flowers develop from the areolar meristems in pricklypear, which can produce either a flower or a cladode (Bowers 1996). Mesquite fruit is set from flower buds formed during the previous growing season (Peinetti et al. 1991).

The influence of rainfall on productivity of pricklypear and mesquite has received limited attention. Based on a four year study of O.
engelmannii in the Sonoran desert, Bowers (1996) suggested that the initial number of flower buds was controlled by intrinsic factors (plant size) and that December-February rainfall affects the proportion of flowers which develop fruit. The objectives of this study were to estimate annual fruit production of pricklypear and mesquite for 10 years (1979-1988) in southern Texas and to analyze variability of productivity in relation to rainfall patterns.

METHODS

Annual production of pricklypear and mesquite was sampled before fruit ripened on a study area of 700 km² located 10-40 km northeast of Laredo, Webb County, Texas, during 12 June-16 July, 1979-1988. Topography, soils, vegetation, climate, and land use for the study area were described by Windberg et al. (1985).

Thirty-two permanently-marked sample plots (7 by 45 m) were systematically spaced ≥3 km apart. The proportion of fruiting plants was estimated annually by recording presence or absence of set fruits on all reproductive plants within plots. Reproductive plants were arbitrarily defined as those ≥2 m in height for mesquite and with ≥20 cladodes for pricklypear. Fruit production per plant was estimated by counting the number of mesquite pods or pricklypear tunas on one reproductive plant of each species nearest the base-corner of each plot. If reproductive plants were absent inside plots, fruits were counted on the nearest reproductive plant ≤50 m outside the plot. Mean numbers of fruit per unit of plant were derived by dividing the (1) number of pods/m of plant height for mesquite and (2) number of tunas/20-cladodes for pricklypear. An annual Fruit Productivity Index (FPI) was calculated by multiplying the proportion of reproductive plants by the mean number of fruits per unit of plant. Monthly rainfall was recorded at two stations near Laredo, Texas (NOAA 1978-1988; IBWC 1978-1988).

Annual estimates of the percentage of plants bearing fruit were analyzed by chi-square tests of 2-way contingency tables. Mean numbers of fruit per unit of plant were analyzed with 1-factor analysis of variance. Mean percentages of plants with fruit were compared between selected years with unpaired t-tests. Relationships between fruit production of the two species, and between fruit-production variables and rainfall, were analyzed by linear correlation.
Table 1. Annual estimates of fruit production for pricklypear and mesquite in southern Texas, 1979-1988.

<table>
<thead>
<tr>
<th>Year</th>
<th>Pricklypear</th>
<th>Mesquite</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Plants with Fruit</td>
<td>No. Fruit per Plant*</td>
</tr>
<tr>
<td></td>
<td>n</td>
<td>%</td>
</tr>
<tr>
<td>1979</td>
<td>224</td>
<td>63</td>
</tr>
<tr>
<td>1980</td>
<td>201</td>
<td>79</td>
</tr>
<tr>
<td>1981</td>
<td>331</td>
<td>50</td>
</tr>
<tr>
<td>1982</td>
<td>248</td>
<td>82</td>
</tr>
<tr>
<td>1983</td>
<td>231</td>
<td>87</td>
</tr>
<tr>
<td>1984</td>
<td>236</td>
<td>86</td>
</tr>
<tr>
<td>1985</td>
<td>253</td>
<td>92</td>
</tr>
<tr>
<td>1986</td>
<td>234</td>
<td>89</td>
</tr>
<tr>
<td>1987</td>
<td>252</td>
<td>89</td>
</tr>
<tr>
<td>1988</td>
<td>266</td>
<td>80</td>
</tr>
</tbody>
</table>

* Number of tunas per 20 cladodes.
** Number of pods per 1 m of plant height.

RESULTS

Annual fruit production of pricklypear and mesquite on the study area varied during 1979-1988 (Table 1; Fig. 1). The percent of pricklypear plants bearing fruit was lowest in 1979 (63%) and 1981 (50%). The percent of mesquite plants with fruit was more variable than pricklypear (CV = 65% and 17%, respectively), and was also numerically lowest in 1979 (0) and 1981 (11%). The annual percentages of fruiting pricklypear and mesquite plants were positively correlated (r = 0.67, t = 2.6, 8 df, P = 0.04).

Mean sizes of reproductive plants sampled during the study were 2.7 m (SE = 0.3) for mesquite and 59.7 cladodes (SE = 2.7) for pricklypear. There was greater annual variability in mean numbers of fruit per unit of plant for mesquite (CV = 87%) than pricklypear (CV = 37%), and no correlation (r = - 0.03) between species (Table 1). The annual percentages of fruiting plants and mean numbers of fruit were positively correlated (r = 0.75, t = 3.2, 8 df, P = 0.01) for pricklypear, but not mesquite (r = 0.47, t = 1.5, 8 df, P = 0.18).

There was no correlation (r = 0.43, t = 1.3, 8 df, P = 0.21) between the annual FPIs for pricklypear and mesquite. There was no relationship between the FPIs in consecutive pairs of years for either
pricklypear \( (r = 0.22) \) or mesquite \( (r = -0.20) \), which indicated that annual productivity was not influenced by fruit production in the preceding year.

Pricklypear and mesquite bloomed and set fruit chiefly during April. There were no detectable relationships \( (t \leq 2.2, \, 8 \, df, \, P \geq 0.07) \) between rainfall during five phenological periods and the three fruit productivity variables for pricklypear and mesquite (Table 2). The phenological periods analyzed were: (1) the prior growing season (Apr.-Oct.); (2) dormant season (Nov.-Mar.); (3) cool season (Dec.-Feb.); (4) pre-flower and flowering (Jan.-Apr.); and (5) flowering and fruit-set (Apr.-May). The strongest trend was a negative relationship between rainfall during January-April and fruit production (Table 2; Fig. 1). However, that relationship was attributable primarily to lower \( (t \geq 2.9, \, 8 \, df, \, P \leq 0.02) \) percentages of pricklypear and mesquite bearing fruit in two years of relatively high rainfall (1979 and 1981). The percentage of mesquite bearing fruit was also low (27%) in another high

Figure 1. Annual Fruit Productivity Indices for pricklypear and mesquite and total rainfall during January-April in Webb County, Texas, 1979-1988.
Table 2. Coefficients ($r$) for relationships between rainfall and fruit production variables of pricklypear and mesquite in Webb County, Texas, 1979-1988.

<table>
<thead>
<tr>
<th>Rainfall Period (Months)</th>
<th>Pricklypear</th>
<th>Mesquite</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>FPI* (%)</td>
<td>% Plants with Fruit</td>
</tr>
<tr>
<td>Prior growing season</td>
<td>-0.01</td>
<td>0.14</td>
</tr>
<tr>
<td>(April-October)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Dormant season</td>
<td>-0.28</td>
<td>-0.04</td>
</tr>
<tr>
<td>(November-March)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cool season</td>
<td>0.21</td>
<td>0.37</td>
</tr>
<tr>
<td>(December-February)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pre-flower and flowering</td>
<td>-0.55</td>
<td>-0.41</td>
</tr>
<tr>
<td>(January-April)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Flowering and fruit-set</td>
<td>-0.52</td>
<td>-0.45</td>
</tr>
<tr>
<td>(April-May)</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

* Fruit Productivity Index (see METHODS).

rainfall year (1985), but productivity of pricklypear was normal (Fig. 1). During the 10-year study, the percentage of mesquite plants bearing fruit was markedly less during three years when rainfall exceeded 15 cm during the pre-flower and flowering period.

**DISCUSSION**

Mature cacti tend to flower every year (Nobel 1988). A high proportion of pricklypear with set fruit was observed each year during this study in southern Texas. In the two years when productivity of pricklypear was markedly less than normal, rainfall was high during the pre-flower and flowering period. This relationship suggested that pricklypear may have responded to the greater precipitation with increased vegetative growth and reduced reproduction. However, the trend was not consistent because productivity was normal during a third year of equally high rainfall (1985). No other relationships were found between annual productivity of pricklypear and rainfall, including precipitation during December-February where Bowers (1996) reported a direct relationship between productivity and rainfall in the Sonoran desert. The more arid climate of that region, compared with the Rio Grande Plains, may have predisposed plants there to respond positively to the effect of cool-season rainfall.

In a review of mesquite phenology, Mooney et al. (1977) reported
that the seasonal timing of blooming is relatively constant annually but
< 3% of flowers initiated fruit development and only one-half to one-third of those subsequently produced fruit. Similarly, Peinetti et al. (1991) reported < 1% of mesquite flowers developed fruit. Phenological observations by Mooney et al. (1977) indicated that flowering and fruiting in *P. glandulosa* and *P. velutina* varied annually. They stated that low soil moisture resulted in heavy flowering, and that high soil moisture suppressed flowering. Nilsen et al. (1991) also reported that water limitation resulted in greater reproduction by *P. glandulosa*, and inferred that reproductive allocation was induced and vegetative growth suppressed during dry years. Lower productivity of mesquite was observed in three years of relatively high rainfall in the pre-flower and flowering period during this study. This notable trend supports the hypothesis that a threshold of soil moisture at time of flowering triggers a plant response of increased vegetative growth and reduced reproduction.

Mooney et al. (1977) suggested that rainfall during the flowering period also resulted in low fruit production by mesquite, but no relationship between annual productivity of either mesquite or pricklypear and rainfall was found during the flowering and fruit-set period in this study. Mooney et al. (1977) mentioned that unusually cold weather in winter and spring adversely affects fruit production in mesquite. Temperatures were generally normal at Laredo in March during 1979-1988 (NOAA 1978-1988), except for a sub-freezing low (- 3°C) on 2 March 1980 when fruit production was normal for pricklypear but relatively low for mesquite.

The xerophytic adaptations of desert shrubs probably tend to negate the effects of variable rainfall on their productivity. Water storage in cladodes of pricklypear assures a relatively constant supply for physiologic requirements. Nobel (1988) estimated that the water requirement for reproduction represented only 6% of the stem water at time of flowering in *Ferocactus acanthodes* (a barrel cactus), which generally occurs during the seasonal drought in spring. The extremely deep root system of mesquite (Solbrig & Cantino 1975) is the mechanism which provides adequate water for survival and reproduction. Yet the positive correlation between the proportion of pricklypear and mesquite plants bearing fruit annually in southern Texas implicates the influence of extrinsic factors. Although this study did not assess any other potential
factors, such as differential pollination and various diseases, there was evidence that heavy rainfall before and during flowering depressed fruit production of pricklypear and mesquite.

ACKNOWLEDGMENTS

Access to private lands for this study was provided by the management of Callaghan Ranch Limited and Killam Ranch Company. The portion of this study prior to 1986 was conducted under the authority of the U. S. Fish and Wildlife Service, Department of Interior.

LITERATURE CITED


GENERAL NOTES

PETROLEUM UTILIZING BACILLUS SPP.
FROM SOIL AT OIL SPRINGS, TEXAS

J. Dickson Ferguson III, Stephen L. Beekman and Thomas G. Benoit
Department of Biology, McMurry University, Abilene, Texas 79697

The first producing oil well in Texas was drilled at Oil Springs. The area is rich in natural petroleum seeps which have been present at least for several hundreds of years, making this an interesting site of chronic petroleum exposure. Crude oil seeps into the freshwater system at Oil Springs. Hydrocarbon degrading bacteria can be isolated from the floating oily mousse at these aquatic seeps (Benoit & Wiggers 1995). Strains of Pseudomonas, Flavobacterium, Alcaligenes and Erwinia have been described. These organisms grow rapidly on aliphatic hydrocarbons in vitro with little or no ability to use aromatics. The Erwinia isolate is unusual in that this genus is not a common hydrocarbon degrading bacterium.

Crude oil also seeps onto the soil at Oil Springs where, unlike the aquatic seeps, it does not wash away. It appeared possible that bacteria with a broader range of substrate use might exist near these terrestrial seeps. Of particular interest were strains of the genus Bacillus that might use hydrocarbons for growth. Bacillus is common in soil and at least one species (B. stearothermophilus from the desert of Kuwait) has been reported to grow on selected aliphatic hydrocarbons (Sorkhoh et al. 1993).

METHODS AND MATERIALS

Hydrocarbon utilizing bacteria were isolated from the soil at Oil Springs by first shaking soil samples for 72 hours at 30°C in one-tenth strength nutrient broth supplemented with a mineral salts mixture (see Benoit & Wiggers 1995). The cultures subsequently were diluted 1:50 into crude oil (1% by volume) / aqueous mineral salts broth and incubated for an additional 72 hours at 30°C. The resulting mixed cultures were streaked onto nutrient agar. Bacillus spp. were identified according to Gordon et al. (1973).

The Bacillus isolates were tested for their ability to grow on crude oil, mineral oil, benzene, toluene, xylene and cyclohexane by adding 50 μL of 18-24 hour nutrient broth cultures to 5 mL of the mineral salts broth supplemented with one percent (v:v) of one of the hydrocarbon substrates.
Incubations were carried out in tightly capped 13 by 100 mm tubes to prevent evaporation. Cultures were scored after incubating for 14 days at 30°C. The appearance of turbidity or suspended colonies, and the microscopic presence of dense cell populations, in the cultures were considered to be indicative of growth. Control cultures in mineral salts broth without hydrocarbons were used for comparison.

**RESULTS AND DISCUSSION**

Two strains of *Bacillus cereus* (MCM1 and MCM3) and one strain of *B. mycoides* (MCM2) were isolated from the soil samples. Each isolate grew as a pure culture with crude oil as the sole source of carbon and energy. Strains MCM1 and MCM2 also grew on mineral oil, toluene and xylene. Strain MCM1 grew on benzene while MCM2 did not. Strain MCM3 grew only on mineral oil in addition to crude oil. None of the strains grew on cyclohexane.

Aliphatics and to some extent aromatics are readily utilizable substrates in crude oil. However, it is unusual to find bacteria like the *Bacillus* isolates which can use both since presumably a monooxygenase and a dioxygenase, and two separate degradative pathways, would be required (Bartha 1986). Growth on cycloalkanes involves an additional oxygenase which almost is never present in strains that use aliphatics (Bartha 1986). It is not surprising, therefore, that the *Bacillus* isolates did not grow on cyclohexane.

In one set of experiments dense cultures of MCM2 were produced by inoculating crude oil/mineral salts broth with spores. This was unexpected since the spores would have to germinate on a component of the oil in order to produce a vegetative cell culture. Common *Bacillus* germinants include monosaccharides and amino acids, molecules structurally unlike those found in crude oil. It is not known which component(s) of the oil may have been used as germinants by the spores.

These *Bacillus* isolates were not the only hydrocarbon users present in the soil. *Pseudomonas*, *Klebsiella* and *Arthrobacter/Rhodococcus* strains also were isolated. These organisms grew on crude oil, mineral oil, and in most cases on at least one of the aromatics.

Chronic exposure to all fractions of crude oil in the soil appears to have selected for greater metabolic capabilities among the soil bacteria than those found at the aquatic seeps. When added together, hydrocarbonoclastic bacteria from soil and water at Oil Springs span a broadly diverse range of genera, probably reflecting the length of time that oil has been present at the site.
NEW RECORDS OF THE EASTERN COTTONTAIL
(SYLVIlagus FLoRIDA NU5) AND BLACK-TAILED JACKRABBIT
(LEpus CALIFORNICUS) IN MÉXICO

Fernando A. Cervantes, Consuelo Lorenzo and *Mark D. Engstrom
Departamento de Zoología, Instituto de Biología, UNAM
Apartado Postal 70-153, Coyoacán. 04510 México, D. F. México and
*Department of Mammalogy, Royal Ontario Museum, 100 Queen’s Park
Toronto, Ontario, Canada, M5S 2C6.

The geographical distributions of the cottontail rabbits (Sylvilagus) and jackrabbits (Lepus) in México are poorly documented. This report represents the first record of the eastern cottontail (Sylvilagus floridanus) from the state of Quintana Roo and of the black-tailed jackrabbit (Lepus californicus) from the state of Tlaxcala. Voucher specimens are deposited with the holdings of the Colección Nacional de Mamíferos (IBUNAM) of the Instituto de Biología, Universidad Nacional Autónoma de México in Mexico City.

Only a few individual specimens of Sylvilagus floridanus have been recorded from the Yucatán Peninsula of México; all are from the states of Campeche and Tabasco (Jones et al. 1974; Hall 1981; Dowler & Engstrom 1988). This species has not been recorded from Quintana Roo (Ramírez-Pulido et al. 1986; Sánchez-Herrera et al. 1986; Ramírez-Pulido & Castro-Campillo 1990) in the eastern region of the Peninsula, although its presence there was suggested by Navarro et al. (1990).

An adult female (IBUNAM-8344) and an adult male (IBUNAM-8345) were collected at Rancho La Ceiba, 2 km SE of Laguna Chichankanab, Municipio José María Morelos, Quintana Roo, on 22 May 1964. Details
on their capture and habitat are unknown. The presence of these specimens extends the range of the species approximately 188 km to the east of Campeche, Campeche, and 102 km to the south of Chichen-Itza, Yucatan, the nearest previously recorded localities.

Selected measurements (mm) of these specimens are (female and male) respectively: total length, 485, —; length of tail, 47, —; length of hind foot, 89, —; length of ear from the notch, 85, —; greatest length of skull, 77.1, 77.0; zygomatic breadth, 37.0, 33.7; mastoid breadth, 22.0, 21.2; length of maxillary toothrow, 14.4, 13.9; width of bulla, 7.3, 7.3. Based on the color of the fur, size of the auditory bullae, and the obvious fusion of the postorbital processes with the cranium (Nelson 1909; Dowler & Engstrom 1988), these specimens are assigned to *S. floridanus yucatanicus*.

In central México, only a few records of *Lepus californicus* have been reported from the states of Queretaro and Hidalgo. This region represents the southernmost known occurrence of this species in North America. Nelson (1909) suggested that *L. californicus* occurred in Tlaxcala and in the extreme northern part of the state of México. The occurrence in the state of México was later confirmed by Ceballos González & Galindo Leal (1984). However, the presence of this species in Tlaxcala has not been documented.

Two adult specimens, a female (IBUNAM-27648) and a male (IBUNAM-27649), were collected near Capulac, Municipio Tlaxco, Tlaxcala, on 2 June 1990. This species was common at this locality based on numerous sightings. The specimens were collected early in the morning in open xeric vegetation dominated by cacti and brush. This record extends the known range for *L. californicus* approximately 58 km to the ESE from Irolo, Hidalgo (type locality of *L. californicus festinus*), the closest recorded locality.

Selected measurements (mm) of the specimens (female and male, respectively) are: total length, 580, —; length of tail, 75, —; length of hind foot, 125, —; length of ear from the notch, 145, —; weight, 2467.5 g, —; greatest length of skull, 94.0, 95.7; zygomatic breadth, 43.6, 43.9; mastoid breadth, 27.0, 26.6; length of maxillary toothrow, 16.4, 16.9; width of bulla, 10.1, 9.4.

The locality of this new record is at the southeastern border of the range of *Lepus californicus festinus* and is geographically separated from that of *L. californicus asellus*. In addition, these specimens exhibit larger ears, a gray nape, and smaller skulls (Nelson 1909) than *L. californicus asellus* and are most similar to *L. californicus festinus*. Accordingly, these specimens are assigned to *L. californicus festinus*. 
In summary, these new records of these two species suggest a poor knowledge of their geographical distribution in Mexico rather than a recent range extension, and lead to a better understanding of their known ranges.

**Acknowledgments**

M. A. Villalba assisted during specimen collection. C. Pozo provided information on leporid holdings of the mammal collection of Centro de Investigaciones de Quintana Roo. J. Ramírez-Pulido, C. Jones and an anonymous reviewer provided valuable comments on an earlier draft. Dirección General de Asuntos del Personal Académico, Universidad Nacional Autónoma de México (grant IN-203793 to B. Villa-R. and F. A. Cervantes), and the IUCN/SSC Lagomorph Specialist Group (grant from the Sir Peter Scott Fund to F. A. Cervantes) supported this research.

**LITERATURE CITED**


Effinger & Lucas (1990) reviewed the fossil record of *Bison* from New Mexico, identifying 30 well-documented records, most of them from the southern High Plains of the eastern part of the state. This study adds to this record a *Bison* fossil from Taos County in northern New Mexico that has been dated by the $^{14}C$ method. This is the first record of *Bison* from Taos County and provides the first direct evidence of the late Pleistocene age of some of the alluvium overlying the Taos Plateau volcanic field. Furthermore, it establishes the presence of Pleistocene *Bison* in the San Luis basin of the Rio Grande rift and represents one of the few New Mexican records of the genus west of the southern High Plains portion of the state.

The *Bison* fossil was collected in the wall of an arroyo in the SE1/4 SE1/4 sec. 16, T24N, R9E, Taos County (UTM coordinates 4018290N, 411880E, zone 13). The fossil consists of the distal end of the right humerus, the articulated proximal end of the co-ossified radius-ulna and the separate ulnar olecranon ossification. These bones were extracted from sandy alluvium approximately 0.3 m below the upland surface. They were articulated, with the distal end of the radius-ulna in the arroyo wall and numerous fragments weathered loose in the arroyo. No cultural material was associated with the fossil. The bones are not abraded and were found in articulation in a relatively fine-grained alluvium, so it seems highly likely they were deposited at the same time as the alluvium and not reworked from an older deposit.

The fossil specimen (112364, Laboratory of Anthropology, Santa Fe, New Mexico) is well mineralized, and in size and morphology conforms to *Bison* as illustrated by Olsen (1960: Figs. 11, 12, 13A & 14A). The species-level taxonomy of *Bison* is based on cranial features (McDonald 1981). The specimen can therefore only be identified as *Bison* sp. The humerus was submitted to Dr. Thomas W. Stafford, Jr. of the Laboratory for Accelerator Radiocarbon Research, University of Colorado at Boulder, for an AMS radiocarbon measurement (specimen NSRL-2796). A date of $24,740 \pm 140$ years before present was obtained on KOH-extracted collagen from cortical bone.

The *Bison* locality is in alluvium deposited over Pliocene tholeiitic lavas.
of the Taos volcanic field. This alluvium represents valley-fill deposits that most workers consider to be of late Pleistocene (Wisconsin) age (Personius & Machette 1984; Kelson 1986; Pazzaglia & Wells 1990). However, direct age control of this alluvium has been lacking until the $^{14}$C age reported in this study.

ACKNOWLEDGMENTS

We thank Mary Ann Elder and Vieterbo Alires of the U.S. Forest Service for locating the site, the Tres Piedras Ranger District for allowing us to study the fossil, John Hawley for discussion and Pete Reser for assistance.

LITERATURE CITED


SGL at: lucas@darwin.nmmnh-abq.mus.nm.us

* * * *

RANGE EXTENSION OF THE FRESHWATER MUSSEL
POTAMILUS PURPURATUS (BIVALVIA: UNIONIDAE) IN TEXAS

Robert G. Howells
Texas Parks and Wildlife Department, Heart of the Hills Research Station
HC07, Box 62, Ingram, Texas 78025

The freshwater bivalve Potamilus purpuratus is a large, distinctive unionid which occurs throughout much of the central and lower Mississippi River Valley (Cummings & Mayer 1993; Vidrine 1993). It is also known to occur in tributaries of the Gulf of Mexico east and west of the Mississippi River (Strecker 1931; Vidrine 1993).

In Texas, this species occurs from the Red River drainage southwest into the Guadalupe/San Antonio River drainage (Howells et al. 1996). Strecker (1931) did not report P. purpuratus from the Nueces or Frio rivers and Murray (1978) did not find it in a survey of Lake Corpus Christi on the
lower Nueces River. Previous reports by Strecker (1931) of this species from the Devils River near its confluence with the Rio Grande were found to represent misidentified specimens (R. Neck & C. Boone, pers. comm.) of the Tampico pearlymussel *Cyrtoniaias tampicoensis*. Metcalf (1982) did not find this species represented in the fossil assemblages of the central Rio Grande and Neck & Metcalf (1988) did not report it from the lower Rio Grande downstream from Falcon Reservoir.

Freshwater mussels not only support important commercial fisheries, but are among one of the fastest declining groups of animals in North America (Neves 1993; Williams et al. 1993). Because of this, the staff of the Texas Parks and Wildlife Department’s (TPWD) Heart of the Hills Research Station began a study of Texas unionid populations in 1992, including statewide distributional surveys. From October 1993 through January 1995, populations of *Potamilus purpuratus* were found at several sites outside their previously known ranges. This study represents an extension of the previously known range of *P. purpuratus* in Texas. Voucher specimens are deposited with the holdings of the Houston Museum of Natural Science (HMNS).

*Potamilus purpuratus* (Lamarck)
(bleufer, blooper or blue mucket)

**Material examined.**—Lake Corpus Christi, Live Oak County, Texas, 5 October 1993, two specimens (HMNS 42487); Amistad Reservoir (near confluence of Devils River), Val Verde County, Texas, 21 December 1994, two specimens (HMNS 42486); Middle Concho River upstream from Twin Buttes Reservoir, Tom Green County, Texas, 3 August 1994, two specimens (HMNS 42485).

**Distributional notes.**—Survey work conducted in Lake Corpus Christi and the Nueces River just upstream of the reservoir in October 1993 revealed that *P. purpuratus* was one of the most abundant unionid taxa in the reservoir. It was represented by very small juveniles (< 15 mm shell length, sl) through mature, gravid adults (> 80 mm sl). However, no large, old adults (> 110 mm sl) were found. Specimens were morphologically similar to specimens from the central and upper Colorado River drainage of Texas. Other collections made further upstream in Choke Canyon Reservoir and the Frio River up and down-stream of the reservoir, Live Oak and McMullen counties, during 1993 and 1994 period failed to yield any specimens of *P. purpuratus*. The survey of Lake Corpus Christi by Murray (1978) was made during drought conditions when the water level was extremely low. If present at that time, specimens of *P. purpuratus* would probably have been found. This suggests an introduction likely occurred in the late 1970s or 1980s.
Several additional bleufer valves were also collected in December 1994 in Amistad Reservoir near the confluence of the Devils River during a drawdown which exposed much of the reservoir bottom. A return trip to the area in January 1995 yielded additional valves as well as three living specimens. These included relatively small juveniles (< 70 mm sl) to larger, older adults (> 125 mm sl). Comparison of the Amistad material to several badly-weathered valves taken by TPWD in January 1992 upstream on the Rio Grande just downstream of San Francisco Creek, Terrell County, indicated the earlier specimens were bleufers as well. Other surveys by TPWD in the Rio Grande downstream of Amistad Reservoir 1992-1995 failed to yield bleufers. Clearly the Amistad population contained larger, older animals than observed in Lake Corpus Christi. Absence of P. purpuratus in the fossil record (Metcalf 1982) from the Rio Grande drainage suggests the Amistad specimens may also represent an introduction, but at a much earlier date.

Biochemical comparisons.—Horizontal starch gel electrophoresis (Morizot & Schmidt 1990) was used to examine tissue samples from Rio Grande and Nueces River specimens to confirm identification. Enzyme systems previously found by Neck & Howells (1994) to show differences between P. purpuratus, P. ohiensis (pink papershell), and P. amphichaenus (Texas heelsplitter) were examined. These included glucose-phosphate isomerase (GPI; E.C. 3.1.1), peptidase (PEP; E.C. 3.4.11. or 3.4.13.), superoxide dismutase (SOD; E.C. 2.7.5.1), malate dehydrogenase (MDH; E.C. 1.1.1.37), and phosphoglucomutase (PGM; E.C. 2.7.5.1). Specimens examined included those from Nasworthy Reservoir, Twin Buttes Reservoir, and Middle Concho River (Concho River drainage, Tom Green County); Concho River (Concho County); Mussel Shoal Creek (Trinity River drainage, San Jacinto County); Lake Buchanan (Colorado River drainage, Llano County); Little Brazos River (Brazos River drainage, Robertson County); and B. A. Steinhagen Reservoir (Neches River drainage, Tyler County) as well as specimens from Lake Corpus Christi, Nueces River, and Amistad Reservoir. An additional specimen from the Pasca-goula River, Jackson County, Mississippi was also included in the comparison. Specimens of P. ohiensis from Lake Arrowhead (Red River drainage, Clay County) and a P. amphichaenus from B. A. Steinhagen Reservoir were also comparatively examined. No significant electrophoretic differences were found among any of the specimens of P. purpuratus and all were distinctly different from P. ohiensis and P. amphichaenus.

Remarks.—Commercial shell fishermen (musselers) have reported deliberately transplanting unionids from one body of water to another (Howells 1993) and inadvertent introductions on glochidia-infected fishes
may also occur (Neck 1982). Although *Potamilus purpuratus* is sometimes taken for shells or pearls, harvest for these purposes is generally very minor when compared to that of other commercially more desirable mussels in Texas (Howells 1993). It is possible that the transplanting of pearl-producing Tampico pearly mussels may have inadvertently introduced specimens of *P. purpuratus* as well because of similarity in appearance of the two species. The only known host fish for the glochidia of *P. purpuratus* is the freshwater drum (Hoggarth 1992). However, freshwater drum (*Aplodinotus grunniens*) are rarely stocked as a sport fish or used as live bait. Consequently, introductions by this method appear unlikely.

**LITERATURE CITED**


RGH at: ams@xtc.com

****
BOOK REVIEW


This is an appealing, reader-friendly review of the speciose and diverse genus *Thamnophis*; in fact, it is the first comprehensive review in nearly ninety years. The book is subdivided into three sections.

Section One is authored by Douglas A. Rossman. This well-written section deals with the taxonomic and systematic relationships of garter snakes, and includes a comprehensive species and subspecies list and key. Particularly helpful is the figure that defines mensural features used to calculate ratios of taxonomic significance in garter snakes.

Section Two is devoted to ecology, behavior and captive care of garter snakes, with Richard A. Seigel providing a thorough treatment of their ecology and conservation. Seigel discusses reproductive ecology, foraging ecology, population ecology and thermal ecology, stressing the contribution of the garter snakes’ ecological plasticity to their success.

Also in Section Two is a chapter on the behavior of garter snakes, written by Neil B. Ford. Ford discusses the value of garter snakes as animal behavior models, and describes the range of behavioral capabilities exhibited by the group. He then discusses, in turn, foraging, thermoregulatory and defense behaviors; orientation and navigational abilities; reproductive, hibernation and aggregation behavior; and the role of learning in garter snakes. Ford concludes the chapter with a review of the role of genetics and evolution in the behavior of garter snakes.

A chapter dealing with the captive care of garter snakes is also authored by Ford. This concise guide is valuable aid for hobbyists and researchers alike. The topics covered include housing, handling and feeding, avoidance and treatment of diseases, and captive propagation.
Section Three, written by all three authors, comprises species accounts for the 30 recognized species of garter snakes. Each account includes a synonymy, identification aids, content and distribution, description, plus comments on life history and ecology. The section includes numerous distribution maps, which, although very useful, would have been even more valuable if individual collection localities had been indicated, rather than more general shaded areas, particularly for some species with very limited distributions.

The color plates are excellent, although they could have been a bit larger, given the amount of space available on the pages. The brief glossary is helpful and clearly written.

This book is a useful addition to any herpetologist’s library. In addition to serving as an up-to-date review of the garter snakes of the United States and Canada, it provides much-needed information about some of the less well-known Mexican species.

R. Kathryn Vaughan
Wildlife & Fisheries Sciences
Texas A&M University
College Station, Texas 77843-2258

RKV at: kvaughan@wfscgate.tamu.edu
INSTRUCTIONS TO AUTHORS

Scholarly manuscripts in any field of science or technology will be considered for publication in *The Texas Journal of Science*. Prior to acceptance, each manuscript will be reviewed both by knowledgeable peers and by the editorial staff. Authors are encouraged to suggest the names and addresses of two potential reviewers to the Manuscript Editor at the time of submission of their manuscript. No manuscript submitted to the *Journal* is to have been published or submitted elsewhere. Excess authorship is discouraged.

Upon completion of the peer review process, the corresponding author is required to submit two typed copies of the final revised manuscript as well as a diskette (3.5 inch) copy.

Format

Except for the corresponding author’s address, manuscripts must be double-spaced throughout (including legends and literature cited) and submitted in TRIPLETYE (typed or photocopied) on 8.5 by 11 inch bond paper, with margins of approximately one inch and pages numbered. The right margin should not be justified. Words should not be hyphenated. The text can be subdivided into sections as deemed appropriate by the author(s). Possible examples are: Abstract; Methods and Materials; Results; Discussion; Summary or Conclusions; Acknowledgments; Literature Cited. Major internal headings are centered and capitalized. Computer generated manuscripts *must* be reproduced as letter quality or laser prints, *not* dot matrix.

References

References must be cited in the text by author and date in chronological (*not* alphabetical) order; Jones (1971); Jones (1971; 1975); (Jones 1971); (Jones 1971; 1975); (Jones 1971; Smith 1973; Davis 1975); Jones (1971), Smith (1973), Davis (1975); Smith & Davis (1985); (Smith & Davis 1985). Reference format for more than two authors is Jones et al. (1976) or (Jones et al. 1976). Citations to publications by the same author(s) in the same year should be designated alphabetically (1979a; 1979b).
Literature Cited

Journal abbreviations in the Literature Cited section should follow those listed in BIOSIS Previews ® Database (ISSN:1044-4297). All libraries receiving Biological Abstracts have this text; it is available from the interlibrary loan officer or head librarian. Otherwise standard recognized abbreviations in the field of study should be used. All citations in the text must be included in the Literature Cited section and vice versa.

Consecutively-paged journal volumes and other serials should be cited by volume, number, and pagination. Serials with more than one number and that are not consecutively paged should be cited by number as well. The following are examples of a variety of citations:

Journals & Serials.—

Books.—

Unpublished.—

In the text of the manuscript, the above unpublished reference should be cited as Davis (1975) or (Davis 1975). Unpublished material that cannot be obtained nor reviewed by other investigators (such as unpublished or unpublished field notes) should not be cited.
Graphics, Figures & Tables

Every table must be included as a computer generated addendum or appendix of the manuscript. Computer generated figures and graphics must be laser quality and camera ready, reduced to 5.5 in. (14 cm) in width and no more than 8.5 in. (20.5 cm) in height. Shading is unacceptable. Instead, different and contrasting styles of crosshatching, grids, line tints, dot size, or other suitable matrix can denote differences in graphics or figures. Figures, maps and graphs should be reduced to the above graphic measurements by a photographic method. A high contrast black and white process known as a PMT or Camera Copy Print is recommended. Authors unable to provide reduced PMT’s should submit their originals. Figures and graphs which are too wide to be reduced to the above measurements may be positioned sideways. They should then be reduced to 9 in. (23 cm) wide and 5 in. (12.5 cm) in height. Black and white photographs of specimens, study sites, etc. should comply with the above dimensions for figures. Color photographs cannot be processed at this time. Each figure should be marked on the back with the name of the author(s) and figure number and top of figure. All legends for figures and tables must be typed (double-spaced) on a sheet(s) of paper separate from the text. All figures must be referred to in text as "Figure 3" or "(Fig.3)"; all tables as "Table 3" or "(Table 3)".

Galley Proofs & Reprints

The principal author will receive galley proofs along with edited typescript. Proofs must be corrected and returned to the Managing Editor within five days; failure to return corrected galley proofs promptly will result in delay of publication. The Academy will provide 100 reprints without charge for each feature article or note published in the Journal. These will be mailed to the senior author or the designated contact person following the publishing of each issue of the Journal. The distribution of reprints among co-authors is the responsibility of the senior author. Authors will have the opportunity to purchase additional reprints (in lots of 100) at the time that the corrected galley proofs are returned to the Managing Editor.
Page Charges

Authors are required to pay $50 per printed page. While members of the Academy are allowed four published pages per year free of charge on publications with one or two authors, all authors with means or institutional support are requested to pay full page charges. Full payment is required for all pages in excess of four. All publications authored by three or four persons will incur full page charges. Nonmembers of the Academy are required to pay full page charges for all pages. The Academy, upon written request, will subsidize a limited number of pages per volume. These exceptions are, however, generally limited to students without financial support. Should a problem arise relative to page charges, please contact:

Dr. Ned E. Strenth
TJS Managing Editor
Department of Biology
Angelo State University
San Angelo, Texas 76909
E-mail: nstrenth@mailserv.angelo.edu

Additional Guidelines

An expanded version of the above author guidelines which includes instructions on style, title and abstract preparation, deposition of voucher specimens, and a listing of standardized abbreviations is available upon request from:

Dr. Jack D. McCullough
TJS Manuscript Editor
Department of Biology - Box 13003
Stephen F. Austin State University
Nacogdoches, Texas 75962
E-mail: f_mccullou@titan.sfasu.edu
THE TEXAS ACADEMY OF SCIENCE, 1996-97

OFFICERS

President: Kenneth L. Dickson, University of North Texas
President Elect: Ronald S. King, University of Texas at Tyler
Vice-President: Dovallee Dorsett, Baylor University
Immediate Past President: Donald E. Harper, Texas A&M University at Galveston
Executive Secretary: Brad C. Henry, University of Texas-Pan American
Corresponding Secretary: Deborah D. Hettinger, Texas Lutheran University
Manuscript Editor: Jack D. McCullough, Stephen F. Austin State University
Managing Editor: Ned E. Strenth, Angelo State University
Treasurer: Michael J. Carlo, Angelo State University
AAAS Council Representative: Sandra S. West, Southwest Texas State University

DIRECTORS

1994 Neil B. Ford, University of Texas at Tyler
Barbara ten Brink, Texas Education Agency
1995 Fred L. Fifer, University of Texas at Dallas
Charles H. Swift, Hutchinson Junior High School in Lubbock
1996 Robert D. Owen, Texas Tech University
Andrew J. Tirpak, Jr., Texas A&M University at Galveston

SECTIONAL CHAIRPERSONS

Anthropology: Mark Glazer, University of Texas-Pan American
Biological Science: Bill Cook, Midwestern State University
Botany: Joan E. N. Hudson, Sam Houston State University
Chemistry: Julio F. Caballero, University of the Incarnate Word
Computer Science: Barbara Schreur, Texas A&M University-Kingsville
Conservation and Management: Michael F. Small, Texas A&M University-Kingsville
Environmental Science: Tom Vaughan, Texas A&M International University
Freshwater and Marine Science: Darrell S. Vodopich, Baylor University
Geography: Drew Decker, Department of Information Resources
Geology: M. Carey Crocker, Stephen F. Austin State University
Mathematics: Patrick L. Odell, Baylor University
Physics: Cyrus D. Cantrell, University of Texas at Dallas
Science Education: Suzette Thorp Johnson, Kealing Jr. High in Austin
Systematics and Evolutionary Biology: Anne Walton, Texas A&M University
Terrestrial Ecology: Monte Thies, Sam Houston State University

COUNSELORS

Collegiate Academy: Jim Mills, St. Edward's University
Junior Academy: Kathy Mittag, University of Texas at San Antonio
MEMBERSHIP.—Any person or member of any group engaged in scientific work or interested in the promotion of science is eligible for membership in The Texas Academy of Science. For more information, please access the Academy’s home page at:

http://www.uttyl.edu/~tas/taswhat.htm

Dues for regular members are $30.00 annually; supporting members, $60.00; sustaining members, $100.00; patron members, $150.00; associate (student) members, $15.00; family members, $35.00; affiliate members, $5.00; emeritus members, $10.00; corporate members, $250.00 annually. Library subscription rate is $50.00 annually.

*The Texas Journal of Science* is a quarterly publication of The Texas Academy of Science and is sent to most members and all subscribers. Payment of dues, changes of address and inquiries regarding missing or back issues should be sent to:

Dr. Brad C. Henry  
Department of Biology  
The University of Texas-Pan American  
Edinburg, Texas 78539  
E-mail: bradhenry@panam.edu

**AFFILIATED ORGANIZATIONS**  
American Association for the Advancement of Science  
Texas Council of Elementary Science  
Texas Section, American Association of Physics Teachers  
Texas Section, Mathematical Association of America  
Texas Section, National Association of Geology Teachers  
Texas Society of Mammalogists

*The Texas Journal of Science* (ISSN 0040-4403) is published quarterly at Lubbock, Texas, U.S.A. Periodicals postage paid at San Angelo, Texas and additional mailing offices. **POSTMASTER:** Send address changes, and returned copies to *The Texas Journal of Science*, Box 43151, Lubbock, Texas 79409-3151, U.S.A. The known office of publication for *The Texas Journal of Science* and The Texas Academy of Science is P. O. Box 10986, ASU Station, San Angelo, Texas 76909, U.S.A.; Dr. Michael J. Carlo, Treasurer.
CONTENTS

Necessary and Sufficient Conditions for Parallel Summable Matrices to be Simultaneously Diagonable.
By Patrick L. Odell and Thomas L. Boullion ........................................ 91

Osteological Specimens of Marine Mammals (Cetacea and Sirenia) from the Western Gulf of Mexico.
By Thomas A. Jefferson and George D. Baumgardner ............................ 97

The Nature of Channel Planform Change: Brazos River, Texas.
By B. Marcus Gillespie and John R. Giardino ...................................... 109

Diet of the Texas Yellow-Faced Racerunner, Cnemidophorus sextineatus stephensi (Sauria: Teiidae), in Southern Texas.
By Mark A. Paulissen, James M. Walker and James E. Cordes ................ 143

Amphibians and Reptiles of the late Pleistocene Tonk Creek Local Fauna, Stonewall County, Texas.
By Dennis Parmley and Russell S. Pfau .............................................. 151

Status of Blarina hylophaga (Insectivora: Soricidae) in North Texas and Southern Oklahoma.
By Frederick B. Stangl, Jr. and Carla B. Carr ..................................... 159

General Notes

By Jeff D. Leach, Harry W. Clark and John A. Peterson ....................... 163

Rafinesque's Big-eared Bat, Plecotus rafinesquii (Chiroptera: Vespertilionidae), from Shelby County, Texas.
By Franklin D. Yancey, II and Clyde Jones ....................................... 166

Age of First Breeding in Golden-fronted Woodpeckers (Melanerpes aurifrons).
By Michael S. Husak ........................................................................... 168

The Bracket Fungus Globiformes graveolens (Aphyllophorales: Polyporaceae) in Northwestern Louisiana.
By Laurence M. Hardy, Larry R. Raymond and Richard K. Speairs, Jr. .... 169

Book Review: Freshwater Mussels of Texas.
By Artie L. Metcalf ............................................................................. 173
THE TEXAS JOURNAL OF SCIENCE
EDITORIAL STAFF

Manuscript Editor:
    Jack D. McCullough, Stephen F. Austin State University
Managing Editor:
    Ned E. Strenth, Angelo State University
Associate General Editor:
    Michael J. Carlo, Angelo State University
Associate Editor for Botany:
    Robert I. Lonard, The University of Texas-Pan American
Associate Editor for Chemistry:
    John R. Villarreal, The University of Texas-Pan American
Associate Editor for Geology:
    M. John Kocurko, Midwestern State University
Associate Editor for Mathematics and Statistics:
    E. Donice McCune, Stephen F. Austin State University
Associate Editor for Physics:
    Charles W. Myles, Texas Tech University

Manuscripts intended for publication in the Journal should be submitted in TRIPLICATE to:
    Dr. Jack D. McCullough
    TJS Manuscript Editor
    Department of Biology - Box 13003
    Stephen F. Austin State University
    Nacogdoches, Texas 75962

Scholarly papers in any field of science, technology, or science education will be considered for publication in The Texas Journal of Science. Instructions to authors are published one or more times each year in the Journal on a space-available basis, and also are available from the Manuscript Editor at the above address.

The Texas Journal of Science is published quarterly in February, May, August and November for $30 per year (regular membership) by THE TEXAS ACADEMY OF SCIENCE. Periodical postage rates (ISSN 0040-4403) paid at Lubbock, Texas. Postmaster: Send address changes, and returned copies to The Texas Journal of Science, PrinTech, Box 43151, Lubbock, Texas 79409-3151, U.S.A.
NECESSARY AND SUFFICIENT CONDITIONS FOR PARALLEL SUMMABLE MATRICES TO BE SIMULTANEOUSLY DIAGONABLE

Patrick L. Odell and Thomas L. Boullion
Department of Mathematics, Baylor University, Waco, Texas 76798 and University of Southwestern Louisiana, Lafayette, Louisiana 70504

Abstract.—In this paper a condition is obtained for which two matrices being parallel summable is equivalent to their being simultaneously diagonable.

Two m x n matrices A and B are said to be parallel summable (p.s.) if their parallel sum

\[ P(A, B) = A(A + B)^g B \]

is invariant with respect to the choice of generalized inverse \((\cdot)^g\).

It is readily shown (Rao & Mitra 1971) that A and B are p.s.

\( \iff R(A) \subseteq R(A + B) \text{ and } R(A^g) \subseteq R(A^g + B^g), \)

\( \iff R(B) \subseteq R(A + B) \text{ and } R(B^g) \subseteq R(A^g + B^g), \)

\( \iff A(A + B)^g B = A(A + B)^g B \text{ for every } (\cdot)^g, \) \hspace{1cm} (1.1)

\( \iff A(A + B)^g (A + B) = A \text{ and } (A + B)(A + B)^g A = A, \) \hspace{1cm} (1.2)

\( \iff B(A + B)^g (A + B) = B \text{ and } (A + B)(A + B)^g B = B, \) \hspace{1cm} (1.3)

where \((\cdot)^g\) is the Moore-Penrose generalized inverse.

If A and B are p.s., then

\[ P(A, B) = P(B, A) \] \hspace{1cm} (1.4)

\[ P(A, B) = A - A(A + B)^g A \] \hspace{1cm} (1.5)
\[ P(A, B) = B - B(A+B)'B \]  

(1.6)

Two \( m \times n \) matrices \( A \) and \( B \) are simultaneously diagonalizable with respect to an equivalence s.d. \( (\sim) \) if there exists non-singular matrices \( S \) and \( T \) such that \( SAT = D_A \) and \( SBT = D_B \) where \( D_A \) and \( D_B \) are diagonal matrices in the sense that \( D = [d_{ij}], d_{ij} = 0 \) for all \( i \neq j \). If \( S = T^{-1} \), then we say that \( A, B \) are simultaneously diagonalizable with respect to a similarity s.d. \((\sim)\).

**Main Results**

**Lemma 1:** Two matrices \( B \) and \( I \) are s.d. \((\sim)\) iff they are s.d. \((\sim)\).

*Proof:* If \( I, B \) are s.d. \((\sim)\), there exists nonsingular matrices \( S \) and \( T \) such that \( SBT = D_B \) and \( SIT = D_I \) are diagonal. This implies \( T^{-1} = S^{-1}D_B' \), thus \( SIS^{-1} = I \) and \( SBS^{-1} = SBTSD_B^{-1} = D_BD_B^{-1} = D \), a diagonal matrix.

Conversely, if \( B, I \) are s.d., \((\sim)\) they are s.d. \((\sim)\) with \( T = S^{-1} \).

**Lemma 2:** Let \( A = \begin{pmatrix} 1 & 0 \\ 0 & 0 \end{pmatrix}, B = \begin{pmatrix} B_{11} & 0 \\ 0 & B_{22} \end{pmatrix} \), then

\( A, B \) are s.d. \((\sim)\) iff \( B_{11} \) is semisimple.

*Proof:* If \( B_{11} \) is semisimple, there exists nonsingular \( S_{11} \) such that \( S_{11}^{-1}B_{11}S_{11} = D_{11} \). Since \( B_{22} \) may be rectangular, let \( U'B_{22}V = D_{22} \) be the singular value decomposition of \( B_{22} \), then

\[
S = \begin{pmatrix} S_{11}^{-1} & 0 \\ 0 & U' \end{pmatrix}, \quad T = \begin{pmatrix} S_{11} & 0 \\ 0 & V \end{pmatrix}
\]

simultaneously diagonalizes \( A \) and \( B \).

**Lemma 3:** If \( A, B \) are square matrices with \( B \) nonsingular, then \( A, B \) are s.d. \((\sim)\) iff \( B^{-1}A \) is semisimple.

*Proof:* If \( A, B \) are s.d. \((\sim)\), there exists nonsingular \( S, T \) such that
SAT = D_A, SBT = D_B. Hence, B^{-1}A = TD_B^{-1}SS^{-1}D_A^{-1} = TDT^{-1} where D is diagonal. Conversely, if B^{-1}A is semisimple, there exists a matrix P such that P^{-1}B^{-1}AP = D. Let S = P^{-1}B^{-1} and T = P, then SAT = D and SBT = P^{-1}B^{-1}BT = I, so A, B are s.d. (~).

**Theorem 1:** Let A, B be square with B nonsingular, then the following two statements are equivalent.

(i) A, B are p.s. and B^{-1}A is semisimple.

(ii) A, B are s.d. (~) and r(A + B) = R(B) = n.

**Proof:** If (i), then (A + B)(A + B)^T = B implies r(A + B) = r(B) = n. By lemma 3, B^{-1}A semisimple iff A, B are s.d. (~). If (ii), then A(A + B)^T = A(A + B)^{-1}B therefore A, B are p.s.

**Theorem 2:** Let A, B be m x n matrices with r(B) = n < m, then the following two statements are equivalent.

(i) A, B are p.s. and B^{-1}A is semisimple.

(ii) A, B are s.d. (~) and r(A + B) = n.

**Proof:** Let U^*(A + B)V = \begin{pmatrix} D_n & 0 \\ 0 & 0 \end{pmatrix} be the singular value decomposition of A + B.

Then (A + B)^* = V(D_n^*|0)U^* and assuming (i) we have B = (A + B)(A + B)^T which implies r(A + B) = n. Also,

\[
B = U \begin{pmatrix} D_n & 0 \\ 0 & 0 \end{pmatrix} (D_n^*|0)U^*B = U \begin{pmatrix} I_n & 0 \\ 0 & 0 \end{pmatrix} U^*B \text{ or }
\]

\[
U^*BV = \begin{pmatrix} I_n & 0 \\ 0 & 0 \end{pmatrix} U^*BV.
\]

Letting \( U^*BV = \begin{pmatrix} B_{11} & B_{12} \\ B_{21} & B_{22} \end{pmatrix} \), we have B_{21} = 0, B_{22} = 0.
Similarly, from $A = (A + B)(A + B)^s A$ we get $A_{21} = 0$, $A_{22} = 0$. Hence, we have

$$U^*BV = \begin{pmatrix} B_1 \\ 0 \end{pmatrix} \text{ and } U^*AV = \begin{pmatrix} A_1 \\ 0 \end{pmatrix},$$
where $B_1$ is $n \times n$ and nonsingular.

Thus,

$$B^*A = VB_1^{-1}A_1V^*.$$  But $B^*A$ semisimple implies $B_1^{-1}A_1$ is semisimple, which by lemma 3 implies $A_1, B_1$ are s.d.($\sim$) and thus A, B are s.d.($\sim$).

Conversely, if $r(A + B) = n$, then $(A + B)^s = (A + B)^*$ and $A, B$ are p.s. Let $SAT = D_1$, $SBT = D_2$, then $B^* = TD_2^{-1}S$ so that $B^*A = TD_2^{-1}SS^{-1}D_1T^{-1}$ and thus $B^*A$ is semisimple.

For the next theorem, let $U^*(A + B)V = \begin{pmatrix} D_r & 0 \\ 0 & 0 \end{pmatrix}$ with $r = r(A + B)$.

Partition $U^*BV = \begin{pmatrix} B_{11} & B_{12} \\ B_{21} & B_{22} \end{pmatrix}$ and $U^*AV = \begin{pmatrix} A_{11} & A_{12} \\ A_{21} & A_{22} \end{pmatrix}$ with $A_{11}, B_{11}$ of size $r \times r$ with $B_{11}$ of rank $r$.

**Theorem 3:** Let $A, B$ be $m \times n$ with $r(A) \leq r(B) = r(A + B) < n \leq m$, then the following two statements are equivalent.

(i) $A, B$ are p.s. and $B_{11}^{-1}A_{11}$ is semisimple.

(ii) $A, B$ are s.d.($\sim$).

**Proof:** Consider the singular value decomposition of $A + B$, say

$$U^*(A + B)V = D = \begin{pmatrix} D_r & 0 \\ 0 & 0 \end{pmatrix}$$

with $U, V$ unitary and $r = r(A + B)$. Then $(A + B)^* = VD^*U^*$. Assuming (i) holds we have $B = B(A + B)^s(A + B) = B(A + B)^*(A + B)$,
which implies \( r(A + B) \geq r(B) \) and thus \( B = BV \begin{pmatrix} I_r & 0 \\ 0 & 0 \end{pmatrix} V' \) and
\[
U'BV = U'BV \begin{pmatrix} I_r & 0 \\ 0 & 0 \end{pmatrix}.
\]
This implies \( B_{12} = 0 \) and \( B_{22} = 0 \). Similarly, from \( B = (A + B)(A + B)'B \) we get \( B_{21} = 0 \) so that \( U'BV = \begin{pmatrix} B_{11} & 0 \\ 0 & 0 \end{pmatrix} \).

From \( A(A + B)'(A + B) = A \) and \( (A + B)(A + B)'A = A \) we get
\[
U'AV = \begin{pmatrix} A_{11} & 0 \\ 0 & 0 \end{pmatrix}.
\]
Thus we have
\[
\begin{pmatrix} A_{11} & 0 \\ 0 & 0 \end{pmatrix} + \begin{pmatrix} B_{11} & 0 \\ 0 & 0 \end{pmatrix} = \begin{pmatrix} D_r & 0 \\ 0 & 0 \end{pmatrix}.
\]

B p.s. implies \( A_{11}, B_{11} \) are p.s. and \( B_{11}^{-1}A_{11} \) semisimple implies \( A_{11}, B_{11} \) are s.d.(~). But this implies A, B are s.d.(~).

Conversely, assuming (ii) holds, let \( SAT = \begin{pmatrix} D_A & 0 \\ 0 & 0 \end{pmatrix} \), \( SBT = \begin{pmatrix} D_B & 0 \\ 0 & 0 \end{pmatrix} \)
where \( D_A, D_B \) are of size \( r = r(A + B) \). Any generalized inverse \( (A + B)^g \) can be expressed as
\[
(A + B)^g = (A + B)^g + U - (A + B)^g(A + B) U (A + B)(A + B)^g \text{ for some } U \text{ where}
\]
\[
(A + B)^g = T \begin{pmatrix} (D_A + D_B)^g & 0 \\ 0 & 0 \end{pmatrix} S. \text{ Hence, } (A + B)^g(A + B) = T \begin{pmatrix} I_r & 0 \\ 0 & 0 \end{pmatrix} T^{-1}
\]
\[
+ U(A + B) - (A + B)^g(A + B) U (A + B) \text{ and}
\]
\[
(A + B)(A + B)^g = S^{-1} \begin{pmatrix} I_r & 0 \\ 0 & 0 \end{pmatrix} S +
\]
\[
(A + B)U - (A + B) U (A + B)(A + B)^g \text{ and thus the product}
\]
\[
B(A + B)^g(A + B) = B \text{ for all } (\cdot)^g \text{ since } D_B I_r = D_B.
\]
Similarly, \( (A + B)(A + B)^gB = B \text{ for all } (\cdot)^g \). Hence, A, B are p.s.
Also, $A, B$ are s.d.($\sim$) iff $A_{11}, B_{11}$ are s.d.($\sim$) and this implies $B_{11}^*A_{11}$ is semisimple.

There are pairs of matrices $A, B$ such that $r(B) > r(A + B)$ and $A, B$ are s.d.($\sim$), but not p.s.; for example, let

$$A = \begin{pmatrix} 0 & 0 & 0 \\ 0 & -1 & 0 \\ 0 & 0 & 0 \end{pmatrix} \quad \text{and} \quad B = \begin{pmatrix} 1 & 0 & 0 \\ 0 & 1 & 0 \\ 0 & 0 & 0 \end{pmatrix}.$$ 

**Literature Cited**


PLO at: Pat_Odell@baylor.edu
OSTEOLOGICAL SPECIMENS OF MARINE MAMMALS (CETACEA AND SIRENIA) FROM THE WESTERN GULF OF MEXICO

*Thomas A. Jefferson and George D. Baumgardner

Department of Wildlife and Fisheries Sciences
Texas A&M University, College Station, Texas 77843-2258

*Present address: Ocean Park Conservation Foundation
Ocean Park Corporation, Aberdeen, Hong Kong.

Abstract.—This report documents the holdings of marine mammal specimens from the western Gulf of Mexico currently deposited in the Texas Cooperative Wildlife Collection at Texas A&M University. These include 124 catalogued specimens of 17 species of cetaceans (nine whales and eight dolphins) and one species of sirenian (manatee). Collection data and relevant information are provided for specimens of each species.

There has been comparatively little research on the marine mammals of the western Gulf of Mexico until recently. This body of water is known to contain at least 31 species of marine mammals, including 28 cetaceans, two species of pinnipeds and one species of sirenian (Schmidly & Melcher 1974a; 1974b; Schmidly 1981; Jefferson et al. 1992; Davis & Schmidly 1994). Of these taxa, many are considered to be protected, threatened or endangered by the Convention on International Trade in Endangered Species of Wild Flora and Fauna and the Texas Parks and Wildlife Department. Most of the literature on the marine mammals of this area (exclusive of the extensive information on the coastal bottlenose dolphin, *Tursiops truncatus*) has been in the form of short notes reporting occasional strandings or opportunistic sightings of offshore oceanic species. Schmidly (1981) compiled and summarized records of cetaceans and pinnipeds from the Gulf of Mexico. Jefferson et al. (1992) updated the taxonomy and distribution maps of Schmidly (1981) and Blaylock et al. (1995) reported stock assessments and population characteristics for cetaceans from this area.

Much of the information comprising these summary publications was obtained from reports of stranded animals or from records for specimens in natural history collections and museums. Yates et al. (1987) listed the Texas Cooperative Wildlife Collection (TCWC) as the 14th largest collection of mammals in North America. The TCWC currently has over 53,000 cataloged specimens obtained from the early 1930’s to present. This collection contains over 150 marine mammal specimens. One hundred twenty-four of these specimens are from the western Gulf.
of Mexico, mostly from Texas waters. The TCWC is the second largest collection of cataloged osteological material of marine mammals from the Gulf of Mexico in the world after the Florida Museum of Natural History, University of Florida, Gainesville, Florida, and is the largest such collection for the western Gulf. It is slightly more extensive and diverse than the collection maintained by the Texas Marine Mammal Stranding Network (TMMSN) in Galveston. Much of the material in the TCWC has been collected during the last decade through efforts of the TMMSN (Tarpley & Marwitz 1986; Tarpley 1987); however, there are a number of animals obtained by workers, supervised by David J. Schmidly during the 1970’s. This facility also houses some of the earliest reported specimens in the literature for the Gulf of Mexico (Gunter 1941a; 1941b; 1946).

The following is a listing of the marine mammal specimens from the western Gulf of Mexico maintained by the TCWC, with a brief summary of their pertinent data. Available data for each specimen are given as to collection locality, date of collection, sex, catalog number, type of material (skull = cranium & lower jaw, skeleton = post-cranial material). Measurements, when available, are total length in cm = TL (obtained from stranding reports or literature) and condylobasal length in mm = CBL (obtained by the senior author, following Perrin 1975 or from the literature). In a few instances there are supplemental remarks regarding specific animals or taxa. Additional details for many localities are available from the TCWC. For most specimens obtained after 1980, additional information regarding circumstances of their recovery and necropsy can be obtained from the TMMSN, 4700 Avenue U, Building 303, Galveston, Texas 77551.

*Balaenoptera acutorostrata* Lacepede

Minke whale

*Material examined.—* TEXAS: MATAGORDA COUNTY, Matagorda Peninsula (4 mi SW of jetty), 30 March 1988, one ♀ specimen (TCWC 52892; skull & skeleton; TL 579 cm).

*Balaenoptera edeni* Anderson

Bryde’s whale

*Material examined.—* LOUISIANA: PLAQUEMINES PARISH, Venice (offshore), 15 January 1975, one ♂ specimen (TCWC 39643; baleen plates; TL 841 cm).
Remarks.—The occurrence of this species of whale from the coast of Louisiana was reported by Shane & Schmidly (1976).

*Feresa attenuata* Gray
Pygmy killer whale

**Material examined.**—**TEXAS:** MATAGORDA COUNTY, West Matagorda Peninsula, 30 March 1989, one specimen (TCWC 52893; skull & skeleton). NUECES COUNTY, Aransas Pass, 19 November 1983, one ♀ specimen (TCWC 45105; skeleton); one ♂ specimen (TCWC 48380; skeleton).

*Globicephala macrorhynchus* Gray
Short-finned pilot whale

**Material examined.**—**TEXAS:** ARANSAS COUNTY, St. Joseph Island, 5 September 1945, one specimen (TCWC 3668; skull; TL 391 cm). Locality unspecified (probably Texas coast), one specimen (TCWC 50848; skull).

*Grampus griseus* (G. Cuvier)
Risso’s dolphin

**Material examined.**—**TEXAS:** ARANSAS COUNTY, San Jose Island, 12 February 1988, one ♂ specimen (TCWC 50948; skull & skeleton; TL 283 cm). MATAGORDA COUNTY, On beach 7.3 mi E of mouth of Colorado River, 17 December 1988, one ♀ specimen (TCWC 52894; skull & skeleton; TL 297 cm).

*Stenella attenuata* (Gray)
Pantropical spotted dolphin

**Material examined.**—**TEXAS:** GALVESTON COUNTY, Bermuda Beach, Galveston Island, 2 July 1988, one ♀ specimen (TCWC 52897; skull & partial skeleton; TL 198 cm). KENEDY COUNTY, Padre Island National Seashore, 3 April 1988, one ♀ specimen (TCWC 52896; skull & skeleton; TL 121 cm). NUECES COUNTY, Locality unspecified, 7 April 1988, one ♀ specimen (TCWC 50941; skull and skeleton; TL 199 cm; CBL 414 mm). Locality unspecified (probably Texas coast), one specimen (TCWC 50851; skull).
Figure 1. Crania of two specimens of *Stenella clymene*, both at various times given the number TCWC 25575. A. "Hildebran's specimen" (currently TCWC 52870). B. LSUMZ 18519. From ventral view, the skulls can easily be distinguished from the broken left pterygoid of LSUMZ 18519.

*Stenella clymene* (Gray)
Clymene dolphin

*Material examined.*—TEXAS: BRAZORIA COUNTY, Bryan Beach, 5 February 1986, one ♂ specimen (TCWC 50934; skull & skeleton; TL 168 cm; CBL 375 mm). GALVESTON COUNTY, Galveston, 14 September 1987, one ♀ specimen (TCWC 50947; skull & skeleton; TL 176 cm). KLEBERG COUNTY, Padre Island National Seashore, 11 March 1985, one ♀ specimen (TCWC 50936; skull & partial skeleton; TL 186; CBL 378 mm); 9 September 1986; one ♂ specimen (TCWC 50937; skull & skeleton; TL 186 cm; CBL 364 mm). NUÉCES COUNTY, Yarbrough Pass, Padre Island, 19 September 1971, one ♂ specimen (TCWC 25576; skull; TL ca. 175 cm; CBL 372 mm); one specimen (TCWC 52870; skull; TL ca. 175 cm; CBL 390 mm). 6.9 mi S. Access Rd., 26 April 1984, one ♂ specimen (TCWC 50938; skull; TL 178 cm; CBL 365 mm). Port Aransas, 27 October 1984, one ♂ specimen
(TCWC 50939; partial skeleton; TL 176 cm); one ♀ specimen (TCWC 50940; skeleton; TL 171 cm). Locality unspecified (probably Texas coast), one specimen (TCWC 50847; skull).

Remarks.—In the past there has been confusion regarding the catalog number of TCWC 52870 and a second specimen (Figure 1). Three dolphins stranded at Yarbrough Pass, Texas in September of 1971 were originally identified as *Stenella frontalis* (cf. Schmidly et al. 1972; Schmidly & Shane 1978). Skulls from two of these dolphins were deposited in the TCWC and were assigned the catalog numbers 25575 and 25576. In 1974, TCWC 25575 was transferred to Louisiana State University Museum of Zoology, where it was renumbered LSUMZ 18519. The skull of the third animal of this stranding was retained for some time at the University of Corpus Christi (now Texas A&M University at Corpus Christi) and was referred to by Schmidly et al. (1972) and Perrin et al. (1981) as "Hildebran’s specimen." This skull appears to have been subsequently deposited in the TCWC. This conclusion is based on information written on a specimen in the TCWC and agreement between measurements of this skull and ones given by Schmidly et al. (1972) for the Hildebran specimen. Upon its deposition in the TCWC, it appears that the Hildebran specimen was mistakenly assigned the TCWC catalog number 25575. Following the realization that this specimen had been given an occupied number, it was reassigned as TCWC 52870. Perrin et al. (1981) reidentified all three of these animals (TCWC 25576, 52870, LSUMZ 18519) as *S. clymene*.

*Stenella coeruleoalba* (Meyen)
Striped dolphin

Material examined.—TEXAS: GALVESTON COUNTY, Bolivar Peninsula, Crystal Beach, 14 April 1986, one specimen (TCWC 50942; skull & partial skeleton; TL 204 cm; CBL 414 mm). JEFFERSON COUNTY, 17 September 1986, one ♂ specimen (TCWC 50935; skull & skeleton; TL 166 cm; CBL 412 mm). NUECES COUNTY, Mustang Island, 20 April 1985, one ♂ specimen (TCWC 50943; skull & partial skeleton; TL 209 cm; CBL 407 mm).

*Stenella frontalis* (G. Cuvier)
Atlantic spotted dolphin

Material examined.—TEXAS: GALVESTON COUNTY, 2 mi W of High Island, 25 February 1967, one specimen (TCWC 21358; skull; CBL 420 mm). NUECES COUNTY, Port Aransas, summer of 1940, one specimen
(TCWC 1543; skull). Padre Island (19 mi SE of Corpus Christi), 3 September 1965, one $\delta$ specimen (TCWC 25577; skull; CBL 449 mm). Locality unspecified (probably Texas coast), one specimen (TCWC 50850; cranium).

Remarks.—The only data directly associated with TCWC 1543 is that of its collector (G. Gunter); however, it is quite likely this animal is the same as that reported by Gunter (1941b) as *Stenella plagiodon*. This conclusion was made because both specimens (TCWC 1543 and that of Gunter, 1941b) have the same collector plus similar measurements and characteristics. The genus *Stenella* was recently revised by Perrin et al. (1987).

*Stenella longirostris* (Gray)
Spiner dolphin

Material examined.—TEXAS: JEFFERSON COUNTY, Sabine Pass Beach, 16 May 1974, one specimen (TCWC 28286; skull, scapula & flippers; TL 156 cm; CBL 361 + mm). KLEBERG or NUECES COUNTY, Padre Island (4 mi S of Malaquite Beach), 3 March 1975, one specimen (TCWC 29035; skull; TL 188 cm; CBL 420 mm). NUECES COUNTY, Mustang Island, 1 June 1987, one $\delta$ specimen (TCWC 50946; skull and skeleton; TL 190 cm; CBL 418 mm).

*Steno bredanensis* (Lesson)
Rough-toothed dolphin

Material examined.—TEXAS: GALVESTON COUNTY, West end of Galveston Island, June 1969, one $?$ specimen (TCWC 50914; skull & skeleton; TL 234 cm). Bolivar Peninsula, Crystal Beach, 6 September 1985, one $\delta$ specimen (TCWC 50915; skull & partial skeleton; TL 254 cm).

Remarks.—The specimen TCWC 50914 is represented by an articulated skeleton that was formerly on display at a marine park (Sea Arama) in Galveston, Texas.

*Tursiops truncatus* (Montagu)
Bottlenose dolphin

Material examined.—TEXAS: ARANSAS COUNTY, Atwell, Aransas Refuge, January 1940, one specimen (TCWC 1071; partial cranium). 2
mi NNE of Fulton, 1958, one specimen (TCWC 9470; skull & miscellaneous skeletal parts). Rockport (N side of Key Allegro Island), 25 March 1988, one ♀ specimen (TCWC 50916; lower jaws & skeleton; TL 225). E side of Aransas Bay, 3 October 1990, one ♀ specimen (TCWC 52903; skull & skeleton; TL 189 cm). BRAZORIA COUNTY, Surfside beach, 15 March 1985, one ♀ specimen (TCWC 50926; skull & skeleton; TL 166 cm). CAMERON COUNTY, South Padre Island, 17 January 1986, one ♀ specimen (TCWC 50917; partial skeleton; TL 221 cm). CHAMBERS COUNTY, 20 mi SW of Sabine Pass, 17 November 1985, one ♀ specimen (TCWC 50918; skull & skeleton; TL 219 cm). GALVESTON COUNTY, 7 mi W of Galveston, 17 March 1939, one ♂ specimen (TCWC 1089; skull). Pelican Island, Galveston Channel, 28 June 1977, one specimen (TCWC 44003; cranium). Galveston, 13 April 1984, one ♂ specimen (TCWC 49004; skull & skeleton; TL 114 cm); 15 December 1984, one ♂ specimen (TCWC 49006; skull & skeleton; TL 147 cm); 22 January 1986, one ♀ specimen (TCWC 50933; partial skeleton; TL 227 cm). Galveston Island, 3 December 1985, one ♂ specimen (TCWC 49010; skull & skeleton; TL 266 cm); 3 January 1985, one ♀ specimen (TCWC 50927; skull & skeleton; TL 247 cm); Beach Pocket Park, 19 April 1984, one ♂ specimen (TCWC 49005; skull & skeleton; TL 225 cm); Stewart Beach, 12 March 1985, one ♀ specimen (TCWC 49007; skull & skeleton; TL 204 cm); East Beach, 12 March 1985, one ♂ specimen (TCWC 49008; skull & skeleton); Big Reef Beach, 19 November 1984, one ♂ specimen (TCWC 50929; skull & skeleton). Bolivar Peninsula, 14 March 1986, one ♀ specimen (TCWC 49012; skull & skeleton; TL 245 cm); Crystal Beach, 12 March 1985, one ♀ specimen (TCWC 49009; skull & skeleton; TL 264 cm); 7 January 1989; one ♀ specimen (TCWC 50931; skeleton; TL 233 cm); High Island, December 1985, one ♀ specimen (TCWC 49011; skull & skeleton; TL 242 cm); 6.5 mi W of Bolivar Ferry Landing, 21 November 1987, one ♀ specimen (TCWC 50919; skeleton; TL 253 cm). Gilchrist, 19 April 1984, one ♂ specimen (TCWC 49014; skeleton; TL 274 cm); 13 March 1988, one ♂ specimen (TCWC 50928; skull & skeleton; TL 212 cm). Gilchrist area, 14 April 1986, one specimen (TCWC 50930; skull & skeleton). HARRIS COUNTY, San Jacinto River, 27 February 1987, one ♂ specimen (TCWC 50920; partial skull & partial skeleton; TL 237 cm). JEFFERSON COUNTY, 20 August 1986, one ♂ specimen (TCWC 49013; skull & skeleton; TL 262 cm). 21.8 mi E of Rollover Pass, 26 July 1987, one ♀ specimen (TCWC 52906; partial skeleton; TL 250 cm). 14.5 mi W of McFaddin National Wildlife Refuge, 22 February 1990, one ♀ specimen (TCWC 52907;
skull; TL 251 cm). KLEBERG COUNTY, Padre Island National Seashore, 1 March 1988, one δ specimen (TCWC 50932; skull; TL 179 cm).

MATAGORDA COUNTY, East Matagorda Bay, 21 January 1990, six ♀ specimens (TCWC 52858; skull & skeleton; TL 240 cm); (TCWC 52862; skull & skeleton; TL 245 cm); (TCWC 52863; skull & skeleton; TL 216 cm); (TCWC 52864; skull & skeleton); (TCWC 52880; skeleton; TL 176 cm); (TCWC 52882; skull & partial skeleton; TL 220 cm); four δ specimens (TCWC 52859; partial skeleton; TL 288 cm); (TCWC 52860; skeleton; TL 270 cm); (TCWC 52861; skull & skeleton; TL 262 cm); (TCWC 52885; skeleton; TL 225 cm); 22 January 1990, three δ specimens (TCWC 52865; skull & skeleton; TL 191 cm); (TCWC 52867; skull & skeleton; TL 216 cm); (TCWC 52868; skull & skeleton; TL 269 cm); five ♀ specimens (TCWC 52866; skull & skeleton; TL 282 ± 5 cm); (TCWC 52869; skull & skeleton; TL 261 cm); (TCWC 52888; skeleton; TL 256); (TCWC 52890; skull, scapula & flippers; TL 207 cm); (TCWC 52891; skull & skeleton; TL 254 cm).

3.5 mi E Colorado River Pier, 21 January 1990, one δ specimen (TCWC 52878; skull & skeleton; TL 198 cm). 6.4 mi E of Colorado River, 21 January 1990, one ♀ specimen (TCWC 52879; skeleton; TL 235 cm). NUECES COUNTY, Corpus Christi ship channel, 23 January 1986, one ♀ specimen (TCWC 50921; partial skeleton; TL 228 cm). Mustang Island, Gulf beach, 1 February 1986, one δ specimen (TCWC 50922; skull & partial skeleton; TL 280 cm). Corpus Christi, 17 September 1986, one δ specimen (TCWC 50923 skull & skeleton; TL 205 cm). Corpus Christi, Oso Bay, 9 October 1986, one δ specimen (TCWC 50924; partial skeleton; TL 144 cm). Corpus Christi Bay, 6 March 1988, one δ specimen (TCWC 52900; skull; TL 115 cm). 1.2 mi N of Padre Island National Seashore, 23 March 1988, one δ specimen (TCWC 52901; skull & skeleton; TL 261 cm). 4.1 mi N of Padre Island National Seashore, 19 May 1987, one δ specimen (TCWC 50925; skull & skeleton; TL 272 cm). Locali-ty uncertain (probably near Victoria, Victoria County), 3 March 1941, one specimen (TCWC 1537; skull). Texas coast, locality unspecified, mid 1970’s, 13 specimens (TCWC 43990, 43991, 43992*, 43993*, 43994*, 43995, 43996*, 43997, 43998, 43999, 44000*, 44001, 44002; skulls or cranium if marked with *); one specimen (TCWC 52911; fully articulated skeleton).

Remarks.—The 20 specimens obtained from east Matagorda Bay in January of 1990 were probably part of the same stranding event. Varansi et al. (1992) reported the results of biochemical analysis of these specimens.
Kogia breviceps (Blainville)
Pygmy sperm whale

**Material examined.**—TEXAS: CALHOUN COUNTY, Port O'Connor, 20 August 1974, one specimen (TCWC 29120; skull; TL ca. 321 cm). GALVESTON COUNTY, Galveston beach, 1 January 1984, one ♀ specimen (TCWC 48381; partial skeleton; TL 288 cm). KLEBERG COUNTY, Padre Island National Seashore, 19 October 1986, one specimen (TCWC 50949; skull & partial skeleton; TL 282 cm).

**Remarks.**—Unique aspects regarding beaching of the specimen from Calhoun County were discussed by Hysmith et al. (1976).

Kogia simus (Owen)
Dwarf sperm whale

**Material examined.**—TEXAS: CALHOUN COUNTY, Matagorda Island, 23 February 1991, one ♂ specimen (TCWC 52908; skull & partial skeleton; TL 216 cm). MATAGORDA COUNTY, Matagorda Peninsula, 3 November 1985, one ♀ specimen (TCWC 50950; partial skeleton; TL 142 cm).

Mesoplodon densirostris (Blainville)
Blainville’s beaked whale

**Material examined.**—TEXAS: Locality unspecified, one ♀ specimen (TCWC 50856; skull).

**Remarks.**—Based on the preparator’s name and number on the tag accompanying this specimen, it is part of a consecutive series of three animals prepared by the same individual. Schmidly (1981) listed Matagorda Island and Nueces County as localities for an unspecified number of specimens of Mesoplodon europaeus housed in the TCWC. At the time of publication of the previous work, these specimens were not cataloged. They were, however, the only representatives of this genus in the TCWC until 1979. It is virtually certain that these specimens are those referred to by Schmidly (1981). This specimen is in all likelihood from either the Matagorda Island or Nueces County localities given above, but assignment to a precise locality can not, however, be determined. Subsequent to Schmidly (1981), the specific identification of the specimen (TCWC 50856) was changed to *M. densirostris*.
Mesoplodon europaeus (Gervais)
Gervais' beaked whale

Material examined.—TEXAS: CAMERON COUNTY, South Padre Island, 11 May 1989, one ♀ specimen (TCWC 52909; skull & skeleton; TL 415 cm); one specimen (TCWC 52910; skull & skeleton; TL 285 cm). Locality unspecified, two ♀ specimens (TCWC 50855; skull); (TCWC 50857; skull).

Remarks.—The circumstances relative to the collection locality of TCWC 50855 and 50857 are discussed under the above Remarks section of Mesoplodon densirostris. While assignment of an exact locality cannot be determined, these specimens are in all likelihood from either the Matagorda Island or Nueces County localities given by Schmidly (1981).

Ziphius cavirostris G. Cuvier
Cuvier's beaked whale

Material examined.—TEXAS: CAMERON COUNTY, Port Isabel, 19 June 1980, one ♀ specimen (TCWC 37054; skull). JEFFERSON COUNTY, 15 km W of Sabine Pass, 19 December 1984, one ♂ specimen (TCWC 51206; skull). KENEDY COUNTY, Padre Island National Seashore, one ♀ specimen (TCWC 50951; skeleton; TL 578 cm).

Trichechus manatus Linnaeus
West Indian manatee

Material examined.—TEXAS: GALVESTON COUNTY, Bolivar Peninsula, 7 February 1983, one ♂ specimen (TCWC 49000; skull & skeleton; TL 274 cm). REFUGIO COUNTY, Copano Bay, July 1928, one ♂ specimen (TCWC 1528; skull & miscellaneous skeletal parts).

Remarks.—The occurrence of this species of manatee in the western Gulf of Mexico was reported by Gunter (1941a) and Fernandez & Jones (1990).

ACKNOWLEDGMENTS

The authors thank Elsa Haubold, Ann Bull and Graham Worthy, of the TMMSN, for assistance in obtaining biological data for a number of
these specimens; John McEachran for the loan of calipers to measure skulls; Bernd Würsig for travel assistance to T. A. Jefferson and the anonymous reviewers and editors of this manuscript for their suggestions.

LITERATURE CITED


GDB at: g-baumgardner@tamu.edu
THE NATURE OF CHANNEL PLANFORM CHANGE: 
BRAZOS RIVER, TEXAS

B. Marcus Gillespie and John R. Giardino
Department of Geology and Geography, Northwest Missouri State University
800 University Drive, Maryville, Missouri 64468 and
Department of Geology and Geophysics, Office of Graduate Studies,
Texas A&M University, College Station, Texas 77843-3147

Abstract.—This study describes the nature of channel planform change that occurred in three contiguous alluvial reaches of the Brazos River, Texas, from the 1930s to 1988. The reaches encompass 260 km and more than 125 bends. A migratory activity index (MAI) developed for the study indicates that the river's rate of migration has decreased substantially since 1939. This change in behavior results from diminished discharges and suspended sediment loads caused by flow regulation and is consistent with previous findings on the effects of flow regulation on channel activity. However, other results are contrary to those found in studies of freely migrating rivers. Although planform controls on migration rates were found, the interaction of variables resulted in poor correlations with migration. Of greatest significance was that 26% of the bends on the river experienced "negative migration," i.e., migration toward the baseline connecting the inflection points that define a bend. This phenomenon, which is not a form of meander cutoff, has not been described before and its significance lies in the fact that it would seem to preclude the development of predictive models of migration and planform evolution.

Since the 1950s, a large amount of fluvial geomorphological research has been directed toward the development of an understanding of meandering rivers. The study of river behavior is based, in part, on the threats rivers pose to structures, such as bridge abutments and flow control structures, and to the land located adjacent to them (Hickin & Nanson 1975). In addition, changes in the amount of sediment either eroded or deposited in the channel because of human-induced land use or discharge changes can alter the flooding frequency of the river and the nature of the riparian and aquatic ecosystems associated with it (Petts 1980).

One of the principal problems currently facing fluvial geomorphologists concerns the nature of meander evolution and migration (i.e., the nature of channel planform change) in alluvial river channels. Previous research indicates that meander evolution is a complex phenomenon for which few universal principles have been discerned. Nonetheless, it has generally been accepted that meander planform size is a function of discharge, that meanders usually grow in size and sinuosity by migrating laterally until cutoff occurs, and that rates of meander migration are often correlated with certain aspects of meander shape.
Based on these and other principles regarding the physics of fluid flow in a meander bend, several models of channel planform evolution have been developed (Howard & Knutson 1984; Ferguson 1984; Parker & Andrews 1985; Furbish 1988; Odgaard 1989). However, these models were developed for freely migrating rivers that exist in homogenous sedimentologic environments, i.e., for conditions that characterize very few rivers. Because of this limitation, additional research is needed to more fully characterize and delimit the wide range of river planform behavior that occurs under more complex environmental conditions. In addition, the models developed to date do not explicitly incorporate information pertaining to the influence of flow regulation on channel behavior. Because the discharge of most of the world’s rivers is regulated, a secondary interest therefore pertains to the nature of channel adjustments that occur in rivers as a result of alterations in their flow regimes associated with either water impoundment or water diversion (Petts 1980).

The Brazos River, Texas can experience rapid planform adjustment (i.e., adjustment within a period of years) to changing environmental conditions throughout much of its length south of Waco, Texas. The alluvial environment in which it occurs is typical of most alluvial rivers in that it is characterized by the presence of dominantly unconsolidated sands, silts and clays interspersed with occasional outcrops of indurated sediments or rock. In addition, it is substantially regulated by dams located on both the river itself and on several of its tributaries. For this reason, it was chosen for purposes of studying and characterizing the planform adjustment of rivers that are impacted by flow regulation and that exist in environments that typify most rivers. Specifically, the research presented in this article attempts to describe the character of three contiguous alluvial reaches of the Brazos River, Texas as a function of discharge and sedimentologic environment, as well as the nature of channel planform evolution that occurred during the period from the late 1930s to 1988.

**STUDY AREA**

The Brazos River Drainage Basin (Fig. 1 inset) covers more than 15% of the state of Texas, with a total area of 112,640 km². The portion of the Brazos River channel located in the study area is approximately 10-18 m deep and averages 110-140 m in width as measured from bank crest-to-bank crest. The floodplain is composed primarily of unconsolidated alluvium, although resistant layers of
indurated sediments and rock are present. Maximum discharge usually occurs in the spring and overbank flooding occurs approximately four to five times per century. Discharge in the study area is regulated by numerous reservoirs located upstream from the study area, nine reservoirs located on tributaries that enter the study area, and approximately 147 flow retarding structures.

The study area (Fig. 1) consists of three contiguous reaches extending
a maximum distance of 260 km and encompassing from 129 to 144 bends. The variation in channel length and bend number reflects changes that occurred in the river during the intervals between successive measurements. The three reaches are defined by confluences with the Little River and Navasota River. The choice of these reaches and the use of confluences to define them was based on the need to: (1) determine the effects of downstream increase in discharge on planform size and behavior; (2) minimize variability in the alluvial environment; (3) have gauging station data for each reach; (4) have suspended load data for the study area; and (5) have approximately contemporaneous photographic coverage of all reaches within the study area.

**METHODOLOGY**

*Map production.*—To measure meander planform and evolution, maps of the channel centerline were created from aerial photographs using a Geographic Information System. The photographs had a nominal scale of approximately 1:40,000, for the 1974 photography, and approximately 1:20,000 for all other years encompassed by the photography, i.e., 1939, 1940, 1941, 1949, 1951, 1965, 1966 and 1988. A total of 213 photographs were used to create the maps. For convenience of reference, those maps derived from photographs that were obtained over a period of more than one year are named as follows: the map derived from photographs obtained in 1939, 1940 and 1941 is referred to as the 1941 map; the map derived from photographs obtained in 1949 and 1951 is referred to as the 1951 map; and the map derived from photographs obtained in 1965 and 1966 is referred to as the 1965 map.

These photographs were originally acquired as part of photographic surveys of the counties in which the study reaches are located. Because the surveys were not always conducted contemporaneously, the photographs used to represent the location of the river at a "specific" point in time could actually encompass a period of up to three years. In addition to this limitation, no photographic survey was conducted for a portion of Study Reach 2 in 1974. Consequently, no coverage was available for 44 bends located in that section of the river at that time. These limitations probably do not compromise the integrity of the maps, as no dams were constructed during the period of overlap encompassed by individual maps. Therefore, no major anthropogenic changes in discharge would have occurred during the period encompassed by any one map, and presumably, no major changes in the form or behavior of the river. Although it is conceivable that natural processes could have
affected the form and behavior of the river during the interval encompassed by a map, this is deemed unlikely given the relatively small time intervals involved. Overlay maps showing the channel in 1941 and 1950, 1950 and 1965, 1965 and 1974, and 1974 and 1988 were printed at approximately 1:37,000 scale.

Discharge characterization.—The discharge for each study reach during each interval of time was characterized in terms of total discharge and maximum annual discharge. In addition, the change in suspended sediment load (percent dry weight silt) was examined using data obtained from the Richmond gauging station located approximately 83 linear km downstream from the study area. The purpose of these procedures was to determine whether the discharge of the river increased significantly in the downstream direction and to determine if the regime of the river had changed significantly through time because of the construction of dams on the Brazos River and its tributaries.

Bank strength characterization.—Previous studies have shown that the rate of channel migration is inversely proportional to the strength of the channel banks. Hickin & Nanson (1984) noted that it has generally been assumed that the grain size of the basal sediment in the outer bank is the most important component of bank strength, and Schumm (1960a; 1960b) considered the silt and clay content to be the most important textural class in defining bank strength. Accordingly, for purposes of this study, bank resistance to erosion was measured in terms of the percent silt and clay comprising the concave wall of a meander bend. Sediment was not obtained from the bed of the channel because of the difficulties of obtaining such measurements and because no historical information regarding bed sediments was available.

To characterize the textural composition of the bank material, three to seven samples of sediment were collected from each accessible, unvegetated cutbank from a zone located just above water level. The samples from each bend were then combined into a composite sample for purposes of textural analysis. The number of samples obtained per bend was determined by the size and accessibility of the cutbank. Although samples were taken only from the base of the banks, the fact that this portion of the banks was frequently covered by slumped material, and the fact that several samples per bend were taken, ensured that the overall composition of the bank was reflected in the composite sample obtained from each bend.

A total of 65 composite sediment samples were collected for textural
Radius of Curvature
(2 Ws)

Amplitude

Arc Length

Upstream Inflection Point

Flow Direction

Downstream Inflection Point

Figure 2. Diagram illustrating the features and measures used to characterize river bends on the Brazos River. (W = channel width, Rc = radius of curvature.) Note that radius of curvature is measured at the point of maximum amplitude. "Area" is that area bounded by the bend arc line and the baseline. The "0.5" in the term "E0.5" reflects the fact that the E0.5 width was measured relative to the mid-point of the amplitude line.

analysis: thirteen from Study Reach 1; twenty-two from Study Reach 2; and thirty from Study Reach 3. These samples were obtained from the entire length of Study Reaches 1 and 3 and half of Study Reach 2. The lower half of Study Reach 2 could not be sampled for a variety of reasons; however, this limitation did not pose a problem because the part of Study Reach 2 that was sampled was approximately equal in length to that of the other study reaches. The textural analysis was done by the Soil Science Lab at Texas A&M.

Planform shape and evolution measures.—The planform character of the bends comprising selected channel reaches at five points in time during the period extending from the late 1930s to the late 1980s was quantitatively described by several morphometric parameters (described below). A meander bend is that portion of a channel located between consecutive inflection points. Inflection points are the points along a channel centerline at which a reversal in the direction of channel curvature occurs.

For purposes of this study, a manual procedure was developed for determining the location of inflection points that consisted of using a rectangular grid, termed an "inflection point identification window", drawn on a transparency. When centered over an inflection point, the upstream and downstream portions of the channel curve away from the center point in opposite directions, and at approximately equal rates.
Examples of its use are shown in Figs. 2 and 3. Once the inflection points that define a given bend were identified, all other bend shape measures could be determined. Five of the 14 bend form measures are illustrated in Fig. 2. These measures include: (1) arc length (Al); (2) baseline length (BLl); (3) Sinuosity (Sin); (4) amplitude (Amp); and (5) area (A). Additional measures requiring explanation are listed and described below:

(6) radius of curvature (Rc) - a measure of bend curvature was obtained by first drawing a series of arcs of different sizes onto a set of transparencies. A total of approximately 70 arcs, ranging in radius of curvature from 55 m to 2,300 m, were used. Each bend was then marked with three points centered on the point of maximum amplitude, and spaced approximately one channel width (110 m) apart (Fig. 2). Once the points were marked, the arcs were used to estimate the radius of curvature of each bend by overlaying the transparencies in such a way that an arc passed through all three points that had been marked on the bends. The radius of curvature of this arc was used as the radius of curvature of the bend;

(7) radius of curvature to channel width (Rc/W) - previous research by Hickin (1977) showed that this ratio is related to migration rates;

(8) asymmetry (As) - the ratio of the area of that part of a bend located on the downstream side of a line drawn perpendicular from the midpoint of the baseline to the apex of the bend (A_d),
to the total area of the bend \( A_t \); thus, asymmetry = \( A_d/A_t \) (Fig. 3). When the value is 0.5, the bend is perfectly symmetrical; when it is greater than 0.5 (positive), the bend is larger in the downstream direction than in the upstream direction; and when it is less than 0.5 (negative), it indicates the opposite. (For purposes of this study, bends with a value of .48 to .52 were considered symmetrical.) Asymmetry was measured because it has been suggested by Raisz (1955) that most bends should be asymmetrical in the downstream direction (i.e., most bends should have an \( A_s \) value greater than 0.5). If so, then the direction of flow could be ascertained from maps and aerial photographs based on the asymmetrical shape of the bends;

(9) channel width \( (W) \) - the width of the channel as measured from bank crest-to-bank crest from points located near the inflection points of the channel. For those cases in which the inflection point occurred near a point bar, the width of the channel was defined as the distance from the top of the cutbank to either a change in slope on the point bar, or to a line of perennial vegetation on the point bar. The change in slope and perennial vegetation were chosen because they are believed to reflect the channel width during the annual flood;

(10a) Simple bends - bends that did not exhibit substantial secondary waveform development along their arc length (Fig. 4)

(10b) Compound bends - bends that exhibited significant secondary
Figure 5. Diagram illustrating the manner in which changes in amplitude were measured. The change in amplitude is obtained by subtracting the length of the amplitude line at time $t_1$ from that at time $t_2$. A negative value would indicate a reduction in amplitude size, whereas a positive value would indicate bend growth.

Waveform development. The key criterion for distinguishing simple bends from compound bends is that the secondary arcs in simple bends are not developed sufficiently enough to cross the baseline that connects the inflection points that define the primary arc (Fig. 4). This division of bends into simple and compound types is based on work by Brice (1974) and is considered important based on the hypothesis that secondary waveform development might reduce rates of lateral migration. This is because it would affect the distribution of force applied to the outside wall of the primary bend arc as a result of flow reversal in the primary bend.

Other planform measures included maximum bend width ($E_{\text{max}}$ width), and bend half width ($E_{0.5}$ width). The manner in which these are defined is illustrated in Fig 3. Maximum extent ratio ($E_{\text{max}}$ ratio), and half bend width ratio ($E_{0.5}$ ratio) were also measured and are obtained by dividing the $E_{\text{max}}$ and $E_{0.5}$ values by the length of the baseline. The measures of bend width and their associated ratios were measured in an attempt to assess the effects of bend "flattening" on migration rates. A flattened bend is one in which the bend is longer in the downvalley direction than in the lateral, or across-valley, direction. The bend shown in Fig. 4 is an example of a flattened, compound bend. It was hypothesized by the authors that bends that exhibited high $E_{\text{max}}$ and $E_{0.5}$ ratios would experience slower migration rates because flattening would result in less curvature in the vicinity of the apex. As discussed by Hickin (1977), low curvature is correlated with lower rates of migration.

Besides form measures, two measures of change were also used that are based on modifications of procedures and concepts originally
Figure 6. Diagram illustrating the manner in which positive and negative lateral migration is measured. Note that the lateral migration distance is measured relative to two lines drawn parallel to the earlier (1941) baseline. The areas that are shaded are examples of the polygons created by the overlay of the channel at successive points in time, and which are used to measure the Migratory Activity Index (MAI).

Changes in amplitude are defined as the difference in amplitude at successive points in time (Fig. 5). Although this definition may at first appear to be synonymous with lateral migration, it is not. The amplitude is measured by a line drawn perpendicularly from the baseline of a bend at a specific point in time. But, as the bend rotates, the orientation of the baseline changes, and as it does, so does the orientation of the amplitude line. Thus, the difference in amplitude at successive points in time does not usually represent a simple change in the extent of the bend.

Inspection of Fig. 6 shows that lateral migration represents the difference in distance between parallel lines drawn tangent to the apexes of a bend at successive points in time and parallel to the baseline at time $t_1$. Stated differently, lateral migration ($LM_{ig}$) is the difference between
Table 1. Channel Slope

<table>
<thead>
<tr>
<th>Year</th>
<th>Study Reach 1</th>
<th>Study Reach 2</th>
<th>Study Reach 3</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>1941</td>
<td>1951</td>
<td>1965</td>
</tr>
<tr>
<td></td>
<td>1 m/3.7 km</td>
<td>1 m/3.7 km</td>
<td>1 m/3.6 km</td>
</tr>
<tr>
<td>Reach</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Reach</td>
<td>2</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>1 m/5.1 km</td>
<td>1 m/5.2 km</td>
<td>1 m/5.2 km</td>
</tr>
<tr>
<td>Reach</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>3</td>
<td>1 m/7.2 km</td>
<td>1 m/7.1 km</td>
<td>1 m/7.0 km</td>
</tr>
</tbody>
</table>

No slope is given for Study Reach 2 in 1974 because photographic and map coverage was incomplete for part of the channel during that period.

The distance \( (d_2) \) measured from the baseline of the bend at time \( t_1 \) to the apex of the bend at time \( t_2 \), and the distance \( (d_1) \) measured from the baseline of the bend to the apex of the bend at time \( t_1 \). So, lateral migration is given by: \( \text{LMig} = d_2 - d_1 \). Lateral migration usually represents a growth in the lateral extent of the bend when the difference is positive.

Lateral migration is not the equivalent of translation, which refers to the movement of the inflection points that define a bend in either the upstream or downstream direction. Two measures of translation were used in this study, but they are not described here because no useful, additional information about bend behavior was obtained by using them.

The MAI involves measuring the area of all the polygons (Fig. 6) created by the overlay of channel centerline traces at successive points in time, and then standardizing the value obtained as a function of time and river length. The equation for the MAI is given as:

\[
\text{MAI} = \left( \frac{\sum A_{\text{avg}}}{L_{t_1}} \right) \times (\text{month m}^{-1})
\]

where \( A_{\text{avg}} = \) average area (obtained by dividing the total area \([m^2]\) of the polygons by the number of months separating the dates on which information regarding the position of the channel centerline was obtained), \( L_{t_1} = \) the length (m) of the channel at time \( t_1 \), \( m = \) meters, and \( m_0 = \) month. (Multiplication by \( m \text{ month}^{-1} \) cancels the units.). The number of months separating the time of acquisition of photographs used to make the maps is used as the basic time interval, rather than years, because this increases the accuracy of the calculation for those instances in which all parts of a study area are not photographed on the same date. Dividing the \( \Sigma A_{\text{avg}} \) term by the length of the river at time \( t_1 \) standardizes the index for river sections of different length. This measure is discussed more thoroughly in Gillespie & Giardino (1996).
Table 2. Descriptive Statistics for Total Monthly Discharge as a Function of Study Reach and Time Interval.

<table>
<thead>
<tr>
<th>Study Reach</th>
<th>Period</th>
<th>n</th>
<th>Min.</th>
<th>Max.</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>1939-1988</td>
<td>1</td>
<td>589</td>
<td>1,610</td>
<td>2,234,000</td>
<td>77,124,440</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>589</td>
<td>6,830</td>
<td>3,237,000</td>
<td>169,823,540</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>589</td>
<td>11,110</td>
<td>11,730,000</td>
<td>243,082,980</td>
</tr>
</tbody>
</table>

n = number of months in interval for which data were available; min = minimum monthly discharge; max. = maximum monthly discharge; total = total discharge for entire period.

Discharge data for Study Reaches 1, 2 and 3 were derived from the Waco, Bryan and Hempstead gauging stations, respectively.

Information regarding channel slope is provided in Table 1. As can be seen, the slope of Study Reach 1 was almost twice that of Study Reach 3 (1 m /3.7 km vs. 1 m/7.2 km), and none of the slope values in any of the study reaches changed substantially over the period covered by this study. Although other factors, such as bedload size and bedload transport, can affect river form (Mangelsdorf et al. 1990), no information was available regarding these variables, so they were not included in this study.

RESULTS AND ANALYSES

The planform behavior of the Brazos River proved to be quite complex as shown by the fact that several results obtained in this study did not support the relationships between planform geometry, discharge, and migratory behavior that have been reported by some researchers. Consequently, it was not possible to discern general principles that could be used to characterize the overall behavior of the river.

Changes in the discharge regime.—As expected, data from the gauging stations in Waco, Bryan, and Hempstead show that there is a definite downstream increase in discharge from one study reach to the next (Table 2). The cumulative discharge in Study Reach 2 for the entire period from 1939 to 1988 was approximately 2.2 times that of Study Reach 1 (169,823,540 acre feet vs. 77,124,440 acre feet), whereas that of Study Reach 3 (243,082,980 acre feet) was approximately 1.4 times greater than that of Study Reach 2. This generalization applies to both the average monthly total discharge per interval, and to the total discharge per interval.

A plot of the total annual discharge of the Brazos River from 1919-1986 (as measured at the Bryan gauging station) shows that the river
experiences substantial variability in annual flow (Fig. 7). However, analysis of the data regarding both total monthly discharge and maximum daily discharge suggests that the discharge regime of the river has changed, and that this change can probably be attributed to flow regulation. Tables 3 and 4 present the results of an ANOVA analysis of total monthly discharge and maximum daily discharge for the 1901-1949 period (i.e., for the period prior to the time dams were constructed near to the study area) and the 1949-1988 period. These results show that both measures of discharge were significantly greater in the period prior to 1949 (p = .0056 and p = .0058, respectively).

Although the first dam on the Brazos River was actually built in 1939, this dam was located more than 250 km from the study area and
Table 3. **ANOVA Comparisons of Monthly Total Discharge (acre-feet) as a Function of Time Interval.**

A. **Total Monthly Discharge Comparisons: Pre-Dam (1901-1939) vs. Post-Dam (1939-1988)**

<table>
<thead>
<tr>
<th>Period</th>
<th>Qavg</th>
<th>Min</th>
<th>Max</th>
<th>ANOVA</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pre-Dam</td>
<td>217,643</td>
<td>167</td>
<td>3,618,000</td>
<td>.277</td>
</tr>
<tr>
<td>Post-Dam</td>
<td>209,633</td>
<td>1,610</td>
<td>3,273,000</td>
<td>.5987</td>
</tr>
</tbody>
</table>

This analysis is based on data from the Waco and Bryan gauging stations only, i.e., Study Reaches 1 and 2 only. No data were available for the Hempstead gauging station prior to 1939.

B. **Total Monthly Discharge Comparisons: Pre-1949 vs. Post-1949**

<table>
<thead>
<tr>
<th>Period</th>
<th>Qavg</th>
<th>Min</th>
<th>Max</th>
<th>ANOVA</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pre-1949</td>
<td>232,976</td>
<td>167</td>
<td>3,618,000</td>
<td>7.676</td>
</tr>
<tr>
<td>Post-1949</td>
<td>192,001</td>
<td>1,610</td>
<td>3,273,000</td>
<td>.0056</td>
</tr>
</tbody>
</table>

This analysis is based on data from the Waco and Bryan gauging stations only. The pre-1949 category includes both the pre-dam (1901-1939) data and the 1939-1949 data. These results are used to support the hypothesis that the lack of significant difference in monthly total discharge obtained for the pre and post-dam periods (shown in Table 3A above) is attributable to the fact that it was not until dams were built near to the study area in the period following the 1940’s that discharge changed significantly.

C. **Total Monthly Discharge Comparisons: Post-1939 Intervals Only**

<table>
<thead>
<tr>
<th>Interval</th>
<th>Qavg</th>
<th>Min</th>
<th>Max</th>
<th>ANOVA</th>
</tr>
</thead>
<tbody>
<tr>
<td>09/39-03/49</td>
<td>389,339</td>
<td>1,870</td>
<td>11,730,000</td>
<td>7.974</td>
</tr>
<tr>
<td>04/49-09/65</td>
<td>241,598</td>
<td>2,510</td>
<td>4,296,000</td>
<td>0.0001</td>
</tr>
<tr>
<td>10/65-05/74</td>
<td>264,600</td>
<td>4,750</td>
<td>2,024,000</td>
<td>39-49 vs. 49-65</td>
</tr>
<tr>
<td>06/74-10/88</td>
<td>251,249</td>
<td>1,610</td>
<td>2,196,000</td>
<td>39-49 vs. 74-88</td>
</tr>
</tbody>
</table>

This analysis is based on data from all three gauging stations. Pairs listed under the Scheffe column are significantly different at the 95 percent level.

Qavg = average discharge; Min = minimum discharge; Max = maximum discharge.

apparently did not significantly affect the discharge in the study area as shown by **ANOVA** tests (Table 3). It was not until dams were built on the Brazos River within 100 km of the study area after 1949 that a significant difference in discharge became apparent. However, the first dam may have affected the suspended sediment load, as suggested by the results shown in Table 5.
Table 4. ANOVA Comparisons of Maximum Daily Discharge (cfs) as a Function of Time Interval.

A. Maximum Daily Discharge Comparisons: Pre vs. Post-Dam Periods

<table>
<thead>
<tr>
<th>Period</th>
<th>Qavg</th>
<th>Min</th>
<th>Max</th>
<th>F-value</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pre-1939</td>
<td>60,315</td>
<td>4,590</td>
<td>172,000</td>
<td>7.84</td>
<td>.0058</td>
</tr>
<tr>
<td>Post-1939</td>
<td>43,532</td>
<td>4,200</td>
<td>155,000</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

This analysis includes only Waco and Bryan gauging station data.

B. Maximum Daily Discharge Comparisons: Post-Dam Time Intervals (All Study Reaches)

<table>
<thead>
<tr>
<th>Interval</th>
<th>Qavg</th>
<th>Min</th>
<th>Max</th>
<th>F-value</th>
<th>P-value</th>
<th>Significant</th>
</tr>
</thead>
<tbody>
<tr>
<td>1940-1949</td>
<td>70,305</td>
<td>8,390</td>
<td>146,610</td>
<td>5.911</td>
<td>.0008</td>
<td>40-49 vs. 50-65</td>
</tr>
<tr>
<td>1950-1965</td>
<td>46,275</td>
<td>4,920</td>
<td>138,000</td>
<td></td>
<td></td>
<td>40-49 vs. 66-74</td>
</tr>
<tr>
<td>1966-1974</td>
<td>36,911</td>
<td>7,760</td>
<td>79,600</td>
<td></td>
<td></td>
<td>40-49 vs. 75-88</td>
</tr>
<tr>
<td>1975-1988</td>
<td>36,823</td>
<td>4,200</td>
<td>80,300</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Qavg = average discharge; min = minimum discharge; max = maximum discharge. The "1940-1949" interval does not include data from Study Reach 3.

The results of these comparisons are important because they show that flow regulation has significantly diminished both the total annual discharge and the average maximum discharges experienced by the river. Given that channel migration is, in part, a function of stream power/discharge (Nanson & Hickin 1983), and that substantial bank erosion is performed by high magnitude discharges because of bank saturation (Pickup & Warner 1976), this suggests that the rate at which the river is migrating should have slowed following dam construction. As will be discussed later, this hypothesis is supported by the average annual lateral migration values and the MAI values.

Changes in the suspended sediment load.—Analysis of suspended sediment load data (Table 5) obtained from the Richmond gauging station located downstream from the study area shows that the suspended sediment load of the Brazos River has decreased substantially over the last 50 years, and that the suspended sediment load in the period prior to 1939 (the year the first dam was built on the Brazos) was significantly greater (p = .0001) than that of the period following 1939. The mean values for percent dry weight of sediment for these periods were 0.491 and 0.208, respectively.
Table 5A. ANOVA Comparison of Sediment Load during Pre and Post-dam Periods.

(Silt load measured as dry silt - percent by weight)

<table>
<thead>
<tr>
<th>Interval</th>
<th>n</th>
<th>Mean</th>
<th>F-value</th>
<th>P-value</th>
<th>Significant Scheffe</th>
</tr>
</thead>
<tbody>
<tr>
<td>1924-1939 Pre</td>
<td>16</td>
<td>.491</td>
<td>54.177</td>
<td>.0001</td>
<td>pre vs. post</td>
</tr>
<tr>
<td>1940-1979 Post</td>
<td>40</td>
<td>.208</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Table 5B. ANOVA Comparison of Suspended Sediment Load as a Function of time Interval.

(Silt load measured as dry silt - percent by weight)

<table>
<thead>
<tr>
<th>Interval</th>
<th>n</th>
<th>Mean</th>
<th>F-value</th>
<th>P-value</th>
<th>Significant Scheffe</th>
</tr>
</thead>
<tbody>
<tr>
<td>1924-1939</td>
<td>16</td>
<td>.491</td>
<td>29.225</td>
<td>.0001</td>
<td>24/39 vs. 50/65</td>
</tr>
<tr>
<td>1940-1949</td>
<td>10</td>
<td>.371</td>
<td></td>
<td></td>
<td>24/39 vs. 66/74</td>
</tr>
<tr>
<td>1950-1965</td>
<td>16</td>
<td>.165</td>
<td></td>
<td></td>
<td>24/39 vs. 75/79</td>
</tr>
<tr>
<td>1966-1974</td>
<td>9</td>
<td>.137</td>
<td></td>
<td></td>
<td>40/49 vs. 50/65</td>
</tr>
<tr>
<td>1975-1979</td>
<td>5</td>
<td>.147</td>
<td></td>
<td></td>
<td>40/49 vs. 66/74</td>
</tr>
</tbody>
</table>

n = number of years of record

Samples were collected in eight ounce narrow-neck bottles at a position approximately one foot below the water surface near midstream. The percentage of suspended sediment by weight obtained from the sample was multiplied by the factor 1.102 to obtain the mean percentage of suspended sediment in the vertical profile.

Data were obtained from the following sources: Texas Water Development Board Reports R299 (Numbers 45, 106, 184, 233, 306) and Reports B936 (Numbers B6108 and 6410).

As the discharge and sediment comparisons suggest, dam construction had no significant effect on discharge in the study area until the 1950s, by which time two dams had been constructed upstream of the study area. However, suspended sediment loads did diminish prior to this period, i.e., following the construction of the first dam (1939), but before the completion of the second dam (1951) which was located much closer to the study area. The change in sediment loads in the 1940s, in spite of a lack of change in discharge, may have resulted from the trapping of sediment by the first dam; however, it also may have resulted from changes in sediment input into the channel that happened to occur during that period.

Bank texture.—Textural analyses indicates that the bank material ranges in composition from sandy loam to clay but that the study reaches do not differ significantly in terms of texture (p = .1833) (Table 6). Also, all three of the reaches exhibit a bimodal distribution in which either the clay or clay loam textural classes are dominant. In spite of the lack of difference in textural composition, the study reaches do,
Table 6A. Descriptive data concerning bank texture (% silt-clay).

<table>
<thead>
<tr>
<th>Study Reach</th>
<th>n</th>
<th>Missing</th>
<th>Mean (%)</th>
<th>Min</th>
<th>Max</th>
<th>SD</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>13</td>
<td>9</td>
<td>68.227</td>
<td>46.32</td>
<td>90.32</td>
<td>13.449</td>
</tr>
<tr>
<td>2</td>
<td>28</td>
<td>56</td>
<td>74.923</td>
<td>44.88</td>
<td>98.88</td>
<td>16.335</td>
</tr>
<tr>
<td>3</td>
<td>32</td>
<td>12</td>
<td>68.699</td>
<td>45.04</td>
<td>92.32</td>
<td>12.250</td>
</tr>
</tbody>
</table>

Table 6B. ANOVA comparisons of sediment texture (% silt-clay) as a function of study reach.

<table>
<thead>
<tr>
<th>Study Reach</th>
<th>n</th>
<th>Mean</th>
<th>F-Value</th>
<th>P-Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>13</td>
<td>68.227</td>
<td>1.739</td>
<td>.1833</td>
</tr>
<tr>
<td>2</td>
<td>28</td>
<td>74.923</td>
<td></td>
<td></td>
</tr>
<tr>
<td>3</td>
<td>32</td>
<td>68.699</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

n = number of bends sampled in a given study reach; min. = minimum; max. = maximum; SD = standard deviation; "missing" refers to bends that were not be sampled because of the presence of thick vegetation.

nonetheless, exhibit differences in the nature of their bank material. These differences are manifested in the number of outcrops of highly resistant layers consisting of either indurated/compacted sediment or rock layers. The necessity of distinguishing resistant layers from unconsolidated alluvium is based on the fact that the resistant layers usually occur in association with the hills bordering the floodplain of the river, are very dense, and form very steep cliffs where exposed. In short, they differ significantly in terms of cliff-forming behavior and appearance though textural analysis did not indicate any difference between these layers and non-indurated alluvial deposits. Where rock layers are present in the channel, they occur near the base of the channel and do not constitute a significant portion of the vertical extent of the channel walls in any location. As will be discussed later, the presence of the indurated sediment layers and rock is a very important control of the size and shape of bends on the river.

Planform size and shape as a function of study reach/discharge.—In the study area, it was found that most bends are asymmetrical. No clear pattern emerges as to the type of asymmetry that dominates, either as a function of study reach or time. When summed across all study reaches and all years, 282 bends (43.6%) show positive asymmetry, 262 (40.5%) show negative asymmetry, and 103 (15.9%) are symmetrical. Because both positive and negative asymmetry occur with approximately equal frequency, it must be concluded that, contrary to expectations based on work by other researchers, bend asymmetry is not a reliable means of
Table 7. *ANOVA* comparisons of bend morphology as a function of study reach.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Study Reach</th>
<th>n</th>
<th>Mean</th>
<th>F-Value</th>
<th>P-Value</th>
<th>Significant Scheffe</th>
</tr>
</thead>
<tbody>
<tr>
<td>Channel Width</td>
<td>1</td>
<td>104</td>
<td>125.3 m</td>
<td>23.81</td>
<td>.0001</td>
<td>1 vs. 3</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>352</td>
<td>128.8 m</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>191</td>
<td>141.3 m</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Arc length</td>
<td>1</td>
<td>104</td>
<td>2311.8 m</td>
<td>10.815</td>
<td>.0001</td>
<td>1 vs. 2</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>352</td>
<td>1723.6 m</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>191</td>
<td>1866.4 m</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Baseline Length</td>
<td>1</td>
<td>104</td>
<td>1550.9 m</td>
<td>11.148</td>
<td>.0001</td>
<td>1 vs. 2</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>352</td>
<td>1231.6 m</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>191</td>
<td>1124.3 m</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Max. Bend Width</td>
<td>1</td>
<td>104</td>
<td>1581.2 m</td>
<td>9.481</td>
<td>.0001</td>
<td>1 vs. 2</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>352</td>
<td>1256.9 m</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>191</td>
<td>1184.0 m</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0.5 Bend Width</td>
<td>1</td>
<td>104</td>
<td>1260.6 m</td>
<td>7.591</td>
<td>.0006</td>
<td>1 vs. 2</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>352</td>
<td>978.1 m</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>191</td>
<td>978.4 m</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Amplitude</td>
<td>1</td>
<td>104</td>
<td>596.2 m</td>
<td>11.089</td>
<td>.0001</td>
<td>1 vs. 2</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>352</td>
<td>426.3 m</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>191</td>
<td>525.9 m</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Rc</td>
<td>1</td>
<td>104</td>
<td>665.5 m</td>
<td>7.243</td>
<td>.0008</td>
<td>1 vs. 3</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>352</td>
<td>572.7 m</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>191</td>
<td>444.9 m</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Asymmetry</td>
<td>1</td>
<td>104</td>
<td>0.508</td>
<td>2.422</td>
<td>.0895</td>
<td>—</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>352</td>
<td>0.506</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>191</td>
<td>0.486</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Area</td>
<td>1</td>
<td>104</td>
<td>0.825 km²</td>
<td>4.561</td>
<td>.0108</td>
<td>1 vs. 2</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>352</td>
<td>0.563 km²</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>191</td>
<td>0.547 km²</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sinuosity</td>
<td>1</td>
<td>104</td>
<td>1.51</td>
<td>15.262</td>
<td>.0001</td>
<td>1 vs. 3</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>352</td>
<td>1.45</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>191</td>
<td>1.74</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Emax Ratio</td>
<td>1</td>
<td>104</td>
<td>1.017</td>
<td>8.084</td>
<td>.0003</td>
<td>1 vs. 3</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>352</td>
<td>1.022</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>191</td>
<td>1.054</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>E0.5 ratio</td>
<td>1</td>
<td>104</td>
<td>.798</td>
<td>13.967</td>
<td>.0001</td>
<td>1 vs. 3</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>352</td>
<td>.785</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>191</td>
<td>.870</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Rc/W</td>
<td>1</td>
<td>104</td>
<td>5.559</td>
<td>10.004</td>
<td>.0001</td>
<td>1 vs. 3</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>352</td>
<td>4.598</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>191</td>
<td>3.264</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Pairs of study reaches listed under the Scheffe column indicate a significant difference at the 95 percent level. When examining this table, recall that discharge increases in the downstream direction and that variables such as wavelength, amplitude, and radius of curvature are usually positively correlated with increasing discharge, not negatively correlated as in the case of that portion of the Brazos River included within the study area.
ascertaining flow direction on the Brazos River.

Simple bends are the dominant type of bends in all study reaches at all times (506 simple bends [78%] vs. 141 compound bends [22%]). As was expected, compound bend development is more likely to occur in larger bends because it is only in such bends that a sufficient distance exists over which flow reversal can develop to any substantial degree. For example, only 6 simple bends (1.18%) exceeded 4000 m in arc length, and none were more than 5000 m in length); however, 31 compound bends (21.98%) exceeded 4000 m in arc length, and the largest was 6755 m.

Two factor ANOVA tests were performed to determine whether the size of the morphological variables differ significantly as a function of both study reach and time. The results indicate that all variables except one, asymmetry, differ significantly as a function of study reach. However, only one variable, channel width, differs significantly as a function of time. Because differences in variable values as a function of time were shown to be insignificant, data from all time periods were combined to perform a single factor ANOVA to determine which study reaches differ significantly in terms of channel planform. The results are presented in Table 7.

Inspection of Table 7 shows that arc length, baseline length, maximum bend width, 0.5 bend width, amplitude, area, Rc, asymmetry, and Rc/W all decrease in the downstream direction. Conversely, channel width, sinuosity, Emax ratio and E0.5 ratio all increase with distance downstream. Most of the planform variables which decrease significantly in value are directly related to bend size, while those that increase in value are ratio variables that can be thought of as more closely related to bend form. Given this distinction between bend size and bend form/ratio variables, one can conclude that bend size decreases with downstream distance, but that measures of bend form, namely, sinuosity and its associated width-ratio variables, increase in value. Principal components analysis also identified the same two variable groupings as principal factors that accounted for 77.6% of the explained variance.

Variables traditionally associated with bend size, such as wavelength and amplitude, usually show a positive relationship with discharge. The relationships among these parameters have been quantified in the form of power functions in various studies and have generally been found to
Table 8. ANOVA comparisons of bend morphology as a function of the presence or absence of indurated layers and rock outcrops.

### SIZE VARIABLES

<table>
<thead>
<tr>
<th>Variable</th>
<th>Channel Material</th>
<th>n</th>
<th>Mean</th>
<th>F-value</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Channel Width</td>
<td>Indurated</td>
<td>80</td>
<td>129.8 m</td>
<td>3.086</td>
<td>.0796</td>
</tr>
<tr>
<td></td>
<td>Alluvial*</td>
<td>361</td>
<td>135.3 m</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Arc Length</td>
<td>Indurated*</td>
<td>80</td>
<td>2555.9 m</td>
<td>20.331</td>
<td>.0001</td>
</tr>
<tr>
<td></td>
<td>Alluvial</td>
<td>361</td>
<td>1882.9 m</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Baseline Length</td>
<td>Indurated*</td>
<td>80</td>
<td>1860.5 m</td>
<td>45.6</td>
<td>.0001</td>
</tr>
<tr>
<td></td>
<td>Alluvial</td>
<td>361</td>
<td>1213.4 m</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Max. Bend Width</td>
<td>Indurated*</td>
<td>80</td>
<td>1895.6 m</td>
<td>41.33</td>
<td>.0001</td>
</tr>
<tr>
<td></td>
<td>Alluvial</td>
<td>361</td>
<td>1257.1 m</td>
<td></td>
<td></td>
</tr>
<tr>
<td>0.5 Width</td>
<td>Indurated*</td>
<td>80</td>
<td>1489.4 m</td>
<td>30.001</td>
<td>.0001</td>
</tr>
<tr>
<td></td>
<td>Alluvial</td>
<td>361</td>
<td>1007.7 m</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Amplitude</td>
<td>Indurated*</td>
<td>80</td>
<td>630.7 m</td>
<td>7.164</td>
<td>.0077</td>
</tr>
<tr>
<td></td>
<td>Alluvial</td>
<td>361</td>
<td>504.3 m</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Rc</td>
<td>Indurated*</td>
<td>80</td>
<td>695.7 m</td>
<td>4.240</td>
<td>.0401</td>
</tr>
<tr>
<td></td>
<td>Alluvial</td>
<td>361</td>
<td>552.6 m</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Area</td>
<td>Indurated*</td>
<td>80</td>
<td>1.160 km²</td>
<td>25.093</td>
<td>.0001</td>
</tr>
<tr>
<td></td>
<td>Alluvial</td>
<td>361</td>
<td>0.597 km²</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Rc/W</td>
<td>Indurated*</td>
<td>80</td>
<td>5.438</td>
<td>3.080</td>
<td>.0800</td>
</tr>
<tr>
<td></td>
<td>Alluvial</td>
<td>361</td>
<td>4.346</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

### FORM VARIABLES

<table>
<thead>
<tr>
<th>Variable</th>
<th>Channel Material</th>
<th>n</th>
<th>Mean</th>
<th>F-value</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sinuosity</td>
<td>Indurated</td>
<td>80</td>
<td>1.396</td>
<td>6.678</td>
<td>.0101</td>
</tr>
<tr>
<td></td>
<td>Alluvial*</td>
<td>361</td>
<td>1.590</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Emax Ratio</td>
<td>Indurated</td>
<td>80</td>
<td>1.015</td>
<td>3.53</td>
<td>.0609</td>
</tr>
<tr>
<td></td>
<td>Alluvial*</td>
<td>361</td>
<td>1.036</td>
<td></td>
<td></td>
</tr>
<tr>
<td>E0.5 Ratio</td>
<td>Indurated</td>
<td>80</td>
<td>0.778</td>
<td>3.81</td>
<td>.0516</td>
</tr>
<tr>
<td></td>
<td>Alluvated*</td>
<td>361</td>
<td>0.823</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Channel material types with * indicate that the size of the variable measured was larger in that material. The term "indurated" refers to indurated sediment layers and rock outcrops. Although asymmetry is a form variable, it does not appear in this or subsequent tables because it is more properly considered a category variable rather than a ratio variable.

take the following forms (Leopold & Wolman 1970; Mangelsdorf et al. 1990):

\[ WL = aQ^f, \]
\[ WL \propto Q^{0.5}, \]
\[ Am = bQ^{g}, \]
where $WL$ is wavelength, $Am$ is amplitude, $Q_b$ is bankfull discharge, $Q$ is dominant discharge, $a$ and $b$ are empirically determined coefficients, $f$ and $g$ are empirically determined exponents, and $\propto$ means "proportional to". However, these relationships are not supported by the results of this study.

Given that the positive relationships between discharge and bend size have been described by many researchers and have been theoretically justified, the failure to observe them in this study suggests that factors other than discharge must be exerting an overriding influence on bend size. It should be emphasized that, although $WL$ (used in the equation above) and arc length (used in this study) are not synonymous, arc length is approximately one half of the wavelength of a meander. Therefore, the nature of the relationship between bend size and discharge should not be affected by the author's use of arc length. The same applies to the definition of amplitude used in this study, which is also approximately one half that of the "amplitude" of an entire meander.

One possible influence on arc length and amplitude was suggested by Hack (1965, cited in Tinkler 1972) who found that meander wavelength in the Cranberry River, Michigan increased by a factor of four when the river crossed from alluvial to bedrock material. Given this, it was hypothesized that bends containing indurated layers or rock would be larger, on average, than those consisting of only unconsolidated alluvium. If so, this might account for the bend-size relationships observed between the study reaches given that the greatest number of indurated layers and rock outcrops decrease from one study reach to the next in the downstream direction. Specifically, 18.18% of bends in Study Reach 1 contain rock and/or indurated sediment layers, whereas only 2.2% of the bends in Study Reach 3 contain such layers. (Study Reach 2 is not listed because the authors were not able to sample approximately half of this reach.) To test this hypothesis, an ANOVA test was performed comparing bend size as a function of the presence or absence of rock outcrops and/or indurated layers. The results of this analysis are presented in Table 8.

As is evident, all measures of bend planform size, excluding width, are significantly greater in those bends containing resistant material. Regarding bend form (i.e., ratio) variables, all exhibit smaller values in the resistant materials, but only sinuosity shows a significant difference. That sinuosity would be lower in bends containing resistant layers is
Table 9. Variation in channel width (m) as a function of study reach and time.

A. Descriptive statistics of channel width (meters') as a function of time and study reach.

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>1988</td>
<td>111</td>
<td>84</td>
<td>141</td>
<td>119</td>
<td>93</td>
<td>178</td>
<td>112</td>
<td>85</td>
<td>158</td>
</tr>
<tr>
<td>1974</td>
<td>132</td>
<td>81</td>
<td>199</td>
<td>128</td>
<td>98</td>
<td>168</td>
<td>151</td>
<td>85</td>
<td>192</td>
</tr>
<tr>
<td>1965</td>
<td>133</td>
<td>103</td>
<td>184</td>
<td>128</td>
<td>87</td>
<td>185</td>
<td>151</td>
<td>118</td>
<td>180</td>
</tr>
<tr>
<td>1951</td>
<td>122</td>
<td>94</td>
<td>166</td>
<td>128</td>
<td>79</td>
<td>218</td>
<td>148</td>
<td>120</td>
<td>224</td>
</tr>
<tr>
<td>1941</td>
<td>129</td>
<td>80</td>
<td>187</td>
<td>140</td>
<td>99</td>
<td>208</td>
<td>147</td>
<td>101</td>
<td>184</td>
</tr>
</tbody>
</table>

B. *ANOVA* comparisons of differences in channel width as a function of time

<table>
<thead>
<tr>
<th>Year</th>
<th>n</th>
<th>Mean (m)</th>
<th>F-Value</th>
<th>P-Value</th>
<th>Significant Scheffe</th>
</tr>
</thead>
<tbody>
<tr>
<td>1941</td>
<td>144</td>
<td>140.62</td>
<td>25.883</td>
<td>.0001</td>
<td>1941 vs. 1951</td>
</tr>
<tr>
<td>1951</td>
<td>136</td>
<td>132.02</td>
<td></td>
<td></td>
<td>1941 vs. 1988</td>
</tr>
<tr>
<td>1965</td>
<td>136</td>
<td>134.52</td>
<td></td>
<td></td>
<td>1951 vs. 1988</td>
</tr>
<tr>
<td>1974</td>
<td>96</td>
<td>137.87</td>
<td></td>
<td></td>
<td>1965 vs. 1988</td>
</tr>
<tr>
<td>1988</td>
<td>135</td>
<td>115.78</td>
<td></td>
<td></td>
<td>1974 vs. 1988</td>
</tr>
</tbody>
</table>

The mean values represent the averages for all bends in the study area for a given year.

explainable in terms of their resistance to erosion. This is because higher sinuosity can be equated with greater change of direction per unit length of a bend. Given that a greater amount of direction change per unit length requires a greater amount of bank erosion per unit length, it follows that sinuosity should be lower in bends containing more resistant material.

*Change in Bend Planform Size.*—A two factor *ANOVA* test of morphology as a function of both time and study reach shows that the only variable that changed significantly during the period encompassed by the study was channel width (Table 9). As discussed earlier, the average width in 1988 was less than that during previous years. This can most readily be explained as a consequence of the reduction in the magnitude and frequency of major floods. Because of this reduction, less energy would be available to erode channel walls.

Finally, as regards the lack of significant change in planform-size variables as a function of time, it is not clear why such change did not occur given the magnitude of the alteration in discharge and suspended sediment loads that have occurred on the river. It may simply be that planform size adjusts more slowly than does channel width and has therefore not had sufficient time to adjust to the new discharge
conditions. Given the relatively short amount of time encompassed by this study, this is a real possibility.

Bend planform evolution.—Before discussing the analyses of change, it should be noted that data from several bends were excluded from this analysis based either on ambiguous boundary overlap between successive map sheets, lack of photographic coverage for bends 37-80 during 1974, and types of change that precluded meaningful analysis. These included cutoffs, the evolution of secondary arcs in compound bends into primary bends, and the evolution of multiple bends into single bends. These types of change could not be included because there were no reference bends at the beginning of the interval from which change could be measured. In addition, bends which exhibited extreme sensitivity to the location of the inflection point were excluded. This situation arose when the transition from one bend to the next occurred over an unusually long section of the channel. Under these conditions, placement of the inflection points was subjective, and minor variations in the placement could substantially alter the dimensions of the bend.

Based on these criteria, data pertaining to a total of 138 bends were deleted from all the analyses involving rates of change. While this appears to represent a substantial diminution of the data base, data from a total of 444 bends (representing all time periods and study reaches) remained and were used in the analyses. Thus, the data base was large in spite of the exclusion of several bends.

As shown in Table 10, all the morphometric variables, as well as measures of migration, experienced negative change at some time during the period encompassed by this study. For morphometric variables, this simply means that some decreased in size during a given interval. That some would undergo this type of change is to be expected. For example, if the bend develops toward a classic horseshoe shape prior to cutoff, one would expect the baseline length to decrease. Similarly, as a bend evolves, its radius of curvature should decrease and, accordingly, so should its $R_c/W$. However, all the literature reviewed by the authors concerning bend growth and development suggests that the vast majority of bends experience an increase in size and sinuosity as a result of growth in amplitude and arc length during the normal course of their evolutionary development until cutoff occurs. Thus, it is surprising to find that the bend evolution examined in this study deviated frequently and substantially from this normal pattern. For example, as shown in
Table 10. Descriptive statistics for direction of change in bend morphology as a function of time interval.

<table>
<thead>
<tr>
<th>Interval</th>
<th>n</th>
<th>AL+ (%)</th>
<th>AL- (%)</th>
<th>BLI+ (%)</th>
<th>BLI- (%)</th>
<th>Amp+ (%)</th>
<th>Amp- (%)</th>
<th>Area+ (%)</th>
<th>Area- (%)</th>
<th>Emax+ (%)</th>
<th>Emax- (%)</th>
<th>Rc+ (%)</th>
<th>Rc- (%)</th>
<th>Sin+ (%)</th>
<th>Sin- (%)</th>
<th>LMig+ (%)</th>
<th>LMig- (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>74-88</td>
<td>93</td>
<td>65.9</td>
<td>34.0</td>
<td>51.7</td>
<td>48.4</td>
<td>53.8</td>
<td>46.2</td>
<td>60.4</td>
<td>39.6</td>
<td>87.9</td>
<td>12.1</td>
<td>54.9</td>
<td>45.1</td>
<td>64.8</td>
<td>35.2</td>
<td>74.4</td>
<td>25.6</td>
</tr>
<tr>
<td>65-74</td>
<td>90</td>
<td>67.0</td>
<td>33.0</td>
<td>54.5</td>
<td>45.5</td>
<td>73.9</td>
<td>26.1</td>
<td>64.8</td>
<td>35.2</td>
<td>91.1</td>
<td>8.9</td>
<td>62.5</td>
<td>37.5</td>
<td>61.4</td>
<td>38.6</td>
<td>76.1</td>
<td>23.9</td>
</tr>
<tr>
<td>51-65</td>
<td>129</td>
<td>55.1</td>
<td>44.9</td>
<td>48.8</td>
<td>51.2</td>
<td>55.9</td>
<td>44.1</td>
<td>56.7</td>
<td>43.3</td>
<td>87.4</td>
<td>12.6</td>
<td>59.8</td>
<td>40.2</td>
<td>49.6</td>
<td>50.4</td>
<td>72.2</td>
<td>27.8</td>
</tr>
<tr>
<td>41-51</td>
<td>132</td>
<td>66.7</td>
<td>33.3</td>
<td>53.0</td>
<td>47.0</td>
<td>68.9</td>
<td>31.1</td>
<td>66.7</td>
<td>33.3</td>
<td>88.6</td>
<td>11.4</td>
<td>53.8</td>
<td>46.2</td>
<td>37.1</td>
<td>62.9</td>
<td>73.3</td>
<td>26.7</td>
</tr>
</tbody>
</table>

AL = arc length; BLI = baseline length; Amp = amplitude; Emax = Emax ratio; Rc = radius of curvature; Sin = sinuosity; LMig = lateral migration. A (+) sign indicates an increase in value and a (-) sign indicates a decrease. The % sign refers to the percentage of bends experiencing the type of change listed. (n) = number of bends.

Bends 37 - 80 are not included in the 1965 to 1974 interval because no photographic coverage of these bends was available during that period.
Table 10, 34% of the bends in the 1974-1988 interval experienced a decrease in arc length, 46.2% experienced a decrease in amplitude, 39.6% experienced a decrease in area, and 35.2% experienced a decrease in sinuosity. This general pattern applies to all time intervals and indicates that from one third to one half of the time, the bends became smaller through time, rather than larger.

**Lateral migration.**—The observations just cited apply to lateral migration as well. Inspection of Fig. 6 shows that, although some bends migrated in the direction of maximum bend curvature \((n = 339)\) as one would expect based on the direction of force applied to the cutbank, others migrated away from the point of maximum curvature \((n = 120)\). The latter type of migration is termed negative migration by the authors, and can be defined as lateral migration of a bend arc toward its baseline. This is not a form of meander cut-off, as cutoffs were excluded from the definition of negative migration.

Instances of negative migration appear to be the result of the net activity of an entire suite of meanders, i.e., of a meander train. Thus, the negative migration results not from the localized activity in a specific bend, but from the complex interplay of flow processes occurring in several contiguous bends. These processes usually cause substantial translation and/or straightening of a bend both of which can lead to negative migration.

In the substantial body of literature reviewed by the authors concerning meandering rivers, no specific mention was made of the phenomenon of negative migration other than that implied by the process of meander cutoff. In fact, a review of this literature leads one to conclude that bends grow in amplitude by the process of positive lateral migration until a cutoff occurs. A few instances of bend reversal were mentioned, but it is not clear whether these occurred following a cutoff, or if they were the result of negative migration as described in this paper.

Because the process of negative migration was not described by other researchers, one immediately wonders if it is an actual phenomenon, or merely an apparent phenomenon resulting from the operational definition used to define it. However, Fig. 6, and the corresponding aerial photographs (not shown), demonstrate that the phenomenon is real. As mentioned earlier, this is not a form of translation in which the inflection
Table 11. *ANOVA* comparisons of average annual rates of change in bend morphology as a function of time interval.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Time Interval</th>
<th>n</th>
<th>Mean</th>
<th>F-Value</th>
<th>P-Value</th>
<th>Significant Scheffe</th>
</tr>
</thead>
<tbody>
<tr>
<td>Arc length</td>
<td>74/88</td>
<td>88</td>
<td>3.4 m</td>
<td>2.385</td>
<td>.0687</td>
<td>—</td>
</tr>
<tr>
<td></td>
<td>65/74</td>
<td>87</td>
<td>3.6 m</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>51/65</td>
<td>120</td>
<td>0.2 m</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>41/51</td>
<td>126</td>
<td>9.9 m</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Baseline Length</td>
<td>74/88</td>
<td>88</td>
<td>-0.1 m</td>
<td>0.192</td>
<td>.902</td>
<td>—</td>
</tr>
<tr>
<td></td>
<td>65/74</td>
<td>87</td>
<td>0.9 m</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>51/65</td>
<td>120</td>
<td>1.2 m</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>41/51</td>
<td>126</td>
<td>1.9 m</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Max. Bend Width</td>
<td>74/88</td>
<td>88</td>
<td>0.3 m</td>
<td>0.259</td>
<td>.8551</td>
<td>—</td>
</tr>
<tr>
<td></td>
<td>65/74</td>
<td>87</td>
<td>0.6 m</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>51/65</td>
<td>120</td>
<td>1.2 m</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>41/51</td>
<td>126</td>
<td>2.6 m</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0.5 Bend Width</td>
<td>74/88</td>
<td>88</td>
<td>1.4 m</td>
<td>3.01</td>
<td>.0301</td>
<td>—</td>
</tr>
<tr>
<td></td>
<td>65/74</td>
<td>87</td>
<td>-1.6 m</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>51/65</td>
<td>120</td>
<td>1.5 m</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>41/51</td>
<td>126</td>
<td>1.4 m</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Amplitude</td>
<td>74/88</td>
<td>88</td>
<td>0.8 m</td>
<td>0.479</td>
<td>.6970</td>
<td>—</td>
</tr>
<tr>
<td></td>
<td>65/74</td>
<td>87</td>
<td>3.4 m</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>51/65</td>
<td>120</td>
<td>0.9 m</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>41/51</td>
<td>126</td>
<td>3.4 m</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Re</td>
<td>74/88</td>
<td>88</td>
<td>0.8 m</td>
<td>3.01</td>
<td>.0301</td>
<td>—</td>
</tr>
<tr>
<td></td>
<td>65/74</td>
<td>87</td>
<td>-2.5 m</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>51/65</td>
<td>120</td>
<td>1.7 m</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>41/51</td>
<td>126</td>
<td>2.1 m</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Asymmetry</td>
<td>74/88</td>
<td>88</td>
<td>-0.001</td>
<td>1.405</td>
<td>.2408</td>
<td>—</td>
</tr>
<tr>
<td></td>
<td>65/74</td>
<td>87</td>
<td>-0.001</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>51/65</td>
<td>120</td>
<td>-0.004</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>41/51</td>
<td>126</td>
<td>-0.020</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Area</td>
<td>74/88</td>
<td>88</td>
<td>0.002 km^2</td>
<td>1.648</td>
<td>.1777</td>
<td>—</td>
</tr>
<tr>
<td></td>
<td>65/74</td>
<td>87</td>
<td>0.003 km^2</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>51/65</td>
<td>120</td>
<td>0.001 km^2</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>41/51</td>
<td>126</td>
<td>0.005 km^2</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sinuosity</td>
<td>74/88</td>
<td>88</td>
<td>0.003</td>
<td>3.078</td>
<td>.0275</td>
<td>41/51 vs. 51/65</td>
</tr>
<tr>
<td></td>
<td>65/74</td>
<td>87</td>
<td>0.003</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>51/65</td>
<td>120</td>
<td>-0.001</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>41/51</td>
<td>126</td>
<td>0.011</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Emax Ratio</td>
<td>74/88</td>
<td>88</td>
<td>0.0003</td>
<td>0.429</td>
<td>.7322</td>
<td>—</td>
</tr>
<tr>
<td></td>
<td>65/74</td>
<td>87</td>
<td>-0.00001</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>51/65</td>
<td>120</td>
<td>0.00040</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>41/51</td>
<td>126</td>
<td>0.00100</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>E0.5 ratio</td>
<td>74/88</td>
<td>88</td>
<td>0.001</td>
<td>0.599</td>
<td>.6426</td>
<td>—</td>
</tr>
<tr>
<td></td>
<td>65/74</td>
<td>87</td>
<td>-0.001</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>51/65</td>
<td>120</td>
<td>0.001</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>41/51</td>
<td>126</td>
<td>0.001</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Re/W</td>
<td>74/88</td>
<td>88</td>
<td>0.055</td>
<td>0.908</td>
<td>.4373</td>
<td>—</td>
</tr>
<tr>
<td></td>
<td>65/74</td>
<td>87</td>
<td>-0.008</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>51/65</td>
<td>120</td>
<td>0.015</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>41/51</td>
<td>126</td>
<td>0.030</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lateral Migration</td>
<td>74/88</td>
<td>88</td>
<td>2.1 m</td>
<td>2.769</td>
<td>.0414</td>
<td>—</td>
</tr>
<tr>
<td></td>
<td>65/74</td>
<td>87</td>
<td>1.9 m</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>51/65</td>
<td>120</td>
<td>1.4 m</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>41/51</td>
<td>126</td>
<td>3.4 m</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Pairs of study reaches listed under the Scheffe column are significantly different at the 95 percent level. Note that the p-value for the lateral migration rate indicates a significant difference though it is not reflected in the Scheffe test.
Table 12. ANOVA comparisons of average rates of change (m yr\(^{-1}\)) in lateral migration for the intervals "1941-1951" and "1951-1988".

<table>
<thead>
<tr>
<th>Variable</th>
<th>Time Interval</th>
<th>n</th>
<th>Mean</th>
<th>F-Value</th>
<th>P-Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Positive Lateral Migration</td>
<td>41/51</td>
<td>93</td>
<td>6.2 m</td>
<td>25.602</td>
<td>.0001</td>
</tr>
<tr>
<td></td>
<td>51/88</td>
<td>222</td>
<td>3.5 m</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Negative Lateral Migration</td>
<td>41/51</td>
<td>45</td>
<td>-3.5 m</td>
<td>5.013</td>
<td>.0265</td>
</tr>
<tr>
<td></td>
<td>51/88</td>
<td>121</td>
<td>-2.2 m</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

points that define a bend simply shift position as the bend moves. It represents a reversal in the direction of the movement of the bend and it is often accompanied by a decrease in the amplitude, or lateral extent, of the bend. This is shown by the fact 37.5% of the bends that were found to exhibit negative migration simultaneously experienced a decrease in amplitude as well. Given that a decrease in amplitude should be highly correlated with negative migration, the fact that the amplitude did decrease in many instances strengthens the findings concerning negative migration.

It must be emphasized that negative migration greatly complicates the study of river migration and evolution because it means that bends can move in directions opposite that expected based on the force applied to a cutbank. Obviously, this makes the prediction of the future location of a bend almost impossible because, if a bend can move in more than one direction across-valley, and if that movement cannot be attributed to a specific factor, such as localized shear stress within the bend, then how can one predict where the bend will be at some point in the future?

Rates of channel planform change and migration as a function of changing discharge.—Rates of planform change were evaluated as a function of both study reach (i.e., as a function of downstream increase in discharge) and time interval. The results show that none of the variables exhibit a significant change as a function of study reach. That almost no differences exist is surprising given that the bends in different study reaches did differ significantly in terms of size. As will be recalled, the proposed explanation for these differences was that the presence or absence of rock and indurated sediment layers exert a dominant control on bend size. If this is the case, one would expect bends located in the resistant materials to migrate substantially slower than those in the unconsolidated alluvium. Apparently, however, this was not the case. Furthermore, when an ANOVA test was done to
Table 13. ANOVA comparisons of yearly average rates of change ($m^2$) in MAI area values as a function of time interval.

<table>
<thead>
<tr>
<th>Interval</th>
<th>n</th>
<th>$M^2$</th>
<th>MIA Index</th>
<th>F-value</th>
<th>P-value</th>
<th>Significant Scheffe</th>
</tr>
</thead>
<tbody>
<tr>
<td>1974-1988</td>
<td>111</td>
<td>5,972</td>
<td>3.503</td>
<td>16.142</td>
<td>.0001</td>
<td>41/51 vs. 51/65</td>
</tr>
<tr>
<td>1965-1974</td>
<td>95</td>
<td>7,513</td>
<td>2.829</td>
<td></td>
<td></td>
<td>41/51 vs. 65/74</td>
</tr>
<tr>
<td>1951-1965</td>
<td>163</td>
<td>4,525</td>
<td>2.902</td>
<td></td>
<td></td>
<td>41/51 vs. 74/88</td>
</tr>
<tr>
<td>1941-1951</td>
<td>169</td>
<td>10,684</td>
<td>7.021</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

The results for both the 1974-1988 interval and the 1965-1974 interval do not include data from bends 37-80 (in Study Reach 2) because data were unavailable for these bends in 1974. The length of the channel used to calculate the MAI for these intervals was adjusted to account for this.

... compare average rates of change as a function of the presence or absence of resistant layers, no statistically significant differences were found for any variable.

Two variables, sinuosity and lateral migration, showed a significant difference in rate of change as a function of time interval, i.e., in terms of temporal changes in discharge (Tables 11 and 12). Of particular interest is the observation that it was the 1941-1951 interval (i.e., the interval before a dam was constructed near the study area) that was responsible for producing the significant differences in these variables and, in most cases, this interval also was characterized by the greatest rates of statistically non-significant change.

ANOVA tests were performed by separately comparing positive and negative migration rates during the 1941-1951 interval with those for the post-1951 intervals. As Table 12 shows, the difference between these intervals was significant for both positive and negative rates of average lateral migration. It is worth emphasizing that the average rate of change in positive lateral migration during the 1941-1951 interval was almost twice as great as that in the 1951-1988 interval ($6.2 \text{ m yr}^{-1}$ vs. $3.5 \text{ m yr}^{-1}$).

Table 13 presents the results of the MAI analyses as a function of time and it, too, shows that there were significant differences in the migratory activity of the river during different time intervals. As with the previous measures of migration, it is the 1941-1951 interval that is responsible for these differences. As with the positive lateral migration rates, the MAI value for this interval was at least twice that of the other intervals ($7.0 \text{ vs. } 2.8, 2.9 \text{ and } 3.5$). This reinforces the previous results on lateral migration, and show that the river’s level of activity has
Table 14. ANOVA Comparisons of average annual positive lateral migration as a function of time, bend type, sinuosity, E0.5 ratio and Rc/W ratio.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Range</th>
<th>n</th>
<th>Mean</th>
<th>F-Value</th>
<th>P-Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Time</td>
<td>1941-1951</td>
<td>93</td>
<td>6.244</td>
<td>25.68</td>
<td>* .0001</td>
</tr>
<tr>
<td></td>
<td>1951-1988</td>
<td>246</td>
<td>3.639</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bend Type</td>
<td>Simple</td>
<td>267</td>
<td>4.305</td>
<td>0.157</td>
<td>.6921</td>
</tr>
<tr>
<td></td>
<td>Compound</td>
<td>72</td>
<td>4.535</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sinuosity</td>
<td>&lt; 1.5</td>
<td>198</td>
<td>3.693</td>
<td>11.197</td>
<td>* .0009</td>
</tr>
<tr>
<td></td>
<td>&gt; 1.5</td>
<td>141</td>
<td>5.282</td>
<td></td>
<td></td>
</tr>
<tr>
<td>E0.5 ratio</td>
<td>&lt; 1.0</td>
<td>291</td>
<td>4.159</td>
<td>4.127</td>
<td>* .0430</td>
</tr>
<tr>
<td></td>
<td>&gt; 1.0</td>
<td>62</td>
<td>5.536</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Rc/W</td>
<td>1) 0.86-2.49</td>
<td>129</td>
<td>4.776</td>
<td>3.386</td>
<td>* .0350</td>
</tr>
<tr>
<td></td>
<td>2) 2.50-3.50</td>
<td>67</td>
<td>5.054</td>
<td></td>
<td>(F:1 vs.3)</td>
</tr>
<tr>
<td></td>
<td>3) 3.51-57.0</td>
<td>143</td>
<td>3.645</td>
<td></td>
<td>(F:2 vs.3)</td>
</tr>
</tbody>
</table>

An asterisk (*) indicates a significant p-value.

diminished since the 1940s. In effect, this means that the river is now more stable than it was in the past.

The set of results regarding changes in the rates of migration during different intervals are logically consistent with the findings concerning changes in discharge and sediment regime through time. As will be recalled, it was found that the discharge regime of the study area did not change significantly until after the 1940s, at which time the frequency and magnitude of major floods decreased, but that the suspended sediment load did begin to decrease significantly in the 1940s. Because of this, one would expect that the rates at which bends change shape and migrate would be greatest in the 1940s, but that they would diminish after this period when the discharge decreased significantly.

Rates of lateral migration as a function of previous bend geometry.— Linear regressions of average annual lateral migration as a function of the measures of bend geometry at the beginning of an interval, i.e., as a function of "previous" bend form, were performed using the combined data from all study reaches and all intervals. The correlations were extremely weak, with the highest $r^2$ being only .015 for both the E0.5 ratio and Rc/W ratio ($p = .0082$ and $p = .0088$, respectively). These correlations did not improve when negative migration rates were excluded from the analyses. Such poor correlations were completely unexpected given that one would expect there to be some relationship between bend form and migration rates based on the effects that form
has on the distribution of forces on the channel walls.

In spite of the poor correlations between bend form and migration rates, further analysis of the effects of previous bend geometry on positive lateral migration rates showed that certain aspects of bend geometry did, nonetheless, affect migration rates (Table 14). Negative migration was excluded from these analyses to determine if the results would be consistent with those obtained by other researchers who dealt only with positive migration. Specifically, the following trends were observed:

1. Average annual positive lateral migration rates were significantly faster \( (p = 0.0009) \) for bends with a sinuosity of greater than 1.5 \( (5.3 \text{ m yr}^{-1} \text{ vs. 3.7 m yr}^{-1} \text{, respectively}) \);

2. Average annual positive lateral migration rates were significantly greater \( (p = 0.049) \) for bends with an \( E_{0.5} \) ratio greater than 1.0 \( (5.5 \text{ m yr}^{-1} \text{ vs. 4.2 m yr}^{-1} \text{, respectively}) \).

3. Average annual positive lateral migration rates were greatest for those bends with a \( R_c/W \) ratio of between 2.5 and 3.5.

The first and third results were anticipated based on previous research; however, the relationship between \( E_{0.5} \) ratio and lateral migration was opposite that hypothesized by the authors. However, a greater \( E_{0.5} \) ratio is closely correlated with greater sinuosity; and so, when viewed from this perspective, the result is understandable. Nonetheless, this seems to be an instance in which competing factors are operating.

Unfortunately, the relationship between these shape measures and positive lateral migration rates is not of such a nature as to be useful in linear regression models relating bend form to migration rates. This seems to preclude the development of such models for purposes of predicting bend migration on rivers such as the Brazos. This is especially true when one considers that negative migration also occurs and cannot be ignored when attempting to develop predictive models.

Because flow regulation had a significant effect on the discharge of the river after the 1941-1951 interval (Tables 3 and 4), it was hypothesized that the correlations between lateral migration rates and previous bend geometry may have changed through time as a result of the change in discharge regime, and that this might account for the poor correla-
tions. Accordingly, it was hypothesized that the correlations would be best for the 1941-1951 interval given that flow conditions in this interval were more natural than those that followed. To test this suggestion, average annual positive lateral migration was correlated with previous bend geometry for the 1941-1951 interval, and with the 1951-1988 intervals. The results showed that the hypothesis was not confirmed.

In summary, the ANOVA results show that there are, indeed, environmental and morphological controls on the rates of positive lateral migration. However, the effects are of such a complicated nature that they preclude the use of any of the measures of bend morphology as predictors of lateral migration based on linear regressions. Examination of the regression plots shows that nonlinear regressions will not improve the correlations either. While it is possible that the measures of bend morphology used in this study were simply inappropriate, this is deemed unlikely given that versions of several of them have been used in previous studies and have been found to be good predictors of lateral migration in many instances. In addition, the sheer number of measures used should have made the identification of meaningful correlations possible if, in fact, such correlations existed.

**CONCLUSIONS**

The Brazos River has experienced a significant reduction in the magnitude and frequency of large discharges, as well as a reduction in the amount of suspended load that it transports as a result of flow regulation. These factors are believed to account for both the decrease in channel width and the decrease in the amount of migratory activity documented in this study. Given the short amount of time that the river has had to adjust to the changes in discharge and sediment regime, it is believed that the river is currently in a state of disequilibrium and that this may account for many of the low correlations between bend shape and migration measured in this study.

Regarding the findings concerning planform, it was shown that the size of bends is apparently influenced more by the presence or absence of resistant layers than by discharge. Because of this influence, bends are larger in the upper reach of the study area than in the lower, which is contrary to what one would expect if discharge were the primary control. The increase in size is ostensibly related to the greater amount of resistance offered by these resistant materials to changes in flow
direction.

Although ranges of certain morphological variables, such as sinuosity and $E_{0.5}$ ratio, were found to be related to migration rates, no significant linear correlations were found between bend morphology and migration rates. Although this may be the result, in part, of the choice of operational definitions used to define the morphological variables, the authors think that the primary reason for the lack of correlation is related to both the heterogeneous nature of the materials the river flows through, and to the changes in discharge regime the river is experiencing.

One additional and very important factor that is believed to be an impediment to the development of these correlations is the process of negative migration. This phenomenon greatly complicates the goal of predicting river migration because it reveals that rivers can move opposite to the direction that standard models pertaining to fluid flow and erosion in a single bend would predict. Given that negative migration in a given bend is often induced by the migratory behavior of upstream bends, it also shows that the behavior of a single bend cannot necessarily be treated as an isolated process as current models of bend migration often seem to do.

In conclusion, the most important implication of the findings in this study is that several principles used to develop models of migration are extremely limited in their applicability. This is apparently because they are based on a very small subset of rivers and bends that exist under conditions that allow for free migration, i.e., conditions that do not characterize those of most rivers. Furthermore, many of the rivers examined by previous researchers are largely unaffected by flow regulation as well, and are thus more likely to be in or near a state of equilibrium. Consequently, some conclusions cited based on the study of idealized rivers are simply not applicable to rivers such as the Brazos that exist in much more complex environments. The results of this study suggest that the processes that control bend evolution appear to be so complex that it may ultimately prove to be impossible to predict river migration and planform change for rivers such as the Brazos.

LITERATURE CITED


BMG at: 0100722@Acad.NWMissouri.edu
DIET OF THE TEXAS YELLOW-FACED RACERUNNER, 
CNEMIDOPHORUS SEXLINEATUS STEPHENSI 
(SAURIA: TEIIDAE), IN SOUTHERN TEXAS

Mark A. Paulissen, James M. Walker and James E. Cordes
Department of Biological and Environmental Sciences, McNeese State University
Lake Charles, Louisiana 70609; Department of Biological Sciences
University of Arkansas, Fayetteville, Arkansas 72701; and Division of Sciences
Louisiana State University at Eunice, Eunice, Louisiana 70535

Abstract.—The diet of Cnemidophorus sexlineatus stephensi was determined from analysis of stomach contents of four samples of lizards collected from Cameron, Kenedy and Brooks counties. Orthopterans and spiders were the most important components of the diet of C. sexlineatus stephensi, though several other kinds of insects were also eaten. Termites were seldom found in lizard stomachs, but when they were, they were often present in large numbers. There was a significant positive correlation between lizard size and total volume of prey consumed, but not between lizard size and number of prey consumed. Overall, the diet of C. sexlineatus stephensi in south Texas resembles the diets of C. sexlineatus populations in the central U.S. more closely than the diet of the closely related unisexual species of the Cnemidophorus laredoensis complex in the Rio Grande Valley.

The six-lined racerunner, Cnemidophorus sexlineatus, is one of the most widely distributed lizards in the United States. Its geographic range extends from the foothills of the Rocky Mountains in Colorado eastward to the Atlantic coast (Conant & Collins 1991). Nearly the entire range of this species is occupied by two subspecies (and their intergrades): Cnemidophorus sexlineatus sexlineatus in the eastern U.S. and C. sexlineatus viridis from the central U.S. westward. Both subspecies occur in Texas forming a poorly defined intergrade zone in eastern and central Texas (Dixon 1987). Recently, Trauth (1992) described a third subspecies of C. sexlineatus from the South Texas Sand Plains and adjacent areas of Kenedy, Brooks, Jim Hogg, Starr and Webb counties and South Padre Island, Cameron County. Cnemidophorus sexlineatus stephensi, or Texas yellow-faced racerunner, is distinguished from the other subspecies in Texas by smaller adult size (<70 mm snout-to-vent length as opposed to 70 mm or greater for the other subspecies), frequent absence of a vertebral stripe (typically present in the other subspecies), and yellowish coloration on the face and neck (Trauth 1992).

There has been surprisingly little study of the ecology of Cnemidophorus sexlineatus in Texas. Laughlin (1958) studied the
ecological relationships between *C. sexlineatus* and *C. gularis* (referred to as *C. sacki*) in San Patricio County; Hoddenbach (1966) reported on reproduction in a population of *C. sexlineatus* in Lubbock County; and Clark (1976) studied ecology and demography of a *C. sexlineatus* population in Brazos County. Based on the locations of these studies, it appears that none involved forms presently allocated to *C. sexlineatus stephensi*. Furthermore, only Laughlin (1958) analyzed lizard stomach contents; that study found that the diet of *C. sexlineatus* consisted almost exclusively of arthropods, especially orthopterans and spiders. Similar studies conducted in Kansas and Oklahoma report that grasshoppers, spiders, and various types of planthoppers constitute the bulk of the diet of racerunners (Fitch 1958; Hardy 1962; Paulissen 1987a). However, a study in Florida showed that termites were the numerically dominant prey in the diet of *C. sexlineatus sexlineatus*, although beetles and various orthopterans made a greater contribution to the total volume of prey consumed (Punzo 1990). Studies conducted in the Rio Grande Valley of Texas have shown that termites comprised the majority of the diet of both species of the parthenogenetic *Cnemidophorus laredoensis* complex (Paulissen et al. 1988). This may be indicative of the diet of *C. sexlineatus stephensi* since the geographic range of the *C. laredoensis* complex in Cameron, Hidalgo, Starr, and Webb counties lies only 45-50 km south of the southern limit of the known range of *C. sexlineatus stephensi* as reported by Walker (1987a; 1987b). Furthermore, the species of the *C. laredoensis* complex arose from hybrids between *C. sexlineatus* and *C. gularis* (cf. McKinney et al. 1973; Bickham et al. 1976). The purpose of this report is to provide the first description of the diet of *C. sexlineatus stephensi* and to compare the diet of this form to that of other *C. sexlineatus* populations as well as to deep south Texas populations of the *C. laredoensis* complex.

**METHODS**

The three sites from which lizard diet data were obtained were as follows: (1) South Padre Island (Cameron County): low dunes, sand flats, and dirt roads adjacent to an electrical substation about 500 meters south of the South Padre Island Convention Center; (2) U.S. Highway 77 (Kenedy County): sandy roadside with patches of sunflowers and sandburs between the highway and a fenced cattle pasture along U.S. Highway 77, 50.1 km south of the junction of Highway 77 and state highway 285; (3) U.S. Highway 281 (Brooks County): sandy roadside with clumps of sandbur, patches of dense grass along a fence row, and
mesquite trees in the center of the highway island at the junction of U.S. Highway 281 and Business 281 (to Encino), 29.8 km south of Falfurrias. The South Padre Island site was sampled on 27 May 1986 and on 3 September 1993 (this sample included four young-of-the-year). The Highway 77 site was sampled 4 September 1993; the Highway 281 site was sampled 27 May 1994. Lizards were collected with BB guns or by noosing, and were preserved; the snout-to-vent length (SVL) was determined to the nearest mm as a measure of lizard size. Later, the stomach contents of each lizard were removed, counted, and identified to the lowest possible taxon (usually family). The volume of intact prey items was estimated either by volumetric displacement of water in a small, calibrated cylinder or by measuring the length and width of prey items and using the following formula (Vitt et al. 1993) for the volume of a prolate spheroid:

\[
\text{volume} = \frac{4}{3} \pi (0.5 \text{ length})(0.5 \text{ width})^2
\]

The former method was used for the South Padre Island samples, the latter for the Highway 77 and Highway 281 samples. Volume estimates of selected prey items computed by the two methods were very close (e.g., for termites, volumetric displacement gives an estimate of 1.6 mm\(^3\); the prolate spheroid formula gives an estimate of 1.4 mm\(^3\)). Correlations between lizard SVL and prey measures were computed using Spearman rank correlations for the pooled samples.

**RESULTS AND DISCUSSION**

A summary of the diet of *Cnemidophorus sexlineatus stephensi* is presented in Table 1. For brevity, the insects are listed by taxonomic order; a complete breakdown of the insect prey listed by family is available from the senior author upon request. Orthopterans and spiders (Araneae) were the dominant prey items in most of the samples in this study. Among the orthoptera, crickets (Gryllidae) were the most important prey items in the May 1986 South Padre Island sample and the September 1993 Highway 77 sample, but short-horned grasshoppers (Acrididae) comprised the bulk of the prey consumed by lizards in the May 1994 Highway 281 sample. By contrast, lizards collected September 1993 from South Padre Island consumed few orthopterans, but one lizard in that sample did consume 10 dictyopharids (a large planthopper: Homoptera). Two lizards in the Highway 77 sample consumed large leaf-footed bugs (Hemiptera: Coreidae); three others consumed several large (12 mm) alate ants (Hymenoptera). Termites (Isoptera) comprised a substantial numerical percentage of lizard diet in three of the samples,
Table 1. Diet of the lizard *Cnemidophorus sexlineatus stephensi* in southern Texas as determined from analyses of stomach contents of four samples (see text for locations and descriptions of the sites). The numerical and volumetric percentage respectively of the prey taxon in the stomach contents sample is given.

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Date</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lizards Sampled</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Prey Taxon</td>
<td>Percent by Number</td>
<td>Percent by Volume</td>
<td>Percent by Number</td>
<td>Percent by Volume</td>
</tr>
<tr>
<td>ISOPODA</td>
<td>1.9%</td>
<td>1.1%</td>
<td>2.6%</td>
<td>3.5%</td>
</tr>
<tr>
<td>AMPHIPODA</td>
<td>1.9%</td>
<td>1.1%</td>
<td>23.4%</td>
<td>28.7%</td>
</tr>
<tr>
<td>ARANEAIE</td>
<td>28.8%</td>
<td>26.3%</td>
<td>7.2%</td>
<td>10.1%</td>
</tr>
<tr>
<td>CHILOPODA INSECTA</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Orthoptera</td>
<td>28.8%</td>
<td>57.7%</td>
<td>1.3%</td>
<td>6.3%</td>
</tr>
<tr>
<td>Isoptera</td>
<td>13.4%</td>
<td>0.8%</td>
<td>46.7%</td>
<td>7.2%</td>
</tr>
<tr>
<td>Hemiptera</td>
<td>3.8%</td>
<td>1.8%</td>
<td>2.7%</td>
<td>20.9%</td>
</tr>
<tr>
<td>Homoptera</td>
<td>15.6%</td>
<td>21.7%</td>
<td>0.9%</td>
<td>&lt;0.1%</td>
</tr>
<tr>
<td>Neuroptera</td>
<td>1.9%</td>
<td>1.4%</td>
<td>2.6%</td>
<td>2.1%</td>
</tr>
<tr>
<td>Coleoptera (Adult)</td>
<td>7.6%</td>
<td>4.2%</td>
<td>2.6%</td>
<td>2.1%</td>
</tr>
<tr>
<td>Coleoptera (Larvae)</td>
<td>5.8%</td>
<td>3.6%</td>
<td>2.6%</td>
<td>9.1%</td>
</tr>
<tr>
<td>Lepidoptera (Larvae)</td>
<td>1.3%</td>
<td>12.1%</td>
<td>4.5%</td>
<td>5.2%</td>
</tr>
<tr>
<td>Hymenoptera</td>
<td>1.9%</td>
<td>0.1%</td>
<td>2.6%</td>
<td>0.2%</td>
</tr>
<tr>
<td>Insect Pupae</td>
<td>1.3%</td>
<td>8.8%</td>
<td>1.8%</td>
<td>&lt;0.1%</td>
</tr>
<tr>
<td>Unidentified</td>
<td>3.8%</td>
<td>2.1%</td>
<td>1.8%</td>
<td>&lt;0.1%</td>
</tr>
</tbody>
</table>
but constitute only a minor percentage volumetrically. This is because termites are small and because few lizards actually consumed termites. Only one lizard in each of the two South Padre Island samples and three lizards in Highway 77 sample consumed termites (and in the latter sample, two of the three lizards had eaten only one termite). Termites are generally patchily distributed; apparently if a racerunner finds a patch of termites, it will eat many of them at a time. However, this obviously happens infrequently given that only 3 of the 34 lizards analyzed for this study had consumed more than one termite. This contrasts with the situation for the *Cnemidophorus laredoensis* complex of unisexual lizards which consume huge numbers of termites (Paulissen et al. 1988). Presumably the difference arises from differences in the availability of termites in *C. sexlineatus stephensi* versus *C. laredoensis* habitats rather than differences in feeding preferences given the close genetic relationship of these lizard species.

There was no significant correlation between lizard SVL and the number of prey consumed \((r = +0.08; P > > 0.05)\). However, there was a significant positive correlation between lizard SVL and total volume of prey consumed \((r = +0.44; P = 0.03)\) and a marginally non-significant positive correlation between lizard SVL and mean volume of individual prey items consumed \((r = +0.33; P = 0.11)\). These relations hold because the September 1993 South Padre Island sample included four small, young-of-the-year individuals which consumed small prey and the lizards in the Highway 281 sample (which were all adult-sized) consumed large grasshopper prey (Table 2). When the four young-of-the-year are removed from the analysis, both the correlation between lizard SVL and total prey volume and the correlation between lizard SVL and mean volume of individual prey items consumed become statistically non-significant \((P > > 0.05)\).

Overall, the results presented here suggest the diet of *Cnemidophorus sexlineatus stephensi* in south Texas is more similar to the diet of other *C. sexlineatus* populations in the central U. S. (San Patricio County of Texas, Kansas and Oklahoma) than to either the diet of *C. sexlineatus* in Florida, or the closely related unisexual species of the *C. laredoensis* complex in the Rio Grande Valley. This similarity may be due to similarities in food preferences and feeding behaviors among populations of *C. sexlineatus* in the central U. S. However, it may be that *C. sexlineatus* populations everywhere are basically generalists, feeding on whatever arthropods they encounter (Paulissen 1987b). If so, diet similarities may reflect nothing more than similarities of the prey base
Table 2. Mean ± standard deviation of lizard snout-to-vent lengths (mm), number of prey per lizard, total volume of prey per lizard (mm³), and mean volume of individual prey items (mm³) from each of the four samples of *Cnemidophorus sexlineatus stephensi*. Numbers in parentheses represent minimum and maximum values.

<table>
<thead>
<tr>
<th></th>
<th>S. Padre</th>
<th>S. Padre</th>
<th>Hwy 77</th>
<th>Hwy 281</th>
<th>All Samples</th>
</tr>
</thead>
<tbody>
<tr>
<td>Snout-to-Vent Length (mm)</td>
<td>56±1.8mm (54-59mm)</td>
<td>47±8.2mm (37-60mm)</td>
<td>60±3.8mm (53-65mm)</td>
<td>59±3.7mm (53-66mm)</td>
<td>56±6.3mm (37-66mm)</td>
</tr>
<tr>
<td>Number of Prey Items</td>
<td>7±4.0 (3-13)</td>
<td>13±13.3 (2-38)</td>
<td>14±17.2 (1-53)</td>
<td>2±1.5 (1-6)</td>
<td>8±11.0 (1-53)</td>
</tr>
<tr>
<td>Total Volume of Prey (mm³)</td>
<td>203±113.7mm³ (68-415mm³)</td>
<td>141±103.3mm³ (13-309mm³)</td>
<td>287±179.5mm³ (18-514mm³)</td>
<td>169±172.8mm³ (46-515mm³)</td>
<td>200±146.2mm³ (13-515mm³)</td>
</tr>
<tr>
<td>Volume of Individual Prey (mm³)</td>
<td>25.6±10.1mm³ (11.5-38.7mm³)</td>
<td>13.7±6.8mm³ (4.6-20.6mm³)</td>
<td>20.4±11.8mm³ (4.3-34.8mm³)</td>
<td>136.1±190.6mm³ (11.5-515.0mm³)</td>
<td>48.0±101.0mm³ (4.3-515.0mm³)</td>
</tr>
</tbody>
</table>
among different areas. Study of other populations of *C. sexlineatus* in Texas is needed to fill in gaps in the understanding of the ecology of this species as well as to clarify the status and distribution of the subspecies in the state.

**ACKNOWLEDGMENTS**

Specimens were obtained under the authority of Scientific Collecting Permits issued to the authors by the Texas Parks and Wildlife Department (1986: number 61; 1993-1994: number SPR-0691-408). Support for travel to Texas was provided by a University of Arkansas, J. William Fulbright College of Arts and Sciences Research Incentive Grant to JMW in 1986 and by the McNeese State University Miller Endowed Professorship of Science awarded to MAP in 1993.

**LITERATURE CITED**


MAP at: mpauliss@acc.mcneese.edu
AMPHIBIANS AND REPTILES OF THE LATE PLEISTOCENE TONK CREEK LOCAL FAUNA, STONEWALL COUNTY, TEXAS

Dennis Parmley and *Russell S. Pfau
Department of Biological and Environmental Sciences
Georgia College, Milledgeville, Georgia 31061 and
Biology Department, Midwestern State University
Wichita Falls, Texas 76308-2099
*Present address:
Department of Zoology, Oklahoma State University
Stillwater, Oklahoma 74078.

Abstract.—The late Pleistocene Tonk Creek local fauna (\(^{14}C\) dated at 13,270 \(\pm\) 110 years before present) of Stonewall County, Texas, has yielded herpetological fossils representing at least two species of amphibians and seven species of reptiles. All of the taxa represent extant species that occur in, or near, the Tonk Creek site today. This is in contrast with the mammalian fauna which contains two extinct and four northern extralimital species. The disjunct composition of the paleofauna suggests more equable climatic conditions at the site during late Pleistocene times.

Amphibians and reptiles are common Pleistocene fossils in Texas, but paleoherpetofaunal assemblages with absolute dates are lacking. A collection of amphibians and reptiles stratigraphically in context with a mammalian fauna \(^{14}C\) dated at 13,270 \(\pm\) 110 years before present, the Tonk Creek Local Fauna of Stonewall County (Pfau 1994), forms the basis of this report. The fossils represent at least two species of amphibians and seven species of reptiles.

SYSTEMATIC PALEONTOLOGY

Identifications of the fossils were made by comparing them with Recent reference skeletons in the collections of Georgia College. Catalogue numbers (in parentheses) refer to the Collection of Fossil Vertebrates of Midwestern State University, and taxonomy generally follows Banks et al. (1987).

Class Amphibia
Order Caudata
Family Ambystomatidae
Ambystoma tigrinum
Tiger salamander

Material examined.—one trunk vertebra (MSU 12970-1).

Remarks.—The vertebra is confidently assigned to A. tigrinum, the only salamander living in Stonewall County today (Dixon 1987), on the
basis of characters given by Holman (1969) and Tihen (1958). The fossil has a widely opened notochordal canal suggesting it represents a larval individual (Rogers 1985).

Order Anura  
Family Ranidae  
*Rana pipiens* complex  
Leopard Frog

*Material examined.*—four left and six right ilia; 2 right and 2 left scapulae (MSU 12970-2).

*Remarks.*—The fossil ilia have smooth vastus prominences and gently sloping ilial crests as in the *R. pipiens* complex (Holman 1964). The elements are identical to those of *Rana blairi*, the species that occurs today in Stonewall County (Dixon 1987). Nonetheless they cannot be confidently separated from ilia of other closely related forms (Parmley 1988a), and consequently, only a "complex" placement is suggested here.

The scapulae of *Rana* do not appear to be diagnostic to species, but at the generic level they may be separated from those of *Bufo* and *Scaphiopus* based on positions of coracoid articular processes (Parmley 1992). In *Rana*, the structures lie near the clavicular articular processes, forming narrow glenoid openings, whereas in *Bufo* and *Scaphiopus* they project laterally, producing wider glenoid openings. The Stonewall scapulae are identical to those of ranid species of about the same size as are represented by the fossil ilia.

Class Reptilia  
Order Squamata  
Family Leptotyphlopidae  
*Leptotyphlops* sp. indet.  
Blind snake

*Material examined.*—one vertebra (MSU 12970-3)

*Remarks.*—Vertebrae of this tiny scolecophidian snake are uniquely distinct at the generic level and easily separated from those of all other small snake genera. The combination of characters that identify the fossil to *Leptotyphlops* include absence of a neural spine; zygosphene wide and thin; prezygapophyseal facets elongated and strongly anteriorly directed; posterior ends of neural arch extended medially; condyle and cotyle dorsoventrally compressed; hemal keel indistinguishable from
centrum; and no subcentral ridges. This is the first fossil record of this tiny fossorial snake from Texas (see Holman 1995). The genus has previously been reported from the Holocene and Pleistocene of Arizona (Van Devender & Mead 1978) and Pleistocene of New Mexico (Van Devender & Worthington 1978). Vertebrae of *L. dulcis* appear to be indistinguishable from those of *L. humilis*, thus no species allocation is suggested here.

Family Colubridae

*Coluber* sp. indet. or *Masticophis* sp. indet.
Racer or Coachwhip snake

*Material examined.*—three trunk vertebrae (MSU 12970-4).

*Remarks.*—These vertebrae are clearly assignable to *Coluber* or *Masticophis* based on their elongated shape; long, relatively thin neural spines; and well developed, uniformly thin hemal keels. One of the fossils has well developed epizygapophyseal spines, which is also characteristic of Recent *Coluber* and *Masticophis*. Vertebrae of *Coluber* are indistinguishable from those of *Masticophis* (Parmley 1990a), and both genera occur in Stonewall County today (Dixon 1987).

*Diadophis punctatus*
Ringneck snake

*Material examined.*—three vertebrae (MSU 12970-10), Figure 1.

*Remarks.*—The vertebrae of *Diadophis* are rather generalized and similar to those of the small colubrid genera *Gyalopion*, *Sonora*,

---

**Figure 1.** Trunk vertebra of *Diadophis punctatus* (MSU 12970-10) in dorsal (A) and ventral (B) view. Line = 1 mm.
Figure 2. Trunk vertebra of *Storeria* cf. *S. dekayi* (MSU 12970-5) in lateral (A) and dorsal (B) view. Line = 1 mm.

*Hypsiglena* and *Tantilla*. Nonetheless, *Diadophis* differs from *Hypsiglena* in having lower neural spines and from *Gyalopion* in having smaller condyles. Vertebrae of *Diadophis* clearly differ from those of *Tantilla* in being shorter, wider, and generally more robust. From *Sonora* they differ in having flatter hemal keels (Holman 1987) and in often having the anterior ends of the neural spines rounded rather than bifurcate (Parmley 1990b).

*Storeria* cf. *S. dekayi*

Brown snake

_Material examined._—four vertebrae (MSU 12970-5), Figure 2.

_Remarks._—Differentiation of the small natricine genera *Storeria*, *Tropidoclonion*, and *Virginia* presents some problems as members of all three genera have low, long neural spines; short, posteriorly directed hypapophyses; relatively wide zygosphenes; and similarly shaped neural arches. Nonetheless, *Storeria* vertebrae differ from those of *Tropidoclonion* in being longer and narrower with longer hypapophyses and shorter, more obliquely positioned accessory process. *Storeria* vertebrae differ from those of *Virginia* in having slightly thicker neural spines that extend past the posterior borders of the neural arches (often referred to as a neural spine overhang). In *Virginia*, the neural spines stop at, or extend only slightly beyond, the posterior borders of the neural arches. It is not possible to confidently separate isolated vertebrae of *Storeria dekayi* and *Storeria occipitomaculata*, but *S. dekayi* is the only species
that currently occurs near Stonewall County; *S. occipitomaculata* occurs far to the east (Dixon 1987). Consequently, a tentative species determination of the fossils is suggested on the basis of current distributions.

*Thamnophis cf. T. proximus*

Ribbon snake

**Material examined.**—one vertebra (MSU 12970-6).

**Remarks.**—This vertebra is well preserved and is placed in the genus *Thamnophis* rather than *Nerodia* (with the exception of *N. harteri*) based on a more elongated vertebral shape; longer, lower neural spine; a more depressed neural arch; and in having a shorter, more posteriorly directed hypapophysis. Moreover, the hypapophysis is not truncated as in *Regina* (Holman 1972). Interestingly, vertebrae of the geographically restricted water snake *Nerodia harteri* are similar to those of *Thamnophis* in having strongly posteriorly directed hypapophyses; low neural spines; and moderately depressed neural arches. Nonetheless, *Thamnophis* vertebrae (and the fossil) differ from those of *N. harteri* in having shorter neural spines and in being longer through the pre- and postzygapophyseal facets.

As pointed out by Parmley (1988b), vertebrae of *Thamnophis proximus* are easily confused with those of *T. sirtalis*, differing only by subtle characters. The accessory processes of *T. proximus* (and the fossil), however, tend to be oblique rather than perpendicular to the long axes of the centra as in *T. sirtalis* (Holman 1964).

*Thamnophis sp. indet.*

Garter or Ribbon snake

**Material examined.**—10 vertebrae (MSU 12970-7).

**Remarks.**—These natricine vertebrae are like Recent *Thamnophis* in that they are elongated, but they are too fragmentary for species determination.

*Nerodia erythrogaster*

Water snake

**Material examined.**—two vertebrae (MSU 12970-9).

**Remarks.**—The vertebrae are well preserved and placed in the genus *Nerodia* based on characters discussed under *Thamnophis proximus*. The specific identification of *Nerodia* vertebrae is difficult, but Parmley
(1990a) and Meylan (1982) give criteria for the separation of this species from *N. sipedon*, *N. rhombifera*, *N. cyclopion*, and *N. fasciata*. The Tonk Creek vertebrae clearly differ from those of *N. harteri* in having higher neural spines and more vaulted neural arches. The species presently occurs in the Tonk Creek area (Dixon 1987).

*Regina grahami*

Graham’s Crayfish snake

*Material examined.*—one vertebra (MSU 12970-9).

*Remarks.*—Holman (1972:93) gives a suite of vertebral characters that separate trunk vertebrae of *Regina grahami* from those of other species of *Regina*, *Nerodia* and *Thamnophis*. Based on comparative specimens available to us, *R. grahami* vertebrae differ from those of *Thamnophis* in being about as long as wide through the zygapophyseal facets rather than longer than wide; in having higher neural arches; and in having more ventrally directed hypapophyses. From *Nerodia*, *Regina grahami* vertebrae differ in having smaller condyles and more truncated hypapophyses.

**CONCLUSIONS AND REMARKS**

As far as can be determined there are no extinct or strongly extralimital species of amphibians or reptiles in the Tonk Creek local fauna. The small natricine *Storeria dekayi* is the only species of the paleoherpetofauna that might be considered extralimital as it is not documented today in Stonewall County (Dixon 1987). Nonetheless, it does occur as close as approximately 45 km to the south in Taylor County (Dixon 1987). Consequently, we can not determine if the Tonk Creek record of this species represents an extralimital occurrence or if simply the species presently occurs there but has yet to be discovered. In strong contrast, the mammalian fauna contains two extinct species (*Camelops* sp. and *Equus* sp.) and four extralimital extant species: *Sorex cinereus, Microtus pennsylvanicus, Synaptomys cooperi* and *Zapus hudsonius* (Pfau 1994). The present distributions of the extant mammals identified to species are considerably north of the Tonk Creek site in an area roughly including eastern Nebraska, Iowa, much of Minnesota, western Wisconsin, and central Illinois (Hall 1981; Fig. 3). Present climatic conditions of this area of sympatry suggest that the late Pleistocene climate of the Tonk Creek area may have been cooler and moister than at the present (Pfau 1994).
If only the Tonk Creek paleoherpetofauna is considered, which is essentially identical to the present herpetofauna, Pleistocene climatic conditions of the area could easily be interpreted to have been about the same as at present. The farthest north of Tonk Creek where all of the herpetological forms are sympatric today is only a small area of south-central Kansas (Conant & Collins 1991; Fig. 3). Thus, while the late Pleistocene Tonk Creek mammals indicate a climate cooler and moister than at the present (Pfau 1994), the stability of the paleoherpetofauna suggests it was not cold or moist enough to displace even the decisively southern genus *Leptotyphlops*. A common explanation for disjunct Pleistocene faunas like the Stonewall fauna has simply been that more equable climatic conditions existed during the time the faunas lived. Milder, less severe summers and winters would have allowed currently allopatric southern and northern species to live together (see Graham & Mead 1987, for discussion on this idea).
ACKNOWLEDGMENTS

We are very grateful to Chris McQuade of Gulf Coast Reptiles, Florida, for generously donating recent comparative specimens used in the identification of the Tonk Creek fossils.

LITERATURE CITED


Parmley, D. 1988b. Early Hemphillian (Late Miocene) snakes from the Higgins local fauna of Lipscomb County, Texas. J. Vert. Paleon., 8:322-327


DP at: dparmley@mail.gac.peachnet.edu
STATUS OF BLARINA HYLOPHAGA  
(INSECTIVORA: SORICIDAE)  
IN NORTH TEXAS AND SOUTHERN OKLAHOMA

Frederick B. Stangl, Jr. and Carla B. Carr  
Department of Biology, Midwestern State University  
Wichita Falls, Texas 76309

Abstract.—Cranial and mandibular measurements of Blarina hylophaga from Oklahoma and Texas were compared with specimens of Blarina brevicaudata from Michigan and Missouri and Blarina carolinensis from Georgia and Texas. The statistical analysis of these measurements are generally consistent with and support the currently known distributions of these three species of shrews. A discussion of the populations in Texas and Oklahoma is presented.

Short-tailed shrews of the genus Blarina occupy southeastern Canada and most of the United States east of the Rocky Mountains. Largest of the three chromosomally distinct (George et al. 1982) and mostly parapatric species is the more northerly occurring B. brevicaudata. The two remaining species are comparably diminutive and are almost indistinguishable by conventional morphological means, although multivariate statistical analyses of cranial characters serve to separate B. carolinensis from B. hylophaga (cf. George et al. 1981; Jones et al. 1984). Present knowledge suggests that B. carolinensis ranges over the southeastern United States, from east Texas to the Atlantic Coast, and that B. hylophaga occupies the greater part of Oklahoma, Kansas and much of Missouri. This latter taxon also occurs in disjunct populations from the deep southeast of Texas (Baumgardner et al. 1992; Schmidly & Brown 1979).

George et al. (1982) proposed a hypothetical boundary paralleling much of the Red River as a dividing line between the eastern ranges of the two cryptic species of Blarina in Texas and Oklahoma. Accordingly, with the exception of the disjunct populations of B. hylophaga from south Texas, specimens from Texas and the extreme southeastern corner of Oklahoma would be referred to B. carolinensis and specimens from the remainder of the range of this genus in Oklahoma would be referred to B. hylophaga. This tentative boundary has since served workers in Texas (Dalquest & Horner 1984; Davis & Schmidly 1994) and Oklahoma (Caire et al. 1989; Stangl et al. 1992) to assign their specimens of Blarina to one species or the other solely on geographic grounds.
This report attempts to validate or refute previous assignments to species of *Blarina* specimens from the eastern margins of the range of this genus in north Texas and southern Oklahoma, an area from which either or both of the cryptic species might be expected to occur.

**METHODS**

Nine cranial and mandibular measurements (following George et al. 1981) were taken from series of adult *Blarina* selected to ensure inclusion of all three species, including *B. brevicauda* for reference purposes. Data were subjected to UPGMA (Unweighted Pair-Group Method Analysis), using the NCSS statistical package (Hintze 1996), to determine the phenetic associations of individual specimens.
STANGL & CARR

MATERIAL EXAMINED

All of the 33 specimens of *Blarina* examined during this study are deposited in the Collection of Recent Mammals at Midwestern State University (MWSU).

*Blarina brevicauda* (n=13).—MICHIGAN: City of Lansing, Ingham County, five specimens (MWSU 16478, 16480, 16481, 16484, 16487); MISSOURI: Booneville, Cooper County, eight specimens (MWSU 18270-18277).

*Blarina carolinensis* (n=9).—GEORGIA: 2.2 mi N of Milledgeville, Baldwin County, six specimens (MWSU 17858-17860, 18373-18375); TEXAS: 4.3 mi S, 2.5 mi E of Spurger, Tyler County, two specimens (MWSU 20271, 20272); Minneola, Smith County, one specimen (MWSU 19826).

*Blarina hylophaga* (n=11).—OKLAHOMA: Wichita Mountains Wildlife Refuge, two specimens (MWSU 11047, 11853); 3 mi W, 2.3 mi S of Cache, Comanche County, one specimen (MWSU 14213); 10.2 km E, 3.7 km S of Fort Sill, Comanche County, one specimen (MWSU 14570); 8.6 km E, 3.3 km S of Fort Sill, Comanche County, two specimens (MWSU 14188, 14570); 3 mi E of Dewar, Okmulgee County, three specimens (MWSU 19364-19366); TEXAS: 8 mi SSE of Montague, Montague County, two specimens (MWSU 11961, 11962).

RESULTS AND DISCUSSION

Based on geographic origins of specimens examined, the three morphometrically distinct subsets (Figure 1) generally agree with the ranges mapped by George et al. (1982) of *Blarina* species. The groupings of shrews appear to verify the assignment to *B. hylophaga* of southwestern Oklahoma shrews (Caire et al. 1989; Stangl et al. 1992) and those from Montague County of north-central Texas (Dalquest & Horner 1984). This latter finding confirms the only record-of-occurrence in Texas of *B. hylophaga*, excepting only the disjunct south Texas populations. While common in Oklahoma and elsewhere, this is clearly one of the rarest of Texas mammals.

One of the six specimens of presumed *B. carolinensis* from central Georgia (MWSU 18375) clustered with *B. hylophaga*. This locality is near the hypothetical boundary between *B. hylophaga* and *B. carolinensis* in that state (George et al. 1982). It is not the intent of this report to claim a possible example of sympathy on the basis of a single,
and possibly aberrant, individual specimen, but the shrews from the
Georgia locality certainly warrant further investigation.

Another necessary study is the determination of the status of _Blarina_
from the southeasternmost corner of Oklahoma. Caire et al. (1989) list
_B. carolinensis_ as a component of that state’s mammalian fauna on the
basis of the map of George et al. (1982). However, until demonstrated
otherwise by a critical review of those specimens listed by Caire et al.
(1989) as _B. carolinensis_, it must be considered equally plausible that _B.
hylophaga_ is the only generic representative of this group in Oklahoma.

**ACKNOWLEDGMENTS**

We thank Clyde Jones and an anonymous reviewer for their
comments on an earlier draft of this manuscript.

**LITERATURE CITED**


State University Press, Wichita Falls, Texas, 254 pp.

Press, Austin, x + 338 pp.

George, S. B., J. R. Choate & H. H. Genoways. 1981. Distribution and taxonomic status

relationships within the short-tailed shrews, genus _Blarina_. J. Mammal., 63:639-645.


Jones, C. A., J. R. Choate & H. H. Genoways. 1984. Phylogeny and paleobiology of

Schmidly, D. J. & W. A. Brown. 1979. Systematics of short-tailed shrews (Genus _Blarina_


FBS at: stanglf@nexus.mwsu.edu
GENERAL NOTES

EVIDENCE FOR MIMBRES-MOGOLLON MORTUARY PRACTICES IN THE DESERT LOWLANDS OF FAR WEST TEXAS

Jeff D. Leach, Harry W. Clark and John A. Peterson
Centro de Investigaciones Arqueologicas, 140 N. Stevens, Brewhouse Towers, Suite 202
El Paso, Texas 79912; El Paso County Historical Commission, 10305 Allway
El Paso, Texas 79925 and Sociology & Anthropology Department,
University of Texas at El Paso, El Paso, Texas 79968

Recent archaeological salvage excavations near Fabens, Texas, uncovered a prehistoric human burial with an associated Mimbres Black-on-white bowl. Mimbres Black-on-white pottery, perhaps one of the most widely recognized prehistoric ceramic types in the American Southwest, is known for its geometric and naturalistic designs painted on the interior of bowls that are commonly found, among other more domestic contexts, as offerings with human burials (Brody 1977; Anyon & LeBlanc 1984; Shafer 1995). An important and equally recognizable trait of Mimbres Black-on-white pottery is its distribution. While complete vessels and sherds of Mimbres pottery can be found in limited numbers throughout much of the American Southwest and northern Mexico, the heartland of Mimbres Black-on-white pottery production can be traced to the Mimbres River drainage and adjacent areas in southwestern New Mexico (Gilman et al. 1994; James et al. 1995; however, see Rugge 1988).

The burial site was exposed after a grade-all was used to refurbish a dirt road following runoff from a recent rainstorm that had washed-out and damaged the road (Clark 1994). The road is situated just above the floodplain of the Rio Grande in the sandhills two miles southeast of Fabens, Texas. The burial was visible in the road as a few scattered bone fragments and the top portion of the cranium (Figure 1). Removal of the loose sand exposed in situ ceramic sherds surrounding the cranium. Limited excavation revealed the sherds to be an almost complete rim portion of a Mimbres Black-on-white bowl (Figure 2) that had been deliberately placed over the cranium as a burial offering. The blading of the road appears to have removed the top 3/4 of the cranium and the bottom-half of the bowl leaving only the rim portion of the vessel. Though difficult to discern because of the ground disturbance and limited excavation, the burial may have been placed in a midden area or possibly underneath a pithouse structure (Clark 1994).
Limited archaeological work at the site (41EP3022) consisted of removal of the burial and limited surface collection. The results of the complete investigations and description of the site can be found in Clark (1994). Due to the poor preservation of the remains, the burial was removed as a complete unit by pedestaling the burial in a bulk-soil column. Following the pedestaling of the burial, the mass was covered in plastic, encased with a large, metal drum, and a mixture of plaster of Paris poured around the pedestal. Once hardened, the form containing the burial was removed to the lab for further processing (Clark 1994:8).

Documentation in the field and complete excavation in the lab revealed that the burial was placed in a pit in an upright position with the knees drawn up into the abdomen or chest (see Figure 1). Due to the extremely poor preservation, sex and stature could not be determined. However, dental analysis identified the remains as probably a 25 - 49 year old adult.

Based on the design elements, the almost complete rim portion of the Mimbres Black-on-white bowl can be typed as a variant of early Mimbres Style III (Mimbres Classic) within the Mimbres painted pottery sequence. Early Mimbres Style III has a known date range of A.D. 1010 to 1080 for the Mimbres River drainage (Shafer & Brewington 1995:Table 1).

A recent review of burial practices in the El Paso area (Miller 1990:65-68) reveals very little patterning in burial positioning, grave architecture, and offerings. Burial offerings that have been reported
include beads and occasional ceramic sherds, but most have no offerings. Owing to preferential preservation, offerings associated with skeletal remains in dry caves have included seed necklaces, sandals, fur-cloth blankets, and other perishable remains (Cosgrove 1947).

The presence of Mimbres Black-on-white pottery in far west Texas is significant in that it demonstrates the movement of Mimbres pottery (see James et al. 1995), and by extension individuals, into the region (a distance of over 100-150 km). This is the first documented occurrence of a Mimbres Black-on-white bowl inverted over the cranium of the deceased in the lowlands of far west Texas, although this practice is common in the Mimbres River drainage (Anyon & LeBlanc 1984; Shafer 1995). The burial described here, and its associated Mimbres Black-on-white bowl, is direct evidence that Mimbres mortuary customs were being practiced between A.D. 1010 to 1080 in the desert lowlands of far west Texas. The complexity of this interaction as documented through ceramic exchange and mortuary practices is not completely understood at this time. It does, however, suggest that the relationship between upland and lowland populations during this time period was both fluid and dynamic.

ACKNOWLEDGMENTS

The authors would like to thank Connie Judkins for examining the skeletal material and Sue Ruth and Harry Shafer for assisting in the identification of the Mimbres bowl. Earlier drafts of this paper were read and commented on by Susanne Green, Raymond P. Mauldin, Sue Ruth, and Bill Lockhart. Anonymous journal reviewers provided comments that improved this paper.
LITERATURE CITED


JDL at: jleach1532@aol.com

* * * * *

RAFINESQUE’S BIG-EARED BAT, PLECOTUS RAFINESQUIII
(CHIROPTERA: VESPERTILIONIDAE), FROM SHELBY COUNTY, TEXAS

Franklin D. Yancey, II and Clyde Jones
Department of Biological Sciences and the Museum
Texas Tech University, Lubbock, Texas 79409-3191

Rafinesque’s big-eared bat (Plecotus rafinesquii) occurs throughout the southeastern United States (Jones 1977; Hall 1981; Choate et al. 1994). It reaches the western limits of its range in extreme eastern Texas (Schmidly 1991). Within this part of Texas, the distribution of P. rafinesquii is rather restricted, the species having been documented previously from only 13 counties (Schmidly 1991; Thies 1994; Horner 1995; Horner & Mirowsky 1996).
This report represents the first record of *P. rafinesquii* from Shelby County, Texas. On 6 June 1996, an adult male (testes, 4 by 3 mm) was captured by a resident in the town of Center, Shelby County, and submitted to the Texas Department of Health (TDH) for rabies testing. Following the rabies assay, which was negative, the bat was sent to the authors at Texas Tech University for identification. The specimen, consisting of skin and skull (TTU 71472) and frozen tissues (TK 54861), is deposited in the Natural Science Research Laboratory at the Museum of Texas Tech University. This record from Shelby County represents the northernmost documented occurrence of *P. rafinesquii* in Texas.

Because of the restricted distribution of *P. rafinesquii* in eastern Texas, the Texas Parks and Wildlife Department (TPWD) lists this taxon as threatened (Jones 1993). Of the 14 counties from which this bat is known, records from four (29%) have been documented only on the basis of specimens submitted to TDH. Thus, TDH specimens have proven vital in mapping the distribution of *P. rafinesquii* in Texas, a task that TPWD considers high priority in its conservation plans for the species (Linam 1995). Furthermore, because of restrictions associated with the collection of threatened species, voucher specimens are few in number and are known only from five counties in Texas. Bats submitted to TDH may be retained readily as vouchers because they must be sacrificed prior to testing for rabies. These important specimens should be preserved and deposited in an appropriate repository whenever possible.

**LITERATURE CITED**


FDY or CJ at: reprints@packrat.musm.ttu.edu
AGE OF FIRST BREEDING IN GOLDEN-FRONTED WOODPECKERS (MELANERPES AURIFRONS)

Michael S. Husak
Department of Biology, Angelo State University
San Angelo, Texas 76909

Few published records exist on the age of first breeding attempts for members of the woodpecker genus Melanerpes. This information is lacking for the Golden-fronted Woodpecker (Melanerpes aurifrons). This report presents observations of four 1-yr-old Golden-fronted Woodpeckers breeding in west-central Texas during 1996.

Observations were made in San Angelo State Park, Tom Green County, Texas. All four individuals (two males, M1 and M2, and two females, F1 and F2) were captured with mist nets and color-banded as hatch year birds during the summer of 1995. Individuals were captured after fledging, but prior to their post-juvenile molt, allowing for age determination by plumage.

The four birds remained within their general area of capture throughout the fall and winter following their capture and successfully found mates and established spring breeding territories in 1996. F1 mated with a banded, after second year (ASY) male. Before completing a nest cavity, both birds abandoned their territory after an extensive area of brush within their territory was cleared and burned. M1 mated with a female of unknown age and also abandoned the territory following the start of a nest, again possibly due to the burning of brush. M2 initially mated with F2; however, F2 disappeared shortly after the start of a clutch. Within one week M2 re-mated with a banded female of unknown age (F3). They began a nest approximately one week after F3’s arrival and were caring for nestlings when M2 abandoned the territory; F3 abandoned shortly afterwards.

It is not known whether or not the nesting failures were due to age related problems, but note that nest failure was common for neighboring ASY pairs as well. One year old individuals were observed to demonstrate behaviors consistent with those observed in older individuals.

Age of first breeding attempts by Golden-fronted Woodpeckers is consistent with that of its congener the Red-bellied Woodpecker, Melanerpes carolinus (cf. Kilham 1961), as well as other non-

**ACKNOWLEDGMENTS**

Financial support was provided by the Rob and Bessie Welder Wildlife Foundation. I thank T. C. Maxwell, R. Conner and an anonymous reviewer for helpful comments on earlier versions of this manuscript. This is Rob and Bessie Welder Wildlife Foundation Contribution 492.

**LITERATURE CITED**


MSH at: aaa136@ramail.angelo.edu

* * * * *

**THE BRACKET FUNGUS GLOBIFORMES GRAVEOLENS (APHYLLOPHORALES: POLYPORACEAE) IN NORTHWESTERN LOUISIANA**

Laurence M. Hardy, Larry R. Raymond and Richard K. Speairs, Jr.

*Museum of Life Sciences, Louisiana State University in Shreveport*
One University Place, Shreveport, Louisiana 71115-2399;
*Walter B. Jacobs Memorial Nature Park, 8012 Blanchard Furrh Road, Shreveport, Louisiana 71107 and Ouachita Mountains Biological Station 281 Polk 615, Mena, Arkansas 71953-9727*

Known rurally as "sweet-knot," the polypore fungus, *Globiformes graveolens* (Schw.) Murr., is rarely encountered in northern Louisiana. At certain times during development, basidiocarps of this species emit a noticeably pleasant, sweet aroma. This fungus has been placed in homes to provide a natural aromatic air freshener (Overholts 1953). The geographic distribution cited by Overholts (1953) includes most of the northeastern United States, but did not include Louisiana,
Fig. 1. The growth habit of the bracket fungus *Globiformes graveolens*. (A) Front view showing shelf thickness and spacing. Each basidiocarp was oblong and broader in the upper half. (B) Top view showing deep red (dark) center and thin creamy-white margin of the top of the pileus. Other shelves, although hidden from view, had similar marginal coloration. (C) Several basidiocarps on the base of a dying oak (*Quercus*). The cluster of smaller shelf fungi to the lower left of the trunk is of another species of Polyporaceae. (D) General habitat of host tree; note pond in background.

Mississippi, or Arkansas. Gilbertson & Ryvarden (1986) noted a Louisiana record on their map but cited no specimens.

On 6 April 1992, while checking salamander traps in a small woodland pond in Walter B. Jacobs Memorial Nature Park (2.5 mi W and 1.0 mi S of Blanchard) in Caddo Parish, Louisiana (see Raymond & Hardy 1990), a distinctive sweet aroma was noticed. The fragrance was suggestive of the scent produced by a large concentration of flowers of the Japanese Honeysuckle, *Lonicera japonica*. A search for a
flowering shrub or tree for the source of the aroma revealed none. The aroma was eventually traced to several basidiocarps of *G. graveolens* growing from the trunk of a dying oak (*Quercus*) located about 3-5 m from the edge of the water (adjacent to pond marker number 129). A specimen (LMH 10116) was collected and deposited with the holdings of the Museum of Life Sciences at Louisiana State University in Shreveport.

This species is not yet known from Arkansas or Mississippi (Gilbertson & Ryvarden 1986) and is considered very rare in Louisiana. This is the first record for the northern half of Louisiana and one of the few known from the state. Dr. Robert L. Gilbertson (pers. comm.) confirmed the presence of a specimen (AZ 10015) from Washington Parish of Louisiana and one (AZ 10017) from Nacogdoches County of Texas among the holdings at the University of Arizona.

The same tree, which is now dead, has been checked regularly (through November 1996) since the time of the original discovery and the sweet aroma or additional growth has not been detected again. The gross morphology and growth form of *G. graveolens* (Fig. 1) was typical of the species (Gilbertson & Ryvarden 1986). Each pileus was brick red, often darker in the center (Fig. 1b), with an outer 5-10 mm margin that was white to creamy white, extending around the entire periphery, including the edge attached to the tree. Basidiocarps appeared white when viewed from the side or from below (Fig. 1a). Aged basidiocarps of *G. graveolens* were very dark brown, almost black.

There were at least nine basidiocarps of *G. graveolens* on the bottom of the tree trunk, from 0.5 to 2.0 m above the ground. All of the pilei were on the SE side of the tree which was located 2-3 m west of a small woodland pond (Fig. 1c,d). Moss and lichens were abundant on the tree from the ground to the lowermost basidiocarp. On the south side of the trunk and at the level of all of the basidiocarps, lichens were abundant and moss was sparse. On the east side of the trunk moss was more abundant than lichens.

Another species of bracket fungus (Polyporaceae) was abundant below *G. graveolens* and on the west side of the trunk (Fig. 1c,d). This species was white with fewer shelves that were thinner than those of the *G. graveolens*. The lower basidiocarps were dark green, apparently from the presence of algae.

The sweet aroma, when present, and the distinctive morphology
makes *G. graveolens* one of the most recognizable bracket fungi in the southeastern United States. Additional discoveries might clarify the geographic distribution in Arkansas, Mississippi, and northeastern Louisiana.

**LITERATURE CITED**


LMH at: lsusmus@prysm.net
BOOK REVIEW


Prior to publication of this work, the only comprehensive treatment of the freshwater mussels of Texas was that of John K. Strecker, Jr., in 1931. It is surely time, after 65 years, for another examination of this fauna. As the authors state, "the need for baseline reference material was clear". That is, research in Texas on freshwater mussels of the family Unionidae has been neither intensive nor extensive in the past. At the same time, populations have suffered decimation related to human activities such as water contamination and excessive harvest of mussels, mainly to obtain nuclei of white shell nacre for the cultured pearl industry. Perhaps the gravest threat that we have imposed on North American unionids is the introduction of Eurasian clams which impact on native species in various negative ways.

In the opening pages of what the authors refer to as a "guide", a useful section provides descriptions of shell and soft tissue anatomy of unionids, accompanied by four pages of helpful diagrams. This is supplemented by a glossary including over 100 terms commonly encountered in the literature concerning unionids. The literature has been thoroughly searched, brought together and summarized.

Many readers may find the most interesting part of the book to be the section (pp. 18-29) dealing with biology, behavior, ecology and the exploitation and commercial importance of unionids. Of interest to readers in various fields is the section "Exploitation and commercial importance". Here, a historical survey is presented, extending back to the utilization of mussels by Native Americans and early Hispanic settlers. Collection methods and gear used in harvesting mussels is discussed and illustrated. Regulations are summarized, and it is hoped that these will aid in the conservation of Texas mussels, which are beset from so many sides.

The greater part of the guide is devoted to accounts of species. Native species comprise 52 unionids and three non-unionid coastal species: Carolina marshclam, Atlantic rangia and dark falsemussel. Accounts of the exotic Asian clam and zebra mussel are also provided,
although the latter species had not yet been reported in Texas at the time of publication of the guide. Species accounts follow a consistent format, in which pertinent aspects can easily be located by salient headings. Common names currently used are indicated. Extensive synonymies are provided. Distributions are summarized in text, and are also mapped. The maps are large and clear, and utilize symbols identifying who made the collection at each site indicated. Inclusion of records from D. W. Taylor's paper of 1967 (*The Veliger*, 10:152-158) would have extended indicated ranges for some species. Descriptions are subcategorized into useful criteria, including size, general shell features, shell teeth, external and internal shell color, and, in some cases, general appearance of soft tissues. Habitat is characterized quite fully, except for a few poorly known species. Several aspects having to do with reproduction are discussed, where information is available, including spawning patterns, a description of glochidia, and species of fish that serve as hosts for various kinds of unionid glochidia.

My only reservation about the guide involves photographs. Black and white photos of adequate size are provided at the head of each species account. Unfortunately, some of these photos are so dark as to obscure important shell features. On the other hand, photos of shells depicted in 16 color plates in Appendix II are very sharp, but are rather small. For example, a 190 mm washboard mussel is reduced to 30 mm. Perhaps accounts might have been made more user-friendly if the black and white photos had been replaced with enlarged color photos, better showing features useful in identification, and also obviating the necessity of flipping back and forth from species accounts to Appendix II. Such larger, color photos enhance the front and back covers of the guide.

The authors are, perhaps, overly modest in regard to reporting their own research, and they are surely candid about what they perceive as the limitations of knowledge concerning the unionids of Texas. However, they should be proud to have produced this study, which will be useful to malacologists, ecologists, conservation workers, archeologists, and people who happen to pick up a mussel shell along a streambank and wonder about it.

Artie L. Metcalf
Department of Biological Sciences
University of Texas at El Paso
El Paso, Texas 79902-0519

ALM at: ametcalf@utep.edu
Errata.—in "A Late Pleistocene (Sangamonian) Vertebrate Fauna from Eastern Texas", Texas Journal of Science 49(1):3-22, the photographs in Figures 2 and 4 were inadvertently reversed.
MEMBERSHIP.—Any person or members of any group engaged in scientific work or interested in the promotion of science are eligible for membership in The Texas Academy of Science. Dues for regular members are $30.00 annually; supporting members, $60.00; sustaining members, $100.00; patron members, $150.00; associate (student) members, $15.00; family members, $35.00; affiliate members, $5.00; emeritus members, $10.00; corporate members, $250.00 annually. Library subscription rate is $50.00 annually.

Application for Membership
(please print or type)

Name
Last
First
Middle
Mailing Address
City State Zip
Type of Membership

Send Application Form and Check or Money Order to:

Dr. Brad C. Henry
TAS Executive Secretary
Department of Biology
University of Texas-Pan American
Edinburg, Texas 78539

Please photocopy this Application Form
THE TEXAS ACADEMY OF SCIENCE, 1997-98

OFFICERS

President: Ronald S. King, University of Texas at Tyler
President Elect: Dovalee Dorsett, Baylor University
Vice-President: James W. Westgate, Lamar University
Immediate Past President: Kenneth L. Dickson, University of North Texas
Executive Secretary: Brad C. Henry, University of Texas-Pan American
Corresponding Secretary: Deborah D. Hettinger, Texas Lutheran University
Manuscript Editor: Jack D. McCullough, Stephen F. Austin State University
Managing Editor: Ned E. Strenth, Angelo State University
Treasurer: Michael J. Carlo, Angelo State University
AAAS Council Representative: Sandra S. West, Southwest Texas State University

DIRECTORS

1995 Thomas Atchison, Stephen F. Austin State University
Charles H. Swift, Hutchinson Junior High School in Lubbock
1996 Robert D. Owen, Texas Tech University
Andrew J. Tirpak, Jr., Texas A&M University at Galveston
1997 Olufisayo Jejelowo, Texas Southern University
Orlan L. Ihms, TU Electric of Dallas

SECTIONAL CHAIRPERSONS

Anthropology: Mark Glazer, University of Texas-Pan American
Biological Science: David Marsh, Angelo State University
Botany: Allan Nelson, Texas A&M University-Kingsville
Chemistry: Delphia F. Harris, University of the Incarnate Word
Computer Science: John A. Ward, Brooke Army Medical Center
Conservation and Management: Michael F. Small, Texas A&M University-Kingsville
Environmental Science: Irene Perry, Sam Houston State University
Freshwater and Marine Science: Cynthia Gorham-Test, Environmental Protection Agency
Geography: David R. Hoffpauir, Sam Houston State University
Geology: Betsy Torrez, Sam Houston State University
Mathematics: Ben Sultenfuss, Stephen F. Austin State University
Physics: Cyrus D. Cantrell, University of Texas at Dallas
Science Education: Suzette Thorp Johnson, Kealing Jr. High in Austin
Systematics and Evolutionary Biology: Jim Collins, Kilgore College
Terrestrial Ecology: Monte Thies, Sam Houston State University

COUNSELORS

Collegiate Academy: Jim Mills, St. Edward’s University
Junior Academy: Kathy Mittag, University of Texas at San Antonio
GENERAL INFORMATION

MEMBERSHIP.—Any person or member of any group engaged in scientific work or interested in the promotion of science is eligible for membership in The Texas Academy of Science. For more information, please access the Academy’s home page at:

http://www.uttyl.edu/~tas/taswhat.htm

Dues for regular members are $30.00 annually; supporting members, $60.00; sustaining members, $100.00; patron members, $150.00; associate (student) members, $15.00; family members, $35.00; affiliate members, $5.00; emeritus members, $10.00; corporate members, $250.00 annually. Library subscription rate is $50.00 annually.

The Texas Journal of Science is a quarterly publication of The Texas Academy of Science and is sent to most members and all subscribers. Payment of dues, changes of address and inquiries regarding missing or back issues should be sent to:

Dr. Brad C. Henry
Department of Biology
The University of Texas-Pan American
Edinburg, Texas 78539
E-mail: bradhenry@panam.edu

AFFILIATED ORGANIZATIONS
American Association for the Advancement of Science,
Texas Council of Elementary Science
Texas Section, American Association of Physics Teachers
Texas Section, Mathematical Association of America
Texas Section, National Association of Geology Teachers
Texas Society of Mammalogists

The Texas Journal of Science (ISSN 0040-4403) is published quarterly at Lubbock, Texas, U.S.A. Periodicals postage paid at San Angelo, Texas and additional mailing offices. POSTMASTER: Send address changes, and returned copies to The Texas Journal of Science, Box 43151, Lubbock, Texas 79409-3151, U.S.A. The known office of publication for The Texas Journal of Science and The Texas Academy of Science is P. O. Box 10986, ASU Station, San Angelo, Texas 76909, U.S.A.; Dr. Michael J. Carlo, Treasurer.
**THE TEXAS JOURNAL OF SCIENCE**

Volume 49, No. 3  
AUGUST, 1997

**CONTENTS**

*Trinacromerum bonneri*, New Species, Last and Fastest Pliosaur of the Western Interior Seaway.  
By Dawn A. Adams .................................................. 179

The Oldest Sclerorhynchid Sawfish (Rajiformes: Sclerorhynchidae) from the Lower Cretaceous of Texas.  
By James R. Branch and John L. Mosley .......................... 199

Characterization of Soil Texture in Mexican Prairie Dog (*Cynomys mexicanus*) Colonies.  
By Julián Treviño-Villarreal, William E. Grant and Américo Cardona-Estrada ....... 207

Predation by Great-Horned Owls on Brazilian Free-Tailed Bats in North Texas.  
By Kristie Jo Roberts, Franklin D. Yancey, II and Clyde Jones ................. 215

Reproduction in the Sonoran Mountain Kingsnake *Lampropeltis pyromelana* (Serpentes: Colubridae).  
By Stephen R. Goldberg ............................................. 219

A Self Stabilizing Algorithm for Shortest Path Trees.  
By A. Kazmierczak .................................................... 223

Plant Cell Wall Degrading Enzymes Produced by the Phytopathogenic Fungus *Sclerotium bataticola*.  
By Jacobo Ortega ..................................................... 235

An Assay for the Determination of a Binding Constant, $K_a$, for the Physiological Electron Transfer Complex between Cytochrome F and Plastocyanin.  
By Kelly A. McKay and Michele R. Harris .......................... 243

The Influence of Habitat Structure upon Diversity and Evenness of Abundance.  
By Daniel M. Brooks .................................................. 247

New Fish Hosts for Nine Freshwater Mussels (Bivalvia: Unionidae) in Texas.  
By Robert G. Howells .................................................. 255

General Note

Noteworthy Records of Mammals from Fannin County, Texas.  
By Frederick B. Stangl, Jr. and Theresa J. McDonough ........................ 259

Annual Meeting Notice for 1998 ..................................... 262

Recognition of Member Support ....................................... 263

Membership Application ............................................... 264
Manuscript Editor:  
Jack D. McCullough, Stephen F. Austin State University  
Managing Editor:  
Ned E. Strenth, Angelo State University  
Associate General Editor:  
Michael J. Carlo, Angelo State University  
Associate Editor for Botany:  
Robert I. Lonard, The University of Texas-Pan American  
Associate Editor for Chemistry:  
John R. Villarreal, The University of Texas-Pan American  
Associate Editor for Geology:  
M. John Kocurko, Midwestern State University  
Associate Editor for Mathematics and Statistics:  
E. Donice McCune, Stephen F. Austin State University  
Associate Editor for Physics:  
Charles W. Myles, Texas Tech University

Manuscripts intended for publication in the Journal should be submitted in TRIPLICATE to:  
Dr. Jack D. McCullough  
TJS Manuscript Editor  
Department of Biology - Box 13003  
Stephen F. Austin State University  
Nacogdoches, Texas 75962

Scholarly papers in any field of science, technology, or science education will be considered for publication in The Texas Journal of Science. Instructions to authors are published one or more times each year in the Journal on a space-available basis, and also are available from the Manuscript Editor at the above address.

The Texas Journal of Science is published quarterly in February, May, August and November for $30 per year (regular membership) by THE TEXAS ACADEMY OF SCIENCE. Periodical postage rates (ISSN 0040-4403) paid at Lubbock, Texas. Postmaster: Send address changes, and returned copies to The Texas Journal of Science, PrinTech, Box 43151, Lubbock, Texas 79409-3151, U.S.A.
TRINACROMERUM BONNERI, NEW SPECIES,
LAST AND FASTEST PLIOSAUR
OF THE WESTERN INTERIOR SEAWAY

Dawn A. Adams
Biology Department, P. O. Box 97388
Baylor University, Waco, Texas 76798-7388

Abstract.—The Pierre Shale represents the final days of the Western Interior Seaway before its regression at the end of the Mesozoic, and records the last of the marine reptiles that dominated the seas much as their contemporary dinosaur counterparts dominated the land. *Trinacromerum bonneri*, n. sp., is the first pliosaur (short-necked plesiosaur) to be described from this formation in the northern Great Plains; as such it represents the final radiation of polycotylid pliosaurs in North America. Pliosaurs have long been regarded as particularly high-speed swimmers, but *T. bonneri* carried this trend to an extreme. Development of the longest wingfins known in pliosaurs maximized its velocity. Unique limb and vertebral structures resisted pressures of the surrounding water that were generated by its own swimming velocity. Such adaptations include tongue-and-groove articular surfaces between critical limb elements and highly interlocking cervical vertebrae.

Plesiosaurs were large marine reptiles of the epicontinental seaways that flooded much of Europe and North America during the Mesozoic. Although contemporaries of dinosaurs, they were both systematically and ecologically very different. Secondarily aquatic and derived from primitive terrestrial diapsids (Storrs 1993:66), plesiosaurs are sauropterygians, all of which generally display a strong evolutionary trend toward an aquatic niche. Specifically, sauropterygians tend to develop long oar-shaped limbs through hyperphalangy. These modified limbs have been referred to variously as paddles, oars, fins, flippers, and wings, and it is unlikely that any one of these terms will gain dominance since each bears disputed functional implications. This paper introduces and uses the term "wingfin" for plesiosaur limbs in an attempt to standardize terminology.

Within the plesiosaurs, members of the pliosaur subtaxon have always been regarded as particularly high-speed swimmers (Williston 1906; Tarlo 1960; Welles 1962; Robinson 1975; 1977; Nicholls & Russell 1991; Bakker 1993). This paper describes and names a new species that exhibits several adaptations for high-velocity subaqueous swimming, including enormous wingfins, unique tongue-and-groove wingfin articular surfaces, and interlocking cervical vertebrae.

Sauropterygians are a monophyletic clade with synapomorphies that
include: "single temporal fenestra (homologous to the upper opening of diapsids), no supratemporal, postparietal, tabular, or lacrimal, retracted nares, a large retroarticular process on the mandible, no trunk vertebral intercentra, three or more sacral vertebrae, no sternum, a divided scapulacoracoid, pectoral and thyroid fenestration, and ... a scapula that lies superficially to the clavicle" (Storrs 1993:66-67). Welles divided pleisosaurs into two infraorders: the long-necked Plesiosauroidea and the Pliosauroidea, the latter defined as short-necked, with large heads, long ischia, and "pendulous propodials" (Welles 1943). While some workers (e.g. White 1940), have argued against the use of neck length as a character of infra-ordinal significance, the dichotomy apparently reflects a basic difference in locomotory adaptations (see Storrs 1993, for review). Generally, the pliosauroids were highly maneuverable animals, capable of changing direction skillfully in pursuit of large prey, whereas plesiosauroids swam steadily and with more endurance, utilizing mobility of the neck to graze upon numerous small prey objects en route (Robinson 1975; 1977). In the absence of a definitive taxonomic revision, however, Storrs (1993) warns that "the traditional Plesiosauroidea ... and Pliosauroidea ... may or may not be valid monophyletic groups."

Within the Pliosauroidea, Welles (1943) originally recognized two families: the Jurassic Pliosauridae and the primarily Cretaceous Polycotylidae, but in an extensive 1962 revision he changed the family name Polycotylidae to Dolichorhynchopidae and relegated 16 of the 19 existing species names as nomina vana. Although not recognized by the International Code of Zoological Nomenclature, the term nomen vanum is commonly used (Thurmond 1968; Chorn & Whetstone 1978), but Welles (1943) used the designation improperly to remove two of the three existing generic names that were based on nomen vanum species, as well as one of the two existing family names that was, in turn, based upon a nomen vanum genus. Considerable confusion regarding the availability of "Polycotylid" generic names and the proper family name for the taxon ensued. Although a definitive taxonomic revision is beyond the scope of this work, it is important to review, evaluate, and stabilize nomenclature itself in this case.

Thurmond (1968) re-referred one group of seven polycotylid species names based on centra, which Welles (1943) considered indeterminate material, to nomen oblitum status. This term, however, refers to a senior synonym that has remained unused for a period of 50 years (ICZN: Article 23), and none of these seven names is a senior synonym.
The appropriate term for a species based on indeterminate material is *nomen dubium*, defined as "a descriptive term meaning name of unknown or doubtful application" (ICZN: Appendices). *Nomina dubia* are still available names, and remain so unless placed on the official index of rejected names published by the Commission (Mayr 1969). Six other "*nomen vanum*" species, *Polycotylus dolichopus*, *Polycotylus ichthyospondylus*, *Polycotylus latipinnis*, *Polycotylus tenuis*, *Trinacromerum anonymum*, and *Trinacromerum latimanus*, are not referable to *nomen dubium* status because each is based on well-described material that is simply not diagnostic at the present time, given the lack of clearly defined genus and species taxonomic characteristics. However, when Welles (1943) removed *Polycotylus latipinnis* as the type species of the genus *Polycotylus*, he also removed the generic name *Polycotylus*. Welles also rejected the genus name *Trinacromerum* because he referred its type species, *T. bentonianum* to *nomen vanum* status as well, but for a different reason: although based on valid material, the specimen had been described inadequately (by Cragin in 1888) and then lost (after a 1908 redescription by Williston), which precluded the possibility of validating the name by a new description (Welles 1962:59).

Only three species and one genus survived Welles’ revision: *Dolichorhynchops osbomi*, *Trinacromerum kirki* and *Trinacromerum willistoni*. Since Williston had previously synonymized *Trinacromerum* and *Dolichorhynchops* (1903; 1908), Welles referred *Trinacromerum kirki* and *Trinacromerum willistoni* to *Dolichorhynchops*. He then changed the family name to Dolichorhynchopidae, since *Dolichorhynchops* had now become the type genus of the family. Welles realized that the change in family name was not consistent with the Code some time before 1968, and communicated to John Thurmond that he had prepared his 1962 revision under the 1926 Code, which allowed such a change of family name in the event of a change in the name of the type genus. Thurmond therefore resurrected the Family Polycotylidae in 1968, the type genus of which remained *Dolichoryhnchos* because of Williston’s synonymy and Welles’ improper designation of *Trinacromerum* as *nomen vanum*. Then, in 1976, the type and paratype specimens of *Trinacromerum bentonianum* Cragin were relocated by the author, through efforts of Marianne Stoller of the Department of Anthropology at Colorado College in Colorado Springs, and Nicholas Hotton of the U.S. National Museum (as briefly reported in Storrs 1981). Both specimens are located at the Smithsonian and catalogued as USNM 10945 and USNM 10946. Each bears an old Colorado College label and notes indicating
that they were the specimens from which Cragin had described *T. bentonianum* (Hotton, pers. comm.).

Since the genus *Trinacromerum* (Cragin 1888) is older than *Dolichorhynchops* (Williston 1902) the synonymy of Williston (1903; 1908) places *Dolichorhynchops* in *Trinacromerum*. Storrs (1981:44) considers the vertebral characters of *Polycotylus latipinnus* to be diagnostic, and therefore recognizes the genus as a valid taxon that "has long been misunderstood and . . . synonymized". If *P. latipinnus* material is diagnostic, and if *Polycotylus* is synonymous with *Trinacromerum*, then *Polycotylus* would be the senior synonym since Cope established the genus in 1869, which antedates the 1888 establishment of *Trinacromerum*. However, Storrs uses the same vertebral characters that validate *Polycotylus* to distinguish it from *Trinacromerum*, meaning that if the genus is valid it is also not synonymous with *Trinacromerum*.

Nomenclature is therefore stabilized at present as follows:

**Family Polycotylidae** Williston 1908  
**Genus Polycotylus** Cope 1869 (type genus)  
*Polycotylus latipinnis* Cope 1869 (type species)  
*Polycotylus dolichopus* Williston 1906  
*Polycotylus ichthyospondylus* Seeley 1869  
*Polycotylus tenuis* Hector 1874  
nomina dubia:  
*Polycotylus balticus* Bogolubov 1911  
*Polycotylus brevispondylus* Bogolubov 1911  
*Polycotylus donicus* Pravoslavev 1915  
*Polycotylus ichthyospondylus* Bogolubov 1911  
*Polycotylus orientalis* Bogolubov 1911  
*Polycotylus ultimus* Bogolubov 1911

**Genus Trinacromerum** Cragin 1888  
*Trinacromerum bentonianum* Cragin 1888 (type species)  
*Trinacromerum anonyum* Williston 1903  
*Trinacromerum (Ceraunosaurus) brownorum* Thurmond 1968  
*Trinacromerum kirki* Russell 1935  
*Trinacromerum latirnanus* Williston 1903  
*Trinacromerum (Dolichorhynchops) osborni* Williston 1902  
nomen dubium:  
*Trinacromerum ichthyospondylus* Pravoslavev 1915
Figure 1. Reconstruction of *Trinacromerum bonneri* in a pose of subaqueous flight. Front and rear limbs move synchronously (Robinson 1975; 1977; Nicholls & Russell 1991; Storrs 1993; Nicholls and Russell have suggested that the limbs may not have been capable of moving dorsally to the degree illustrated.) Estimated length of approximately 3.5 m.

Museum abbreviations: KUMNH = University of Kansas Museum of Natural History, Lawrence, Kansas; TAMU = Texas A&M University, College Station, Texas; USNM = United States National Museum, Washington D.C.

**SYSTEMATIC PALEONTOLOGY**

Order Sauropterygia Owen 1860
Suborder Plesiosauria de Blainville 1835
Family Polycotylidae Williston 1908
*Trinacromerum bonneri*, new species
(Figures 1-8 and 10-14)

_Disposition of types._—Holotype (KUMNH 40002), complete skeleton minus skull (Figs. 2-6 and 10-14); Paratype (KUMNH 40001), skull, lower jaws, first three cervical vertebrae (articulated), pubes and ischia, left humerus and femur, vertebrae and ribs (Figs. 2, 5-8 and 14).

_Type locality._—Johnson Ranch, 3 mi NE of Redbird, Niobrara County, Wyoming; 1 mi E of the ranch house, about 10 ft above the Ardmore Bentonite.

_Paratype locality._—Wallace Ranch, Section 16, T35N, R57W, Fall River County, South Dakota, 10 ft below the Ardmore Bentonite; approximately 4 mi from type locality.
Figure 2. A. Atlas-axis of *Trinacromerum bonneri*, KUMNH 40002. Abbreviations: na\(_x\) = axial neural arch, na\(_t\) = atlal neural arch, zy = zygapophyses, c\(_x\) = axial centrum, c\(_t\) = atlal centrum, i\(_x\) = axial intercentrum, i\(_t\) = atlal intercentrum. B and C. Maxillary teeth of *T. bonneri*, KUMNH 40001, labial (B) and lingual (C) views. Scale = 5 cm.

Figure 3. Cervical vertebrae of *Trinacromerum bonneri*, KUMNH 40002, preserved in articulation. Note size and orientation of zygapophyses in middle region of the neck. Scale = 5 cm.
Figure 4. Vertebrae of *Trinacromerum bonneri*, KUMNH 40002. A. 20th dorsal, posterior view. B. Same, anterior view. C. Same, left lateral view. D. 15th caudal, anterior view. E. Same, ventral view. F. Caudal vertebrae 8-11, in situ. Scale = 5 cm.

Figure 5. Reconstructed girdles of *Trinacromerum bonneri*, KUMNH 40002 and 40001, dorsal view. A. Reconstructed pectrum. Abbreviations: cl = clavicle, i = interclavicle, c = coracoid, sc = scapula. B. Reconstructed pelvis. Abbreviations: p = pubis, is = ischium, il = ilium. Scale = 5 cm.
Figure 6. A - C. Proximal ends of humeri of *Trinacromerum bonneri*. A. Ventral view, KUMNH 40002. B. Ventral view, KUMNH 40001. C. Lateral view, KUMNH 40002. D. Detail of phalangeal arrangement of distal portion of left rear wingfin. I, II, III, IV, and V denote digit numbers. E. Longitudinal section through anterior and proximal portion of front or rear wingfin of *T. bonneri*. Abbreviations: h-f = humerus or femur, propodial; ru-tf = radius/ulna or tibia/fibula, first row of epipodials; c-t = first carpal or tarsal, second row of epipodials. Tongue and groove articular surfaces occur between h-f and ru-tf and between ru-tf and c-t. Scale = 5 cm.

Figure 7. Dorsal ribs of *Trinacromerum bonneri*, KUMNH 40001. A and B. Anterior dorsals. C and D. Posterior dorsals. Scale = 5 cm.
Figure 8. Reconstructed skull and lower jaw of *Trinacromerum bonneri*, KUMNH 40001. Abbreviations: pm = premaxilla, m = maxilla, f = frontal, n = nasal, pf = prefrontal, po = postorbital, p = parietal, sq = squamosal, j = jugal, q = quadrate, d = dentary, ang = angular, sur = surangular, art = articular. Scale = 5 cm.

Figure 9. Right pubis, ischium, and ilium of *Trinacromerum kirki* pelvis, dorsal view. The truncated pubis and ischium medial articular region and the unique anterolateral pubic border are drawn with heavy lines for emphasis. Compare to Figure 5B. Medial to left. Drawn from photograph in Russell 1935. Scale = 5 cm.
Figure 10. Pectrum elements of *Trinacromerum bonneri*, KUMNH 40002. A. Left scapula, ventral view. B. Interclavicle, ventral view. C. Left clavicle, ventral view. D. Right coracoid, dorsal view. Scale = 5 cm.
Figure 11. Humeri and associated epipodials of *T. bonneri*, KUMNH 40002. A. Left humerus and epipodials, dorsal view. B. Right humerus and epipodials, dorsal view. Scale = 5 cm.

Figure 12. Pelvis elements of *T. bonneri*, KUMNH 40002. A. Right pubis, dorsal view. B. Left ischium, dorsal view. C. Right ilium, anterior view. D. Same, posterior view. Scale = 5 cm.
Figure 13. Femora and associated epipodials of *T. bonneri*, KUMNH 40002. A. Left femur and wingfin, dorsal view. B. Right femur and wingfin, ventral view. Scale = 5 cm.

Figure 14. Skull and lower jaws of *Trinacromerum bonneri*, KUMNH 40001. Scale = 5 cm.
Type horizon.—Sharon Springs Member of Pierre Shale.

Age.—Campanian.

Referred specimens.—TAMU 3001, Taylor Marl of McLennan County, Texas, referred to *Trinacromerum* cf. *T. kirki* (Storrs 1981), in Texas Memorial Museum, Austin, Texas; fragmentary materials collected in 1966 at the South Dakota Wallace Ranch locality: USNM 50144 (adult) and USNM 55810 (juvenile), and proximal end of juvenile humerus at University of Nebraska.

Diagnosis.—Wingfins equal in length to dorsal spinal column; "tongue-and-groove" propodial-epipodial articulation; cervical vertebrae closely interlocked by zygapophysis-neural spine embrasures. Nineteen cervical vertebrae (including atlas and axis). Twenty-eight dorsal vertebrae (3 pectoral and 3 sacral); sacral vertebrae not fused, contra "many species of polycotylids" (Bonner 1964); dorsal vertebrae with very small paired nutrient foramina neither set in depressions nor separated by keel, contra *T. osbomi* (Williston 1908). Nineteen caudal vertebrae, most with unexpectedly long neural spines. Humerus:femur ratio >1, unlike almost all other pliosaurs (Storrs 1993). Pubis and ischium borders meet at angle caused by tapering curves at sutural ends of both bones, as in description of TAMU 3001; pubis-ischium symphysis is not truncated as it is in *T. osbomi, T. kirki, T. willistoni* and reconstruction of TAMU 3001 (Storrs 1981; Russell 1935). Prominent short spur on anterior edge of posterior coracoid process. Pubis margin smooth rather than emarginated as in *T. kirki* (Figs. 5B and 9).

Etymology.—The name proposed for the new species is in honor of Orville Bonner, preparator at the University of Kansas. Mr. Bonner has devoted most of his life to the collection, preparation, and study of the rich faunas of the Niobrara Chalk and Pierre Shale. His considerable preparation skills and wide knowledge of Great Plains paleontology have proven invaluable to graduate students at the University of Kansas for many years.

Remarks.—The skeleton KUMNH 40002 has been designated as holotype and the skull KUMNH 40001 as paratype because only postcranial characters have heretofore been used in pliosaur systematics. Measurements of *Trinacromerum bonneri* are given in Table 1.
Table 1. Measurements of *Triacromerum bonneri*.

<table>
<thead>
<tr>
<th>Measurement</th>
<th>40002R</th>
<th>40002L</th>
<th>40001</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Skull (KUMNH 40001)</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total length, snout to posterior edge of quadrate</td>
<td>93.5 cm</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Height (dorsoventral, along squamosal-quadrate)</td>
<td>29.5 cm</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Lower jaws (KUMNH 40001)</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Length (anteroposterior)</td>
<td>98.3 cm</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Symphysis length</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total width, both mandibles in articulation</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>at snout</td>
<td>5.2 cm</td>
<td></td>
<td></td>
</tr>
<tr>
<td>at posteriormost point of symphysis</td>
<td>10.7 cm</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Interclavicle (KUMNH 40002)</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Length</td>
<td>21.6 cm</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Width</td>
<td>20.8 cm</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Greatest width of foramen</td>
<td>2.1 cm</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Length of foramen</td>
<td>6.0 cm</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Clavicle (KUMNH 40002, right)</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total length</td>
<td>36.9 cm</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Length of external margin</td>
<td>27.0 cm</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Scapula (KUMNH 40002, left)</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Length, shortest part of anterior edge to end</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>of dorsal process</td>
<td>39.5 cm</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Length, anterior edge to articulation with glenoid</td>
<td>34.4 cm</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Coracoid (KUMNH 40002, right)</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Length (to top of suture)</td>
<td>71.5 cm</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Greatest width at glenoid</td>
<td>33.5 cm</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Humerus</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Length</td>
<td>52.6 cm</td>
<td>54.5 cm</td>
<td>57.8 cm</td>
</tr>
<tr>
<td>Diameter at head (anteroposteriorly)</td>
<td>13.0 cm</td>
<td>14.5 cm</td>
<td>12.4 cm</td>
</tr>
<tr>
<td>Diameter at distal end</td>
<td>32.0 cm</td>
<td>32.5 cm</td>
<td>36.0 cm</td>
</tr>
<tr>
<td><strong>Pubis</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Width, side-to-side as articulated</td>
<td>43.4 cm</td>
<td>44.0 cm</td>
<td>43.6 cm</td>
</tr>
<tr>
<td>Anteroposterior extent</td>
<td>43.0 cm</td>
<td>43.0 cm</td>
<td>44.4 cm</td>
</tr>
<tr>
<td>Width of neck</td>
<td>17.0 cm</td>
<td>16.4 cm</td>
<td>17.3 cm</td>
</tr>
<tr>
<td>Length of symphysis</td>
<td>38.0 cm*</td>
<td>40.2 cm</td>
<td>35.0 cm</td>
</tr>
<tr>
<td><strong>Ischium</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Length, to bar</td>
<td>46.2 cm</td>
<td>46.1 cm</td>
<td></td>
</tr>
<tr>
<td>Width, anterior end</td>
<td>28.2 cm</td>
<td>28.1 cm</td>
<td></td>
</tr>
<tr>
<td><strong>Ilium</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Length</td>
<td>28.5 cm</td>
<td>26.7 cm*</td>
<td>29.6 cm</td>
</tr>
<tr>
<td>Diameter of shaft at middle</td>
<td>6.3 cm</td>
<td>7.5 cm</td>
<td>6.0 cm</td>
</tr>
<tr>
<td>Diameter of base, largest</td>
<td>9.3 cm</td>
<td>9.0 cm</td>
<td>10.0 cm</td>
</tr>
<tr>
<td><strong>Femur</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Length</td>
<td>51.5 cm</td>
<td>53.0 cm</td>
<td>52.0 cm</td>
</tr>
<tr>
<td>Diameter at capitulum (greatest)</td>
<td>14.8 cm</td>
<td>12.5 cm*</td>
<td>12.0 cm*</td>
</tr>
<tr>
<td>Diameter at distal end (greatest)</td>
<td>30.0 cm</td>
<td>28.0 cm</td>
<td></td>
</tr>
</tbody>
</table>

* indicates measurement is an estimate
+ indicates measurement is too short due to breakage of measured area
— indicates portion measured is absent
**FUNCTIONAL IMPLICATIONS**

Wingfins of *Trinacromerum bonneri* are much longer relative to body size than those of any other polycotylid. Index of thorax length to hind wingfin length for *T. bonneri* is 1.03 (thorax length = 148 cm; wingfin length = 144 cm), compared to indices of 1.50 in the *T. kirki* type specimen and 1.65 in the Fort Hayes *T. osborni* specimen. *T. bonneri* wingfin elongation occurred within the epipodial regions (radius/ulna and tibia/fibula, plus first and second supernumaries), rather than via lengthening of humerus or femur. The femur of the complete hind wingfin of *T. bonneri* comprises only 35.7% of the total wingfin length, whereas it averages 41.2% of the wingfin in *T. kirki* and *T. osborni*. (*Trinacromerum kirki* type = 41.5%; *T. osborni* type = 41.2%; Ft. Hayes *T. osborni* = 41.3%). A unique "tongue-and-groove" articulation between propodials and epipodials, however, effectively increased the functional length of the propodial, since very little (if any) movement could have occurred at this type of joint. If tibia and fibula lengths are added to femur length in *T. bonneri*, the resulting length of the "functional propodial" accounts for 40% of total wingfin length, remarkably close to the 41% values for other members of the genus.

Tongue-and-groove articulation characterizes both fore and hind wingfins of *T. bonneri*, differing only in depth of the articular surfaces (Fig. 6). Elements of the first (most proximal) row of epipodials articulate at four distinct facets on the propodial, and elements of the second epipodial row articulate against the propodials just proximal to them. The articular facets are long, slender, concave "grooves", into each of which fits a projecting epipodial "tongue" (analogous to a tongue-and-groove carpentry joint). The epipodial tongue is bounded by a small but distinct rim that marks the distal extent of the propodial over it when the two are articulated. The longest and deepest of these tongue and groove facets are on the leading edges of the wingfins. Those of the fore wingfin are better developed than those of the hind (2 cm deep on humero-radius facet), and the more proximal facets are deeper and more well-developed than are those between the first and second epipodial rows. Generally tight fitting of epipodials and phalanges throughout the wingfins amplifies the overall effect.

Torsion and bending of the wingfin surface caused by resistant water pressure during the attack stroke phase of propulsion is a critical factor in plesiosaur mechanical adaptations (Robinson 1975; 1977; Nicholls & Russell 1991). While hyperphalangy increased wingfin length and therefore wingloading (which increased swimming efficiency and speed),
the fact that so much of the wingfin was composed of a pavement of numerous small elements laid essentially side-by-side made the wingfin more subject to torsion and bending along the numerous joint surfaces. Previous studies have noted offset joint rows and slight lapping of phalangeal articulations as adaptations that reduced torsion and bending of the wingfin in the epipodial region of earlier pliosaurs (Robinson 1975; 1977). The tongue-and-groove articular system seen in *T. bonneri* further increased wingfin strength and rigidity along the longitudinal axis and minimized torsion of the wingfin surface as a whole, which permitted the development of longer wingfins with more wingloading area and greater propulsive power. Water pressure resistance was highest during the attack stroke at the leading edge of the wingfin, which corresponds to the location of the deepest tongue-and-groove facets. Torsion resistance was further enhanced by the perpendicular orientation of the anteriormost (radius or tibia) articular facets to the long axis of the articulating propodial. The tongue-and-groove facet rim that projects distally beyond the articulation surfaces also projects past the angles between the facets, further reducing the possibility of torsion and bending at these joints.

The neck region of *T. bonneri*, particularly size, shape, and facet orientation of the cervical zygapophyses mid-neck, also displays remarkable adaptations to resist torsion and bending caused by water resistance (Fig. 3). Each zygapophysis is extraordinarily robust, broader and thicker in the area of articulation than in the area of origin on the centrum, and each bears a very large, flat, horizontal articular surface (as opposed to inclined articulating surfaces on dorsal vertebrae). Each pair of posterior zygapophyses tightly embraces the anterior edge of the neural spine of the vertebra to which it articulates. Horizontal zygapophyseal articular facets are commonly reconstructed as facilitating lateral (side-side) movement (Romer 1956), but the tight embrasure between neural spines and zygapophyses precludes lateral motion between individual cervical vertebrae. The broad horizontal zygapophyseal facets may instead be interpreted as adaptations to resist dorso-ventral bending (by reducing vertically oriented stresses at the joints, since stress = force per unit area), while the neural spine embrasures would have resisted lateral bending between individual cervicals. Taken together, these vertebral modifications would have resisted torsion and bending of the neck by water resistance. Smaller and less robust zygapophyses near the head and body ends of the neck presumably facilitated the mobility requirements at these major points. This agrees with Storrs' reconstruction of *Trinacromerum* neck flexi-
bility based on the fact that intervertebral cartilage in the TAMU 3001 specimen (now referred to T. bonneri) thins posteriad (Storrs 1981). It also agrees with the general perception of pliosaurs as extremely manuveurable swimmers, since high-speed directional changes would produce the type of water resistance forces the neck is designed to reduce and resist.

PHYLOGENETIC IMPLICATIONS

Some postcranial characters commonly considered diagnostic in pliosaurs, specifically hindlimb:forelimb ratios and pelvis morphology, should not be heavily weighted. The proposal that hindlimbs are larger than forelimbs in pliosaurs (and the opposite in long-necked plesiosaurs, or elasmosaurs) fails when applied to T. bonneri, in which the humerus is longer than the femur. Humerus: femur values for the Trinacromerum osborni type and Fort Hayes specimens and the type of T. kirki are 0.90, 0.98 and 0.96, respectively, while the value for T. bonneri is 1.06. Humerus length exceeds femoral in Trinacromerum sp., MDM P80.06.14 as well (figured in Nicholls & Russell 1991). As can be seen, humerus:femur ratios are not even distributed very far to either side of 1.00 in polycotylids, although statistical significance is impossible to evaluate due to small sample size.

Pelvic element morphology, such as pubis-ischium midline symphysis shape, may also prove to be nondiagnostic in pliosaurs, but for different reasons. Ventral placement and plate-like morphology of the pelvic elements, together with the possibility of live-bearing, makes sexual dimorphism a likely source of variation in this region.

Many workers believe that the use of postcranial characters in pliosaur systematics is generally problematic. Despite numerous revision attempts (Williston 1903; 1906; 1907; 1908; Welles 1943; 1962; Riggs 1944; Tarlo 1958; Persson 1963; Sues 1987; Storrs 1993; Bakker 1993), the state of chaos lamented by Williston nearly 100 years ago persists: "There are few orders of reptiles so long and so widely known . . . of which our knowledge is more unsatisfactory . . . Very few figures or adequate descriptions have been published of our numerous and diverse types. Not only are the specific characters of the descriptions almost wholly undecipherable, but the generic characters even can be satisfactorily made out in but few . . . " (Williston 1903:3). A data base of cranial characters might help resolve problems of pliosaur phylogeny, but there is "little reliable information on the cranial structure . . . and many characters (such as the presence or absence of
nasal and quadratojugal) have yet to be confirmed on better preserved and (or) prepared skull material" of plesiosaurs (Sues 1987:129). The lack of data reflects, in part, real ambiguities in the bones. Nasal and prefrontal sutures, for example, are essentially obliterated by heavily rugose striations anterior and dorsal to the external nares in polycotylids (including *T. bonneri*). This region, as well as similar areas on the maxilla below the naris, may indicate the presence of strong muscles that closed the nostril and kept it watertight during submerged high-speed swimming.

It is commonly argued that postcrania display primarily functional or gradal characters that are unsuitable for constructing hypotheses of phylogenetic relationships, and that cranial characters provide more reliable indicators of common ancestry (for example see Bakker 1993). The possibility that at least some pliosaur cranial characters may also reflect adaptations to swimming and diving suggests the more probable non-dualistic nature of character distribution, with morphology of any particular character being determined by a combination of function, phylogeny, and developmental constraint, regardless of whether the element is cranial or postcranial. Because of the rich interplay of function and phylogeny in pliosaur morphology, future revisions of pliosaurs may therefore contribute not only to our understanding of the taxon itself, but to our understanding of the interface between functional and phylogenetic processes in evolution.

**Conclusions**

*Trinacromerum bonneri*, a member of the final radiation of polycotylid plesiosaurs in the North American Western Interior Seaway, displays a unique set of structural adaptations for high-speed swimming. The wingfins are the longest known in polycotylid plesiosaurs, each being approximately the same length as the thorax. This lengthening was accomplished via elongation of the epipodial region relative to the propodium, which effectively increased wingloading and therefore swimming velocity. Development of tongue-and-groove articulation within the first two rows of epipodials reduced and resisted the increased torsion and bending of the wingfin hydrofoil otherwise caused by the increase in its surface area. The cervical vertebrae also show adaptations to high-speed swimming. A combination of massive zygapophyseal and neural spine embrasures on all but the most anterior and posterior cervicals resisted hydraulic forces generated by swimming and high-speed directional changes.
The "truncated" and "normal" pubis-ischium contacts of the medial symphysis region in *T. kirki* and *T. bonneri*, respectively, and the differences between the shapes of their anterolateral pubic borders, may be sexually dimorphic rather than phylogenetically significant. The significance of this variation cannot be evaluated in the absence of a database of cranial characters in the taxon, however. Compilation of such a database may have been hindered by the very types of high-speed swimming adaptations that have drawn the search for apomorphies to pliosaur postcrania. However, this problematic interplay of function and phylogeny in pliosaur morphology may eventually contribute to our understanding of the interface between functional and phylogenetic processes in evolution.

**ACKNOWLEDGMENTS**

Thanks are due to many people, including David S. Brown, Ken Carpenter, the late Theodore Eaton, Nicholas Hotton III, Larry D. Martin, Elizabeth L. Nicholls, Benjamin Pierce, Jane A. Robinson, Samuel P. Welles, Kenneth Wilkins and Daniel E. Wivagg. Parts of this work appeared in an earlier manuscript that comprised my Master’s thesis at the University of Kansas.

**LITERATURE CITED**


DAA at: Dawn_Adams@baylor.edu
THE OLDEST SCLERORHYNCHID SAWFISH
(RAJIFORMES: SCLERORHYNCHIDAE)
FROM THE LOWER CRETACEOUS OF TEXAS

James R. Branch and John L. Mosley
Department of Biology and Department of Geology
Baylor University, Waco, Texas 76798

Abstract.—The earliest known oral teeth of the sclerorhynchid sawfish, Onchopristis sp., are reported from the Early Cretaceous of Central Texas. These teeth were recovered from the uppermost Glen Rose Formation of the Trinity Group. In addition to the sawfish teeth, this bed contains a concentration of disarticulated fish remains, selachian teeth and denticles, crocodile teeth, and plant remains. Previous reports place the earliest occurrence of sclerorhynchids in the overlying Fredericksburg Group. These teeth move the earliest known occurrence of sclerorhynchid sawfish back several million years.

Sawfish of the Family Sclerorhynchidae closely resemble modern sawfish of the Family Pristidae. Both families are characterized by a highly elongate rostrum with sharp spinelike teeth along its lateral margins. However, the two families can be separated by comparing the morphology of the rostra. Pristid rostral teeth are set in alveoli while the notched bases of the rostral teeth of sclerorhynchids rest on the surface of the rostrum.

Modern sawfish (pristids) inhabit warm, shallow tropical marine environments. Sclerorhynchids presumably frequented the same type of environment based on taphonomic evidence. Both are quite similar in outward body form and represent an example of parallel evolution among cartilaginous fishes (Welton & Farish 1993).

MATERIALS AND METHODS

A 15 kg sample of the limestone bonebed from the Whiteway locality in Hamilton County (Figure 1) was collected and dissolved it in dilute formic acid (~10%). The remaining residue was wet sieved through number 10, 18, and 30 mesh standard sieves. Identifiable bone fragments were removed from the associated debris with the aid of a dissecting microscope. The illustrations were photographed through a scanning electron microscope. Specimens collected and examined during
Figure 1. Map of Hamilton County and measured geologic section of the Thorp Springs and Upper Members of the Glen Rose Formation illustrating the location and stratigraphic position of the Whiteway Bonebed.

This study are deposited in the Shuler Museum of Paleontology, Southern Methodist University, Dallas, Texas (SMUSMP).

**SYSTEMATIC PALEONTOLOGY**

Class Chondrichthyes  
Subclass Elasmobranchii  
Order Rajiformes Berg 1940  
Family Sclerorhynchidae Cappetta 1974  
Genus *Onchopristis* Stromer 1917

*Description.*—Oral teeth of *Onchopristis* sp. from the Early Cretaceous Glen Rose Formation are characterized by a lingually
Figure 2. Scanning electron micrographs of an anterior tooth, *Onchopristis* sp. (SMUSMP 74627) in labial (A), lingual (B), occlusal (C), and lateral (D) views. Posterior tooth (SMUSMP 74628) is illustrated in labial (E), lingual (F), lateral (G), and occlusal (H) views. Scale bar = 0.5 mm.

directed central cusp (Figure 2). Five teeth from the Whiteway Bonebed (SMUSMP 74627-74632) are referred to this taxon. The teeth range from 0.75 to 1.75 mm in width, and 0.50 to 1.00 mm in height. The tooth crown is roughly triangular in lingual view (Figure 2b & f). A cutting blade descends from the central cusp to the lateral margins of the crown (Figure 2d). The pendant labial process is the most prominent feature of the crown (Figure 2a & e). The root is hemiaulacrohizous as described by Casier (1947a; 1947b; see also Welton & Farrish 1993), crown width slightly exceeding root width. Based upon specimens examined during this study, tooth form probably varied from the front
Occurrence.—Teeth of sclerorhynchid sawfish occur throughout the Middle and Late Cretaceous of the Gulf Coast area in the United States (Stromer 1917; Meyer 1975; Werner 1989; Welton & Farish 1993). Sclerorhynchid skeletal material is known from the Late Cretaceous of Lebanon (Cappetta 1980). Oral and rostral teeth referred to the Genus *Onchopristis* are known from the Fredericksburg Group and younger Cretaceous rocks of central Texas (Thurmond 1972; Welton & Farish 1993), the Late Cretaceous of Arizona (Williamson et al. 1993), and the Late Cretaceous of Georgia (Case & Schwimmer 1988). Thus, the genus has a Tethyan distribution in Cretaceous marine sediments. The Glen Rose specimens extend the range into the uppermost Trinity Group.

Geology.—The Lower Cretaceous Comanchean Series is exposed in Central Texas strikes NNE and dips gently to the east (Figure 3). The outcrop band is bound on the east by the Balcones Fault Zone and is
truncated on the west by erosion that exposes Paleozoic rocks. Therefore, the general trend in Central Texas is that of older rocks in a westward direction (Figure 3). The Whiteway Bonebed occurs within this Cretaceous outcrop belt and is well exposed in several places in Hamilton County, Texas (Figure 1).

In Hamilton County, the Glen Rose Formation ranges in thickness from 67 meters to 43 meters and thins from the northeast to the southwest. Three formal members are recognized, and ascending order, are Lower Glen Rose Member, the Thorp Springs Member, and the Upper Glen Rose Member. The Whiteway Bonebed occurs within the highest sand-free limestone of the Upper Glen Rose. The bonebed is overlain by the Lake Merritt Member of the Paluxy Formation. In the study area, the Upper Glen Rose Member is about 18 meters thick and consists of limestone, sandy limestone and marl. The limestone commonly contain mollusk fragments intraclasts, pellets, ostracods and miliolid foraminifera. Cross-bedding, bored surfaces and burrows are also present. Siltstones and sandstones are common in the upper portion of this unit. The Lake Merritt Member of the Paluxy Formation is about 2.7 meters thick in the study area and consists of thin sandstones and shales. The sandstones are fine-grained, subrounded and well sorted (Arnold 1988:Fig. 6; Brothers 1976; Tarrant 1969).

The Glen Rose/Paluxy contact is conformable and consists of an increasing sandstone and shale content up section. Thin sandstones and shales interfinger and intergrade with sandy and silty marls over a three meter interval. For convenience, the Glen Rose/Paluxy contact is placed at the top of the last sand-free limestone. This commonly coincides with the Whiteway Bonebed.

The Upper Glen Rose Member represents deposition in an offshore, shallow marine environment. As deposition progressed, the relative amount of mud, silt and sand became a greater volume of the sediment and suggests an increasing proximity to shore. The increase in intraclasts in the limestone and the cross-bedding in the sandstones indicates an increase in wave and/or current energy associated with a shallowing sea. The presence of miliolid foraminifera, low biodiversity and terrigenous clastics indicates a highly variable salinity (Arnold 1988). Terrigenous clastic influx during deposition resulted in the
abandonment of carbonate production. This package of rocks records deposition on a shallow carbonate shelf during a protracted regressive event.

**DISCUSSION**

Sclerorhynchid sawfish fossils are known from many Upper Albian and later Cretaceous marine fossil localities (Cappetta 1987). However, they are quite rare in earlier deposits (Thurmond 1972; Cappetta 1987). The collection of nine oral teeth from the Whiteway Bonebed represents the earliest known occurrence of sclerorhynchid sawfish in the Early Cretaceous. The teeth are morphologically identical to material assigned to *Onchopristis dunklei* by other researchers (Cappetta 1987; Welton & Farish 1993). However, Werner (1989) erected a new genus and species, *Sechmetia cruciformis*, based on similar specimens from the Upper Cenomanian of Egypt. The Whiteway Bonebed teeth examined during this study are assigned to the Genus *Onchopristis* based on the morphological similarities to more complete sclerorhynchid material from the Late Cretaceous of Lebanon (Cappetta 1980).

In addition to producing the earliest known sclerorhynchid sawfish teeth, the Whiteway Bonebed and associated sediments provide a clear picture of the paleoecology of the upper member of the Glen Rose Formation. The bonebed is the last sand free carbonate in this section and represents a final episode of marine deposition in this area. Following the deposition of this material, clastic deposition dominated, as seen in the sands of the Paluxy Formation.

Two general conclusions can be made on this study of the Whiteway Locality. First, the Whiteway Bonebed contains the earliest known representatives of the Genus *Onchopristis* (Rajiformes: Sclerorhynchidae). Second, bonebed geology indicates a normal marine environment suggesting a warm, shallow depositional environment.

**ACKNOWLEDGMENTS**

We would like to acknowledge the departments of Geology and Biology at Baylor University for granting us the freedom to pursue projects beyond our thesis and dissertation topics while using
departmental equipment and supplies. Also, thanks to our committee
ing chairs, Dawn A. Adams and Robert C. Grayson, Jr., for their patience
and instruction. Phillip A. Murry (Tarleton State University), Louis L.
Jacobs and Dale A. Winkler (Southern Methodist University) allowed us
to examine material processed in their labs. Special thanks to Mark
Grimson and the Department of Biology, Texas Tech University, for
graciously allowing John Mosley to use the scanning electron
microscope and darkroom facilities. Finally, we would like to thank
Melinda Mosley for her organizational help.

LITERATURE CITED


Brothers, J. 1976. Stratigraphy and Environments of the Marginal Glen Rose
Limestone, Glen Rose Formation (Lower Cretaceous), North-Central Texas. Unpub.


Cappetta, H. 1987. Chondrichthyes II. Mesozoic and Cenozoic ELASMOBRANCHII,
in Schultze, H. P. and Kuhn, O. (eds.), Handbook of Paleoichthyology. Fischer,

Case, G. R. & D. R. Schwimmer. 1988. Late Cretaceous fish from the Blufftown
Formation (Campanian) in western Georgia. J. Paleont., 62(2):290-301.

Casier, E. 1947a. Constitution et evolution de la racine dentaire des Euselachii. II.

Casier, E. 1947b. Constitution et evolution de la racine dentaire des Euselachii. III.

Meyer, R. L. 1975. Late Cretaceous Elasmobranchs from the Mississippi and East
Methodist University, Dallas, Texas, 419 pp.

Stromer, E. 1917. Ergebnisse der Forschungsreisen Prof. E. Stromers in den Wusten
Agyptens. II. Wirbeiter-Peste der Baharije-Stufe (unterstes Cenoman). 4. Die Sage
des Pristiden Onchopristis numidus Haug sp. und uber die Sagen der Sagehare: Abh.

Tarrant, E. 1969. The Paluxy-Glen Rose Contact in Hamilton and Comanche Counties
and Southward into Burnet County. Unpub. bachelors thesis, Baylor University., 66


JRB at: BRANCHJ@baylor.edu
CHARACTERIZATION OF SOIL TEXTURE IN MEXICAN PRAIRIE DOG (*Cynomys mexicanus*) COLONIES

Julián Treviño-Villarreal, *William E. Grant and Américo Cardona-Estrada

*Instituto de Ecología y Alimentos, Universidad Autónoma de Tamaulipas*
Blvd. A. López Mateos # 928, 87040 Cd. Victoria, Tamaulipas, México and
*Department of Wildlife and Fisheries Sciences, Texas A&M University College Station, Texas 77843-2258*

Abstract.—The Mexican prairie dog (*Cynomys mexicanus*) is an endangered species that is endemic to the northeastern Mexican states of Coahuila, Nuevo León and San Luis Potosí. Soil texture was characterized from samples collected from 21 colonies throughout this geographic range. All colonies examined were found in loamy soils. The majority (>60%) of colonies were found in silt loam soils low in clay, medium in sand, and medium to high in silt.

Resumen.—El perrito llanero mexicano (*Cynomys mexicanus*) es una especie en peligro de extinción y endémica del noreste de México (Coahuila, Nuevo León y San Luis Potosí). En esta investigación se obtuvieron muestras de suelo de 21 colonias de perritos llaneros mexicanos a lo largo de su distribución geográfica y se caracterizó la textura del suelo donde estaban presentes las colonias de esta especie. Todas las colonias de perritos llaneros se distribuyeron en suelos limosos. La mayoría (>60%) de las colonias se localizaron en suelos de textura tipo migajón-limosa con porcentajes bajos en arcilla, medios en arena, y medio-altos en migajón.

The Mexican prairie dog (*Cynomys mexicanus*) is an endangered species (IUCN 1990; USFWS 1991; CITES 1992; SEDESOL 1994) primarily due to destruction/fragmentation of its natural habitat (Treviño-Villarreal & Grant in press). Ninety-eight percent of the present geographic range of the Mexican prairie dog is found in the Mexican states of Coahuila and Nuevo León, with the remaining 2% found in San Luis Potosí (Treviño-Villarreal & Grant in press). The only colony (Cienega de Rocamontes) reported for the state of Zacatecas (Matson & Baker 1986) is now extinct (Treviño-Villarreal 1988; 1994; Treviño-Villarreal et al. 1996; Ceballos & Mellink 1990; Ceballos & Navarro 1991; Ceballos et al. 1993).

Mexican prairie dog habitat is confined to valleys, prairies and intermontane basins at elevations of 1600-2000 m associated with gypsum and xerosol soils that are dominated by grasses, forbs and bare soil (Treviño-Villarreal 1990). The influence of different soil texture on the geographic distribution of Mexican prairie dogs (*C. mexicanus*)
is poorly known. Scott-M. (1984) found that Mexican prairie dogs were restricted to gypsic grasslands at El Tokio, Nuevo León, México, although she did not conduct soil analyses. According to Ceballos et al. (1993), Mexican prairie dogs are associated strongly with gypsum soils throughout their geographic range, except in Rancho Los Angeles, Coahuila, where they are found in alluvial soils. The objective of this study was to characterize soil texture within Mexican prairie dog colonies.

**METHODS**

All 94 active and inactive Mexican prairie dog colonies reported by Treviño-Villarreal (1994) were plotted on 1:50,000-scale edaphological maps from the Instituto Nacional de Geografía y Estadística (INEGI; Map codes: G14 C33-35, G14 C43-46, G14 C53-56, G14 C62-66, G14 C74-76, G14 C84-85 and F14 A14). Three colonies were randomly chosen within each of seven soil types. Soil samples were collected during June 1992 and from December 1992 to August 1993. One soil sample was collected at a depth of 30 cm and another at a depth of 60 cm (except two colonies were not sampled at the 60 cm depth) at the center of each prairie dog colony in a position where prairie dog mounds had not altered the composition of the soil. Soil texture was characterized by the amounts of sand, clay and silt they contained by the Laboratorio de Suelos del Gobierno de Tamaulipas, México in Cd. Victoria (LSGT) following the hydrometer method of Downhower & Hall (1966).

**RESULTS**

Seventeen of the 21 Mexican prairie dog colonies sampled were found in alluvial soils 2 to 10 m deep and four colonies (Artecillas, Cienega del Toro, El Porvenir and El Castillo) in colluvial soils 2 to 5 m deep (INEGI; Edaphology map codes: G14 C33-35, G14 C43-46, G14 C53-56, G14 C62-66, G14 C74-76, G14 C84-85 and F14 A14) (Table 1). The majority of the colonies sampled at a depth of 30 cm (66.7%) and 60 cm (63.2%) (Table 1) were found on silt loam soils low in clay, medium in sand, and medium to high in silt (Fig. 1). All soil samples were gravel-free.

**DISCUSSION**

It is suggested by the results that Mexican prairie dog colonies are found primarily on loamy soils. According to Reading & Matchett (in press), prairie dogs prefer sandy loams; very sandy soils are not favora-
Table 1. Latitude, longitude and origin of soil at the localities, listed from northwest to southeast, where soil samples where collected. Soil depth, texture and classification also are presented.

<table>
<thead>
<tr>
<th>Colony Name, State</th>
<th>Latitude (N)</th>
<th>Longitude (W)</th>
<th>Soil Origin</th>
<th>Depth cm.</th>
<th>Texture (%)</th>
<th>Soil Class</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Clay</td>
<td>Silt</td>
<td>Sand</td>
</tr>
<tr>
<td>Artecillas, Coah.</td>
<td>25°14'12&quot;</td>
<td>100°43'48&quot;</td>
<td>Colluvial</td>
<td>30</td>
<td>16</td>
<td>52</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>60</td>
<td>NA</td>
<td>NA</td>
</tr>
<tr>
<td>El Castillo, Coah.</td>
<td>25°11'42&quot;</td>
<td>100°37'40&quot;</td>
<td>Colluvial</td>
<td>30</td>
<td>6</td>
<td>60</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>60</td>
<td>20</td>
<td>64</td>
</tr>
<tr>
<td>R. Los Angeles 4, Coah.</td>
<td>25°08'55&quot;</td>
<td>101°05'09&quot;</td>
<td>Alluvial</td>
<td>30</td>
<td>23</td>
<td>40</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>60</td>
<td>17</td>
<td>38</td>
</tr>
<tr>
<td>El Porvenir, N.L.</td>
<td>25°07'35&quot;</td>
<td>100°21'44&quot;</td>
<td>Colluvial</td>
<td>30</td>
<td>4</td>
<td>56</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>60</td>
<td>2</td>
<td>76</td>
</tr>
<tr>
<td>R. Los Angeles 3, Coah.</td>
<td>25°07'20&quot;</td>
<td>100°01'05&quot;</td>
<td>Alluvial</td>
<td>30</td>
<td>36</td>
<td>42</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>60</td>
<td>21</td>
<td>32</td>
</tr>
<tr>
<td>Rancho Nuevo, N.L.</td>
<td>25°05'28&quot;</td>
<td>100°36'27&quot;</td>
<td>Alluvial</td>
<td>30</td>
<td>6</td>
<td>58</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>60</td>
<td>NA</td>
<td>NA</td>
</tr>
<tr>
<td>Providencia 2, N.L.</td>
<td>25°05'00&quot;</td>
<td>100°37'00&quot;</td>
<td>Alluvial</td>
<td>30</td>
<td>4</td>
<td>40</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>60</td>
<td>6</td>
<td>40</td>
</tr>
<tr>
<td>C. del Toro, N.L.</td>
<td>25°04'40&quot;</td>
<td>100°20'10&quot;</td>
<td>Colluvial</td>
<td>30</td>
<td>13</td>
<td>56</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>60</td>
<td>11</td>
<td>62</td>
</tr>
<tr>
<td>San Rafael, N.L.</td>
<td>25°00'00&quot;</td>
<td>100°35'00&quot;</td>
<td>Alluvial</td>
<td>30</td>
<td>4</td>
<td>50</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>60</td>
<td>4</td>
<td>52</td>
</tr>
<tr>
<td>Las Hormigas, Coah.</td>
<td>24°58'32&quot;</td>
<td>100°51'00&quot;</td>
<td>Alluvial</td>
<td>30</td>
<td>16</td>
<td>54</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>60</td>
<td>25</td>
<td>40</td>
</tr>
<tr>
<td>Gómez Farías, Coah.</td>
<td>24°57'00&quot;</td>
<td>101°03'40&quot;</td>
<td>Alluvial</td>
<td>30</td>
<td>6</td>
<td>56</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>60</td>
<td>9</td>
<td>50</td>
</tr>
<tr>
<td>E. de Guzmán, Coah.</td>
<td>24°48'30&quot;</td>
<td>101°04'00&quot;</td>
<td>Alluvial</td>
<td>30</td>
<td>17</td>
<td>56</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>60</td>
<td>9</td>
<td>54</td>
</tr>
<tr>
<td>El Potosí-Pocitos, N.L.</td>
<td>24°47'00&quot;</td>
<td>100°18'30&quot;</td>
<td>Alluvial</td>
<td>30</td>
<td>9</td>
<td>58</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>60</td>
<td>3</td>
<td>68</td>
</tr>
<tr>
<td>C. de Rocamontes, Zac.</td>
<td>24°45'29&quot;</td>
<td>100°35'30&quot;</td>
<td>Alluvial</td>
<td>30</td>
<td>5</td>
<td>42</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>60</td>
<td>7</td>
<td>38</td>
</tr>
<tr>
<td>La Ventura O, Coah.</td>
<td>24°44'00&quot;</td>
<td>100°53'00&quot;</td>
<td>Alluvial</td>
<td>30</td>
<td>9</td>
<td>50</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>60</td>
<td>9</td>
<td>54</td>
</tr>
<tr>
<td>El Tokio, N.L.</td>
<td>24°41'00&quot;</td>
<td>100°14'13&quot;</td>
<td>Alluvial</td>
<td>30</td>
<td>9</td>
<td>54</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>60</td>
<td>11</td>
<td>56</td>
</tr>
<tr>
<td>N. Primavera, N.L.</td>
<td>24°37'30&quot;</td>
<td>100°12'21&quot;</td>
<td>Alluvial</td>
<td>30</td>
<td>13</td>
<td>64</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>60</td>
<td>7</td>
<td>66</td>
</tr>
<tr>
<td>San Urbet, N.L.</td>
<td>24°36'14&quot;</td>
<td>100°11'18&quot;</td>
<td>Alluvial</td>
<td>30</td>
<td>13</td>
<td>60</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>60</td>
<td>7</td>
<td>70</td>
</tr>
<tr>
<td>Loma Güera, S.L.P.</td>
<td>24°28'26&quot;</td>
<td>100°47'56&quot;</td>
<td>Alluvial</td>
<td>30</td>
<td>7</td>
<td>48</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>60</td>
<td>13</td>
<td>34</td>
</tr>
<tr>
<td>Refugio de Ibarra, N.L.</td>
<td>24°27'30&quot;</td>
<td>100°23'30&quot;</td>
<td>Alluvial</td>
<td>30</td>
<td>13</td>
<td>40</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>60</td>
<td>33</td>
<td>34</td>
</tr>
<tr>
<td>Rancho A, S.L.P.</td>
<td>24°07'30&quot;</td>
<td>100°55'30&quot;</td>
<td>Alluvial</td>
<td>30</td>
<td>25</td>
<td>50</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>60</td>
<td>5</td>
<td>54</td>
</tr>
</tbody>
</table>

...ble to prairie dogs. However, black-tailed prairie dogs (Cynomys ludovicianus) prefer areas of hard soils and low-growing vegetation in western Kansas (Bee et al. 1981), while half of the black-tailed prairie dog colonies in North Dakota were found on clay loam soils and several more were on silt loams (Reid 1954). In contrast, Koford (1958) found that black-tailed prairie dogs dig burrows in many types of soil; he therefore concluded that the distribution of black-tailed prairie dog colonies is not restricted by soil texture. Individuals of Cynomys
mexicanus observed during this study exhibited exploratory burrowing behavior in rocky ground or loose sands as described by King (1955) for black-tailed prairie dogs in undisturbed habitats. According to Osborn (1942), soil texture apparently had little influence upon the local distribution of black-tailed prairie dogs after a habitat disturbance, implying that they could build burrow systems in sandy or rocky soil if more favorable areas were not available.

Many researchers have noted that prairie dogs avoid steeply sloped areas because these areas did not facilitate the detection of predators (King 1955; Hoogland 1979; 1981; Cable & Timm 1988; Hoogland et al. 1988). However, prairie dogs may also avoid steeply sloped areas because these soils are generally very rocky due to soil erosion. During
the present study, soil was sampled in four small marginal Mexican prairie dog colonies (El Castillo, El Porvenir, Artecillas and C. del Toro) where cropland activity has pushed Mexican prairie dogs to establish in steep slopes in shallow (2 to 5 m) colluvial soils. Although it is not known if prairie dogs were previously established on those steeply sloped colluvial soils, it appears that even on steep slopes Mexican prairie dogs build their burrow systems in loamy soils.

Mexican prairie dogs also were found in a silt loam soil (El Potosí-Pocitos) that had once been tilled. Koford (1958) also found silt loam soil in two large black-tailed colonies towns where the land once had been used as a cropland. Therefore, these results would indicate that black-tailed and Mexican prairie dogs are able to colonize or re-colonize former croplands if those soils still provide favorable depth and structural support for the construction of burrow systems. However, detailed soil texture studies on former croplands colonized or re-colonized by prairie dogs are needed to support this hypothesis.

The only inactive colony (C. de Rocamontes) surveyed in this study exhibited a sandy loam soil. This colony may have been abandoned due to either direct or indirect effects of cattle overgrazing within the colony and in the adjacent desert scrub community (Mellink 1989; Ceballos et al. 1993; Treviño-Villarreal 1994). Erosion caused by cattle overgrazing may have changed the soil to a sandy loam texture. Therefore, abandonment of the C. de Rocamontes colony could be explained by the inability of sandy loam soils to be compact enough to sustain burrows.

Only one colony (Refugio de Ibarra) sampled exhibited a clay loam soil at 60 cm depth. The area where this colony is located is classified on a 1:50,000-scale topographical map from INEGI (Map code: G14 C75) as an area of potential flooding during long rainy periods because of the low porosity and high permeability. However, according to Reading & Matchett (in press), clay loam soils are well-drained, so they are less likely to flood.

Conclusions

In conclusion, it appears that Mexican prairie dogs establish their colonies primarily in loamy soils, although field observations indicate that Mexican prairie dogs carry out exploratory burrowing behavior in rocky, sandy and clayey soils.
ACKNOWLEDGMENTS

We would like to thank M. Corson, who provided the final version of Figure 1. A. García, A. Mora-Olivo, J. L. Mora-López, J. Sifuentes-S., E. Andarade-Limas, L. Corral-Pérez, S. Niño-Maldonado and C. Monreal-Guevara (Instituto de Ecología y Alimentos, Universidad Autónoma de Tamaulipas) helped with field work. Our special thanks go to our field assistants Quique and Paco from Ejido El Tokio, Galeana, Nuevo León. Lodging was provided during field work by G. Luna, El Tokio, Nuevo León.; L. M. González-Villarreal, Rancho Santa Ana, Vanegas, San Luis Potosí.; F. Alfaro-Calvillo, Ejido La Ventura, Coahuila.; J. Saldaña, Providencia, Nuevo León.; R. Avila-Salazar, El Salado, San Luis Potosí.; D. Bustos-Arevalo, Las Hormigas, Coahuila.; J. Gómez-Bustos, Gómez Farías, Coahuila. We also thank the Universidad Autónoma Agraria Antonio Narro for allowing us to carry out field work at the Rancho Los Angeles Rangeland Management facilities. The study was funded by the Sixteenth Joint Committee Meeting, Mexico-U.S.A. for the Conservation of Wildlife. Dr. E. Ezcurra from the Dirección General de Aprovechamiento Ecológico de los Recursos Naturales (DGAERN) at the Instituto Nacional de Ecología (INE), Secretaría de Desarrollo Social (SEDESOL), kindly provided permits No. 0866 and No. 05865 in support of the project titled "Investigaciones prioritarias para la creación de un área protegida para el perro mexicano de las praderas (Cynomys mexicanus)".

LITERATURE CITED


JT-V at: jtrevill@hotmail.com
PREDATION BY GREAT-HORNED OWLS ON BRAZILIAN FREE-TAILED BATS IN NORTH TEXAS

Kristie Jo Roberts, Franklin D. Yancey, II and Clyde Jones
The Museum and Department of Biological Sciences
Texas Tech University, Lubbock, Texas 79409-3191

Abstract.—A colony of Brazilian free-tailed bats (Tadarida brasiliensis) inhabiting a former railroad tunnel (Clarity Tunnel) at Caprock Canyons State Park, Floyd County, Texas, has been under regular observation since mid-March 1996. Numerous interactions between great-horned owls (Bubo virginianus) and the bats were observed from 23 May through 1 October 1996. Number of owls present, success rate of predation, and intervals between predation attempts were recorded and correlated with general weather conditions, exit times of the bats, and several other factors. Results from statistical analyses indicate that there are no significant differences in time intervals between successful and unsuccessful predation attempts. Based upon the time periods throughout the year that owls preyed upon the bats, one may conclude that Brazilian free-tailed bats may serve as an important and convenient source of food for great-horned owls during part of the year in North Texas.

Predation by great-horned owls (Bubo virginianus) on Brazilian free-tailed bats (Tadarida brasiliensis) has been documented upon the basis of both analyses of owl pellets (Twente 1956; Perry & Rogers 1964; Taylor 1964) and direct observations (Constantine 1948; Caire & Ports 1981). While several investigators have reported on the recovery of owl pellets containing remains of bats, there have been few publications on consistent, direct observations of predation by these birds on T. brasiliensis. Previous reports have been based on only one or two sightings; details of predation by great-horned owls on these bats are poorly understood (Caire & Ports 1981). Herein, are presented some details of the predation by these owls on a colony of bats.

STUDY SITE

An estimated 50,000 Brazilian free-tailed bats inhabit a former railroad tunnel (Clarity Tunnel) in Floyd County, Texas. Clarity Tunnel is managed by officials of Caprock Canyons State Park under the jurisdiction of the Texas Parks and Wildlife Department. The interior of the tunnel consists of a wooden frame built into a rock escarpment. The length of the tunnel is approximately 700 feet long. The bats roost mostly between the wooden infrastructure and the surrounding rock. The colony of bats in the tunnel has been under regular observation since mid-March of 1996. Great-horned owls appear to nest in the vicinity, perhaps on the eastern part of the rock embankment surrounding the tunnel. Additionally, while T. brasiliensis is generally considered a migratory species, some members of this colony remain in the
tunnel year-round.

**METHODS AND MATERIALS**

Observations of animals were made by use of night vision binoculars and standard binoculars, as well as the naked eye. Times and time intervals were recorded from readings of a standard wrist watch and stopwatch. Monitoring of the ends of the tunnel usually began about one hour prior to the estimated time of the flight of bats.

General weather conditions and exit times of bats from the tunnel were recorded. Activities of owls were monitored with regard to the number of attempts made to capture bats as they emerged from the tunnel. Attempts by owls to capture bats were classified as either successful or unsuccessful based upon whether or not an owl returned to a perch with a captured bat. Intervals of time were measured from the moment a bat was either captured or unsuccessfully attacked by an owl until the owl attempted a subsequent capture of a bat. All statistical analyses were conducted using SAS®.

**RESULTS AND DISCUSSION**

Interactions between great-horned owls and bats at Clarity Tunnel were observed from 23 May through 1 October 1996 (Table 1). Frequently, at about the time that the bats would begin to exit, one or more owls would appear on perches (usually trees) near the entrances to the tunnel.

Each assault that an owl made consisted of it flying directly into the column of bats exiting from tunnel, positioning its body vertically, extending the talons, and attempting to capture a bat. Following a successful capture of a bat, an owl would return to a perch (rock ledge or tree) where the owl would either consume the bat, fly out of sight for a time, or transfer the prey to another owl. If an attack on the bats was not successful, the owl either would make another attempt almost immediately or remain on the perch for an unspecified period of time (Table 2). Attempts to distinguish between the owls with regard to sex or age were unsuccessful because there were no notable size differences between the individual owls.

There was some relationship between the amount and success of the predation by owls in relation to the number of bats exiting at the same time from the tunnel. For example, the owls were more successful at predation when there was a dense column of bats flying from the tunnel than when the bats emerged erratically from the roost. Also, it was observed that when an owl attempted to attack a bat outside of the column, the owl was normally unsuccessful because the bat was able to
Table 1. Number of great-horned owls present, success rate of predation, general weather conditions, time of bat flight, and time of sunset at the Clarity Tunnel, Floyd County, Texas.

<table>
<thead>
<tr>
<th>Date</th>
<th>Owls</th>
<th>Success Rate</th>
<th>Weather</th>
<th>Flight Time</th>
<th>Sunset Time</th>
</tr>
</thead>
<tbody>
<tr>
<td>23 May</td>
<td>1</td>
<td>6 / 11</td>
<td>Clear</td>
<td>2050</td>
<td>2045</td>
</tr>
<tr>
<td>29 May</td>
<td>1</td>
<td>2 / 7</td>
<td>Cloudy / No Rain</td>
<td>2055</td>
<td>2049</td>
</tr>
<tr>
<td>30 May</td>
<td>0</td>
<td>—</td>
<td>Partly Cloudy</td>
<td>2108</td>
<td>2050</td>
</tr>
<tr>
<td>5 Jun</td>
<td>2</td>
<td>4 / 5</td>
<td>Clear</td>
<td>2050</td>
<td>2053</td>
</tr>
<tr>
<td>6 Jun</td>
<td>2</td>
<td>4 / 4</td>
<td>Cloudy/Windy</td>
<td>2051</td>
<td>2054</td>
</tr>
<tr>
<td>16 Jun</td>
<td>0</td>
<td>—</td>
<td>Rainy/No Wind</td>
<td>2117</td>
<td>2058</td>
</tr>
<tr>
<td>18 Jun</td>
<td>1</td>
<td>—</td>
<td>Cloudy</td>
<td>—</td>
<td>2059</td>
</tr>
<tr>
<td>20 Jun</td>
<td>1</td>
<td>—</td>
<td>Clear</td>
<td>2122</td>
<td>2059</td>
</tr>
<tr>
<td>21 Jun</td>
<td>1</td>
<td>1 / 2</td>
<td>Clear</td>
<td>2116</td>
<td>2059</td>
</tr>
<tr>
<td>24 Jun</td>
<td>2</td>
<td>3 / 6</td>
<td>Partly Cloudy/ Low Wind</td>
<td>2111</td>
<td>2100</td>
</tr>
<tr>
<td>25 Jun</td>
<td>1</td>
<td>0 / 1</td>
<td>Cloudy</td>
<td>2109</td>
<td>2100</td>
</tr>
<tr>
<td>26 Jun</td>
<td>0</td>
<td>—</td>
<td>Clear</td>
<td>2117</td>
<td>2100</td>
</tr>
<tr>
<td>16 Jul</td>
<td>0</td>
<td>—</td>
<td>Clear</td>
<td>2115</td>
<td>2057</td>
</tr>
<tr>
<td>17 Jul</td>
<td>1</td>
<td>—</td>
<td>Clear</td>
<td>—</td>
<td>2056</td>
</tr>
<tr>
<td>18 Jul</td>
<td>0</td>
<td>—</td>
<td>Clear</td>
<td>—</td>
<td>2056</td>
</tr>
<tr>
<td>1 Aug</td>
<td>1</td>
<td>—</td>
<td>Partly Cloudy/ No Wind</td>
<td>2107</td>
<td>2046</td>
</tr>
<tr>
<td>4 Aug</td>
<td>0</td>
<td>—</td>
<td>Partly Cloudy</td>
<td>2050</td>
<td>2043</td>
</tr>
<tr>
<td>5 Aug</td>
<td>1</td>
<td>—</td>
<td>Clear/Windy</td>
<td>—</td>
<td>2042</td>
</tr>
<tr>
<td>13 Aug</td>
<td>0</td>
<td>—</td>
<td>Clear</td>
<td>2057</td>
<td>2034</td>
</tr>
<tr>
<td>19 Aug</td>
<td>1</td>
<td>—</td>
<td>Clear</td>
<td>2039</td>
<td>2028</td>
</tr>
<tr>
<td>1 Sep</td>
<td>3</td>
<td>4 / 5</td>
<td>Cloudy/Windy</td>
<td>2015</td>
<td>2011</td>
</tr>
<tr>
<td>2 Sep</td>
<td>3</td>
<td>4 / 5</td>
<td>Partly Cloudy/ Windy</td>
<td>2015</td>
<td>2010</td>
</tr>
<tr>
<td>7 Sep</td>
<td>0</td>
<td>—</td>
<td>Cloudy/No Wind</td>
<td>2015</td>
<td>2003</td>
</tr>
<tr>
<td>14 Sep</td>
<td>3</td>
<td>2 / 2</td>
<td>Rain/No Wind</td>
<td>2005</td>
<td>1953</td>
</tr>
<tr>
<td>17 Sep</td>
<td>0</td>
<td>—</td>
<td>Windy</td>
<td>—</td>
<td>1949</td>
</tr>
<tr>
<td>21 Sep</td>
<td>1</td>
<td>—</td>
<td>Clear</td>
<td>—</td>
<td>1943</td>
</tr>
<tr>
<td>1 Oct</td>
<td>2</td>
<td>5 / 14</td>
<td>Windy/Clear</td>
<td>1933</td>
<td>1930</td>
</tr>
</tbody>
</table>

avoid being captured.

The number of owls that participated in predation on bats was somewhat variable, and success rates were greatest when more than one owl was involved (Table 1). However, it seemed that one owl was considerably more adept at capturing bats that the other owls, and another appeared especially inept. However, the inability to ascertain individual identifications on a regular basis necessitates the need for more observations.

No obvious and definite relationships were apparent between amount and success rate of predation by owls on bats in relation to some of the general weather conditions (Table 1). However, it seemed that owls were more successful at capturing bats during windy conditions that at some other times (Table 1).

Intervals of time between successful and unsuccessful captures of bats by owls varied (Table 2). As mentioned previously, successful captures
Table 2. Time intervals between predation attempts by great-horned owls on Brazilian free-tailed bats at the Clarity Tunnel, Floyd County, Texas.

<table>
<thead>
<tr>
<th>Date</th>
<th>Success Rate</th>
<th>Time Interval (Seconds)</th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>After Failure</td>
<td>After Success</td>
<td></td>
</tr>
<tr>
<td>23 May</td>
<td>6 / 11</td>
<td>30 - 60</td>
<td>60 - 90</td>
<td></td>
</tr>
<tr>
<td>29 May</td>
<td>2 / 7</td>
<td>10 - 95</td>
<td>70 - 105</td>
<td></td>
</tr>
<tr>
<td>5 Jun</td>
<td>4 / 5</td>
<td>71</td>
<td>68 - 240</td>
<td></td>
</tr>
<tr>
<td>21 Jun</td>
<td>1 / 2</td>
<td>180</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>24 Jun</td>
<td>3 / 6</td>
<td>105 - 120</td>
<td>15 - 75</td>
<td></td>
</tr>
</tbody>
</table>

\[p > |T| = 0.8245 \text{ with variances equal}\]

of bats resulted in other activities by the owls. However, after failed attempts to capture bats, the owls usually made other attempts at predation within one to one and a half minutes (Table 2). Despite the variation in the intervals between successful and unsuccessful attempts, there was no significant statistical difference \((p = 0.8245)\). On one occasion, an owl was observed to grasp its prey in a column of bats, but as the owl turned in flight, the bat escaped; the owl turned immediately back into the column and captured another bat.

Brazilian free-tailed bats may serve as an important source of food for great-horned owls (Twente 1956; Perry & Rogers 1964; Taylor 1964). However, inasmuch as predation by these owls on this species of bats was not consistent throughout the year, it seems that the bats may be alternative and convenient sources of food for great-horned owls, especially during the spring and the summer, in North Texas.

**ACKNOWLEDGMENTS**

Financial assistance was provided by the Natural Resources Program (David Riskind, Director), Texas Parks and Wildlife Department. Logistical support was provided by the personnel of Caprock Canyons State Park (Geoffrey Hulse, Superintendent). Assistance in the field was provided by Mary Ann Abbey and Richard W. Manning.

**LITERATURE CITED**


SAS Institute, Inc., Cary, NC, USA.


REPRODUCTION IN THE SONORAN MOUNTAIN KINGSNAKE
*LAMPROPELTIS PYROMELANA* (SERPENTES: COLUBRIDAE)

Stephen R. Goldberg
Department of Biology, Whittier College
Whittier, California 90608

Abstract.—Gonadal tissue was examined in 34 museum specimens of *Lampropeltis pyromelana* collected from Arizona, New Mexico and Sonora, México. The results of this examination supports the premise that this species of kingsnake exhibits a reproductive cycle in which sperm formation occurs in late summer/autumn and is stored overwinter; mating occurs in the spring.

The Sonoran mountain kingsnake, *Lampropeltis pyromelana*, occurs from central Utah and eastern Nevada south in the mountains of Arizona and southwest New Mexico to southern Chihuahua, México; it is a mountain dweller (850-2800 m elevation) and ranges from piñon/juniper woodland to pine/fir forest (Stebbins 1985). There are only brief accounts of reproduction for this species (Stebbins 1954; 1985; Wright & Wright 1957; Zweifel 1980; Tanner & Cox 1981; Painter 1985; Behler & King 1988; Williamson et al. 1994; Rossi & Rossi 1995). Other aspects of the biology of this species are summarized in Tanner (1983). The purpose of this investigation is to report on a histological examination of gonads from *L. pyromelana* in order to provide information on the reproductive cycle.

**METHODS AND MATERIALS**

Reproductive data presented is based upon an examination of 34 museum specimens (17 male, Mean Snout-Vent Length, SVL = 599.1 mm ± 20.1 SE, 443-745 mm range and 17 female, Mean SVL = 594.7 mm ± 20.0 SE, 475-735 mm range) of *L. pyromelana* collected from Arizona, New Mexico and Sonora, México. The left gonad and a portion of the male kidney were removed for histological examination, embedded in paraffin and sectioned at 5 μm. Slides were stained with Harris’ hematoxylin followed by eosin counterstain. Testes slides were examined to determine the spermatogenic stage of the male cycle; ovary slides were examined for the presence of yolk deposition (vitellogenic granules). Histology slides are deposited in the herpetology collection of the Natural History Museum of Los Angeles County.

**Material examined.**—Specimens examined are listed by county from herpetology collections at the Natural History Museum of Los Angeles
County (LACM), Museum of Southwestern Biology (MSB) and the University of Arizona (UAZ).

ARIZONA: COCHISE COUNTY, eight specimens (UAZ 25109, 30625, 34696, 42066, 42071, 42074, 43109, 48860); COCONINO COUNTY, two specimens (LACM 20322; UAZ 37827); GILA COUNTY, two specimens (UAZ 25111, 25117); MOHAVE COUNTY one specimen (UAZ 14654); PIMA COUNTY, four specimens (LACM 138156; UAZ 25114, 25119, 42063); SANTA CRUZ COUNTY three specimens (UAZ 41236, 42058, 42061); YAVAPAI COUNTY, one specimen (UAZ 25112).

NEW MEXICO: CATRON COUNTY, two specimens (MSB 416, 26397); GRANT COUNTY, one specimen (MSB 60123); HIDALGO COUNTY, five specimens (LACM 2463; MSB 4192-4193, 25360, 48880, 49251).

MÉXICO: SONORA, four specimens (LACM 127794; UAZ 28177, 38655, 47792).

RESULTS AND DISCUSSION

Data on the male *L. pyromelana* testicular cycle are presented in Table 1. Testicular histology was similar to that reported in the colubrid snakes *Masticophis taeniatus* and *Pituophis melanoleucus* by Goldberg & Parker (1975). In the regressed testes, seminiferous tubules contained spermatogonia and Sertoli cells. During recrudescence there was renewal of spermatogenic cells characterized by spermatogonial divisions; primary spermatocytes, secondary spermatocytes and spermatids were occasionally present. In spermiogenesis, metamorphosing spermatids and sperm were present.

It appears (Table 1) spermiogenesis (sperm formation) occurred in late summer/early autumn. The smallest male to undergo spermiogenesis measured 443 mm SVL. Sperm is apparently stored over-winter in *L. pyromelana* as the vasa deferentia of three May males with regressed testes contained sperm. Sperm was present in the vasa deferentia of six August-September males and two October males with regressed testes. This suggests the *L. zonata* testicular cycle is aestival (sensu Saint Girons 1982) with sperm stored in the vas deferens through winter and mating in the spring. Kidney sexual segments were enlarged and contained secretory granules in May males which had regressed testes and sperm in the vasa deferentia, as well as in other spermiogenic males. Johnson et al. (1982) reported elevated blood testosterone levels coincided with hypertrophy of the kidney sexual segment in the cotton-
Table 1. Monthly distribution of conditions in seasonal testicular cycle of Lampropeltis pyromelana. Values shown are the numbers of males exhibiting each of the three conditions.

<table>
<thead>
<tr>
<th>Month</th>
<th>N</th>
<th>Regressed</th>
<th>Recrudescence</th>
<th>Spermiogenesis</th>
</tr>
</thead>
<tbody>
<tr>
<td>May</td>
<td>4</td>
<td>3</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>June</td>
<td>2</td>
<td>1</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>July</td>
<td>2</td>
<td>1</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>August</td>
<td>4</td>
<td>0</td>
<td>1</td>
<td>3</td>
</tr>
<tr>
<td>September</td>
<td>3</td>
<td>0</td>
<td>0</td>
<td>3</td>
</tr>
<tr>
<td>October</td>
<td>2</td>
<td>2</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>

mouth Agkistrodon piscivorous. This would agree with reports of L. pyromelana mating in the spring (Stebbins 1954; Painter 1985; Behler & King 1988). The presence of sperm in the vasa deferentia and granules in the kidney sexual segments of males from October raises the possibility that some L. pyromelana mating may also occur in the fall. Goldberg (1995) reported similar timing for the testis cycle of the California mountain kingsnake Lampropeltis zonata.

Histological examination of ovaries from 16 females (May N = 1; July = 2; August = 6; September = 3; October = 4) did not reveal any reproductive activity (yolk deposition or enlarged follicles) nor were oviductal eggs present. Thirteen of these were from a time (August-October) when females would not have been expected to be reproducitively active. No histology was done on the ovary of one female (SVL = 612 mm) collected 8 June which contained three enlarged follicles (7-9 mm diameter) indicating a clutch size of three eggs. This is within the range of other reports of L. pyromelana clutch sizes in the literature: 3-8 eggs laid in middle to late spring (Williamson et al. 1994); 3-6 eggs laid June to July (Stebbins 1985; Behler & King 1988; Rossi & Rossi 1995); 3-6 eggs, mean 4.4 eggs (Zweifel 1980); 5 eggs (Tanner & Cox 1981); 6 eggs (Stebbins 1954).

CONCLUSIONS

Lampropeltis pyromelana appears to exhibit a reproductive cycle similar to that of other North American colubrid snakes (see Goldberg & Parker 1975) in which sperm formation occurs in late summer/autumn and is stored overwinter in the vas deferens; mating occurs in the spring. The related California mountain kingsnake L. zonata appears to have a similar reproductive cycle (Goldberg 1995).
ACKNOWLEDGMENTS

I thank Robert L. Bezy, Natural History Museum of Los Angeles County, Charles H. Lowe, The University of Arizona and Howard L. Snell, Museum of Southwestern Biology, University of New Mexico for permission to examine specimens of *L. pyromelana*. Estella J. Hernandez assisted with histology.

LITERATURE CITED


SRG at: sgoldberg@whittier.edu
A SELF STABILIZING ALGORITHM FOR SHORTEST PATH TREES

A. Kazmierczak
Department of Computer Science, University of Texas at Tyler
Tyler, Texas 75799

Abstract.—The literature on distributed algorithms has seen a number of works on self stabilizing algorithms. This paper presents a self stabilizing algorithm for shortest path trees. The algorithm allows a network to recover from unexpected disturbances without external intervention. Self stabilization can be used when dealing with communication networks where the criterion for message routing is the path of least cost.

Self stabilizing algorithms are receiving much interest in the recent research literature (Brown et al. 1989; Burns & Pachl 1989; Dolev et al. 1990; Kurijer 1979). They have addressed a variety of situations, including leader election (Dolev et al. 1991; Flatebo & Datta 1991), finding a maxima (Lin & Ghosh 1991), graph coloring (Ghosh & Karaata 1991), maximal matching (Hsu & Huang 1992), and distributed reset (Arora & Gouda 1990). Algorithms have been designed to be memory efficient (Afek et al. 1990) and adaptive (Anagnostou et al. 1992).

Several algorithms are designed to work on graphs with a restricted topology, such as rings (Burns & Pachl 1989; Israeli & Jalfon 1990) and trees (Chen et al. 1991; Huang & Chen 1992). The tree structure is of special interest to message passing systems because of its importance in routing tables for the underlying communications network. In this context, the most important structures are shortest path (Ramarao & Venkatesan 1992) and minimum weight spanning trees (Gallager et al. 1983). Both trees are very useful in the design of routing algorithms and tables for computer communication networks where the major criterion is the lowest cost route. The message complexity needed to make the network self stabilizing may be far more attractive than that required to rebuild the routing table. Self stabilization is entirely feasible in momentary power losses, such as in an electrical storm.

A shortest path tree is a spanning tree with the property that, along all the tree edges, each node has a minimum weighted distance to the
root. A self stabilizing algorithm gives the system the capability to automatically recover from errors, which gives it some degree of fault tolerance. The system can start in any state, even an illegitimate state. Within a finite number of moves, it converts to a legitimate state. Once in a legitimate state, the system remains there until an error condition occurs, when it will automatically initiate the algorithm and move to a legitimate state. The concept of self stabilization was introduced by Dijkstra (Dijkstra 1974) and has been applied to different tree structures (Chen et al. 1991; Huang 1989).

This paper presents a self stabilizing algorithm for a shortest path tree of a connected weighted undirected graph and contains sections addressing the following major topics: the network model, the algorithm, proof of correctness, message complexity and conclusions.

**THE NETWORK MODEL**

An asynchronous network is a point-to-point (or store-and-forward) communication network described by an undirected graph $G = (V, E, W)$. The set of nodes $V, |V| = n$, represents the processors of the network. The set of edges $E, |E| = m$, represents bidirectional non-interfering communication channels operating between processors. $W$ represents some characteristic of the communication lines, such as the congestion on the line. This weight information is particularly useful when designing distributed routing tables since no common memory is shared by nodes in the network.

Processors which are connected by a communications link are called neighbors. Each node processes messages received from its neighbors, performs some local processing, and sends messages to its neighbors. All these actions are assumed to be performed in negligible time compared to message transmission time. All messages have a fixed length and may carry only a bounded amount of information. Each message sent by a node to its neighbor arrives within some finite but undetermined time. Multiple messages sent by a node arrive in the order sent.

The proposed algorithm, which appears in a later section, maintains a shortest path spanning tree in which each node knows its parent in the tree, the distance to the root, and its level in the tree. It is assumed that each node has some "special property" (SP) that exists when the system
is in a legal and consistent state. In previous papers this special property has been called "breadth-first-search" (BFS) (Huang & Chen 1992) and "general spanning tree" (GSP) (Chen et al. 1991). In this paper the special property is called the "shortest path tree" (SPT) property. Hereafter, it will be referred to as SP. Whenever a node does not have the SP, it can make one of several moves into a state where it does. When a node does not have SP it has the "privilege". When a node attains SP, we say the node is stable. Many nodes may not have SP at one time and thus many nodes will have the privilege. Only one node is allowed to execute its privilege at any one time. Only one node is allowed to execute its privilege at one time because the change of state of the node may affect the rule another node needs to execute when it executes its privilege. The node chosen to execute its privilege makes a move into a new state. The new state is a function of the node’s old state and its neighbors’ states.

The proposed algorithm will always restore SP to all nodes in the network after a finite number of moves. All nodes eventually attain SP and the algorithm terminates with the system in a globally legal and consistent state. The system remains so until it is disturbed again. The node having the choice of which node gets to execute its privilege next is called the "daemon" and can either be distributed or centralized Ramarao & Venkatesan (1992). The proposed algorithm is based on a centralized daemon.

The proposed algorithm consists of a set of rules available at each node which tells it how to make moves. Each rule has two parts, the condition or privilege and the move. The condition is defined as a boolean function based on each node’s state and that of its neighbors. When the condition is true, the node has the privilege and may, if selected, make its move.

The existence of a central daemon is assumed. The set of nodes having the privilege next depends on the states resulting from the last move. The rules are atomic. No node is allowed to evaluate its condition and then wait for other nodes to move before making its move. After one node makes its move, it is up to the central daemon to select the next node to make a move.

In the proposed algorithm, each node \(i\) keeps three local variables:
$D(i)$, its distance to the root, which is the sum of the weights of edges of the shortest path tree; $L(i)$, its level; and $P(i)$, a pointer to its parent. The value of $D(i)$ remains in a range that is reasonable for the weights in the network. The value of $L(i)$ will be in the range \{0, \ldots , n - 1\}. The system is in a legitimate state if the parent pointers form a spanning tree of $G$ rooted at a node labelled $r$. Each node except the root has a distance that is equal to its parent's distance plus the weight of the edge to its parent. This weight is the smallest possible. Any other state is illegitimate.

The proposed algorithm is self stabilizing because the system can start in any illegitimate state and, regardless of the sequence of moves, will converge to a legitimate state. Each node determines its parent in the tree, its distance to the root, and its level in a finite number of moves. When the system reaches a legitimate state, the algorithm terminates. If the system again enters an illegitimate state, the algorithm is automatically restarted.

The proposed algorithm meets the following requirements:

1. In an illegitimate state, at least one node will have the privilege and one of these nodes is selected to make a move. If the system enters an illegitimate state as the result of any changes in the system, the algorithm is restarted with no outside intervention.

2. When the system enters a legitimate state, no node has the privilege and the algorithm terminates.

3. Starting from any initial state and applying an arbitrary rule each time, the system will enter a legitimate state after a finite number of moves.

It has been observed that showing a self stabilizing algorithm to be correct is sometimes a very difficult task (Dijkstra 1986; Kessels 1988). Kessels proposed a straightforward approach. First, show that the system can always make some move as long as the system is in an illegitimate state. Then, provide a bounded evaluation function whose value decreases after each move. This approach is used to prove the correctness of this algorithm.
THE ALGORITHM

A distributed system can be modeled by a connected undirected weighted graph $G(V, E, W)$. Node $r$ is selected as the root. The algorithm builds from $G$ a shortest path tree rooted at $r$ with each node knowing its distance from the root, its parent and its level.

For each node $i$, let $N(i)$ be the set of neighbors of $i$. Each node keeps the following variables:

- $D(i)$: the distance of $i$ from $r$
- $P(i)$: the parent of $i$
- $L(i)$: the level of $i$

where $D(i) \leq \infty$ and $P(i) \in N_i$, the symbol $\infty$ representing a distance larger than reasonably expected. The initial value of the variables is unpredictable. The root node always has $D(r) = 0$, and $L(r) = 0$.

The following rules construct a shortest path tree rooted at $r$. Throughout the tree, $D(i) = D(P(i)) + W(e_{P(i)}|i)$, where $W(e_{P(i)}|i)$ is the weight of the edge from node $i$ to its parent for any node $i$. To retain the property of being a shortest path tree, it is required that \[D(P(i)) + W(e_{P(i)}|i) = \min\{D(j) + W(e_{j}) \mid j \in N_i\}\].

The system is in a legitimate state when

\[SPT = (\forall i, i \neq r: D(P(i)) + W(e_{P(i)}|i) \wedge D(P(i)) + W(e_{P(i)})) \]

\[SPT = \min(\{D(j) + W(e_{j}) \mid j \in N_i\})\]

No rules apply to the root since it has constant depth and never changes state.

A node whose distance is not equal to its parents distance plus the weight of the edge to its parent should make a move by changing its distance, (rule $R0$). In a legitimate state, a node cannot be at distance $\infty$. If any node has a distance $\infty$, it cannot be a parent node. Any child of this node must make a move (rule $R1$). In a legitimate state, every node must have a parent with a distance that is shortest among all its neighbors. Therefore, a node having a parent not at the shortest distance must make a move (rule $R2$).
For any node other than the root, the following rules apply.

\[ R0: \quad \text{if } D(i) \neq D(P(i)) + W(e_{pi}) + \infty \lor L(i) \neq L(P(i)) + 1 \]
\[ \rightarrow D(i) = D(P(i)) + W(e_{pi}) \land L(i) = L(P(i)) + 1 \]

\[ R1: \quad D(i) \neq \infty \land D(P(i)) = \infty \lor L(P(i)) = n \lor L(i) = n \]
\[ \rightarrow D(i) = \infty \land L(i) = n \]

\[ R2: \quad \text{Let } k \in N_i \text{ be such that} \]
\[ D(k) + W(e_k) = \min\{D(j) + W(e_j) \mid j \in N_i\} \]
\[ \text{then} \]
\[ D(k) + W(e_k) < D(P(i)) + W(e_{pi}) \]
\[ \rightarrow P(i) = k \land L(i) = L(P(i)) + 1 \land D(i) = D(P(i)) + W(e_{pi}) \]

Figure 1 is an example of a connected weighted graph \( G(V, E, W) \). The set of nodes is \( V = \{a, b, c, d, e\} \) with node \( a \) the root. The weights of each edge are shown next to the edge. The distance of each node from the root is shown next to the node. The level of each node is shown in parentheses next to the node. The abbreviation "inf" is used to represent infinity, a distance far too large for the weights of the edges in the tree. The arrows on the edges show the parent pointers. The rules by which a node has the privilege are also shown. The rule marked by the asterisk is the rule selected for the next move. After seven moves, the system moves to a legitimate state. A different moving sequence may be applied, but the result would be the same shortest path tree.

PROOF OF CORRECTNESS

The algorithm must now meet the requirements stated in the network model section. By definition of the SPT property, the algorithm meets requirement 2.

The proof takes the following approach. Before SPT becomes true, some node has the privilege and may make a move, thus satisfying requirement 1. An evaluation function \( F \) over the states of the system will then be defined. When a node makes a move, the value of the function decreases. Thus, SPT will eventually evaluate to true. When SPT evaluates to true, the system is in a legitimate state. Therefore, the algorithm meets requirement 3. The rules are applied a finite number of times until the system reaches a legitimate state.
Define a "Correct Parent" (CP) pointer to be a pointer \( i \rightarrow P(i) \) if \( D(P(i)) \neq \infty, D(i) \neq \infty, \) and \( D(i) = D(P(i)) + W(e_{P(i)}) \). In any state, only CP pointers need to be considered. The nodes of the graph are partitioned into several sets, each set being a shortest path subtree. A CP set is defined as the set of nodes in each subtree.

For the initial state shown in Figure 1, the pointer \( b \rightarrow e \) is a CP pointer while \( c \rightarrow b, d \rightarrow b \) and \( e \rightarrow c \) are not. The nodes are partitioned into four trees defined by these pointers. Therefore, there are four disjoint CP sets. By definition, any node \( i \) with \( D(i) = \infty \) constitutes a CP set by itself and has its level set to \( n, L(i) = n \).

For each CP set \( S \) there is a directed spanning tree. Let \( i, i \in S \), be the node with the minimum distance in \( S \). The subtree is thus rooted at \( i \). According to the rules, only the root node of a subtree has the privilege at any time, for example, node \( b \) in the second tree in Figure 1. Therefore, let \( S^{(i)} \) denote the CP set rooted at \( i \), where \( L(i) \) is the level of \( i \). Continuing the example from Figure 1, the initial state set: \( S_{a}^{0} = \{ a \}, S_{c}^{5} = \{ c \}, S_{d}^{1} = \{ d \}, S_{e}^{1} = \{ e, b \} \).

That the algorithm satisfies requirement 1 is now ready to be proven.

**Theorem 1.**—Before the SPT property evaluates to true, some node \( i \) in the system has the privilege.

**Proof.**—Before the SPT property becomes true, there must exist some CP set \( S_{i}^{L(i)}, i \neq r \). Two cases are considered.

**Case 1:** \( D(i) \neq \infty \) for a CP set \( S_{i}^{L(i)}, i \neq r \). If \( D(P(i)) \neq \infty \), node \( i \) has the privilege by rule \( R0 \). If \( D(P(i)) = \infty \) node \( i \) has the privilege by rule \( R1 \).

**Case 2:** \( D(i) = \infty \) for every CP set \( S_{i}^{L(i)}, i \neq r \). There must exist at least one edge between a node \( j \) in \( S_{i}^{0} \) and some node \( i, i \neq r \) where \( S_{i}^{L(i)} = S_{i}^{j} = \{ j \} \), because \( G \) is connected. By definition, any node \( j \) in \( S_{i}^{0} \) must have \( D(j) < \infty \) and \( W(e_{j}) \) finite. Node \( i \) must have the privilege by rule \( R2 \).

In both cases, node \( i \) has the privilege.

In the evaluation function of \( F \), any state can be arbitrarily chosen.
Let $t_k$, $0 \leq k \leq n$, be the number of CP sets $S_i^{L(i)}$ such that $L(i) = k$. The evaluation function for this state is defined by

$$t_0, t_1, t_2, \ldots, t_n, 0 \leq t_i \leq n.$$ 

This is why it is necessary to keep track of the nodes level. It allows the use of an evaluation function that has a bounded length. In Figure 1, the level of each node is shown in parentheses.
Table 1. Evaluation function for example of Figure 1.

<table>
<thead>
<tr>
<th>Step</th>
<th>$S_a^0$</th>
<th>$S_b^0$</th>
<th>$S_c^0$</th>
<th>$S_d^0$</th>
<th>$S_e^0$</th>
<th>$F$</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>${a}$</td>
<td>${e, b}$</td>
<td>${d}$</td>
<td>${c}$</td>
<td></td>
<td>$(1,2,0,0,0,1)$</td>
</tr>
<tr>
<td>1</td>
<td>${a}$</td>
<td>${d}$</td>
<td>${b}$</td>
<td>${e}$</td>
<td>${c}$</td>
<td>$(1,1,1,0,0,2)$</td>
</tr>
<tr>
<td>2</td>
<td>${a}$</td>
<td>${b, d}$</td>
<td>${e}$</td>
<td>${c}$</td>
<td></td>
<td>$(1,0,1,0,0,2)$</td>
</tr>
<tr>
<td>3</td>
<td>${a}$</td>
<td>${d}$</td>
<td>${b}$</td>
<td>${e}$</td>
<td>${c}$</td>
<td>$(1,0,1,0,0,3)$</td>
</tr>
<tr>
<td>4</td>
<td>${a, b}$</td>
<td>${d}$</td>
<td>${c}$</td>
<td>${e}$</td>
<td></td>
<td>$(1,0,0,1,0,2)$</td>
</tr>
<tr>
<td>5</td>
<td>${a, b, c}$</td>
<td>${d}$</td>
<td>${e}$</td>
<td></td>
<td></td>
<td>$(1,0,0,1,0,1)$</td>
</tr>
<tr>
<td>6</td>
<td>${a, b, c, d}$</td>
<td>${e}$</td>
<td></td>
<td></td>
<td></td>
<td>$(1,0,0,0,0,1)$</td>
</tr>
<tr>
<td>7</td>
<td>${a, b, c, d, e}$</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>$(1,0,0,0,0,0)$</td>
</tr>
</tbody>
</table>

The values of $F$ are measured and compared lexicographically: $(a_0, a_1, \ldots) > (b_0, b_1, \ldots)$ if there exists some $j$ such that $a_i = b_i$ for $0 \leq i \leq j$ and $a_j > b_j$. The evaluation function is a bounded function with maximum value $(1, n-1, 0, \ldots, 0)$ and minimum value $(1, 0, \ldots, 0)$. For any initial state $L(i) = 0, i \in s^0$ with all other nodes having a level greater than 0, $t_0 = 1$ for all system states.

Continuing with the example from Figure 1, Table 1 shows how the evaluation function decreases as the system moves towards a legitimate state. Step 0 is for the initial step. Subsequent steps correspond to the moves shown in Figure 1.

From the example in Table 1, the system converges towards the legitimate state where $F = (1, 0, \ldots, 0)$. The system moves towards a single CP set $S_r^0$. Each time a node makes a move, the evaluation function decreases.

**Theorem 2.**—Each time a node applies one of the rules $R0$, $R1$, or $R2$, the evaluation function decreases.

**Proof.**—Each of the rules $R0$, $R1$, $R2$ will be applied by the root node $i$ of some CP set $S_i^{L(i)}$.

Case $R0$: If rule $R0$ is applied by node $i$, it gets appended to some existing CP set. If the set contained more than node $i$, the CP set will be split into one or more such sets with $L(j) = L(i) + 1$ after the move. In this case, $t_j$ decreases by one and $t_j$ may increase.

Case $R1$: If rule $R1$ is applied by node $i$, it becomes a CP set by
itself. If $S_i^{L(i)}$ contained more than node $i$, the rest of the set will be split into one or more sets with $L(j) = L(i) + 1$ after the move. In this case, $t_i$ decreases by one and $t_j$ may increase.

Case $R2$: If rule $R2$ is applied by node $i$, the set node $i$ is appended to an existing CP set. In this case $t_i$ decreases. In all cases, the evaluation function decreases.

**Theorem 3.**—The system converges to a legitimate state in a finite number of moves.

**Proof.**—The largest initial value of the evaluation function is finite, as is the smallest value. Hence, $F$ can be decreased only a finite number of times. Since each application of one of the rules causes $F$ to decrease, the rules can be applied only a finite number of times. When $F$ reaches its smallest value, the predicate SPT becomes true. By definition, when SPT becomes true, the system is in a legitimate state.

**Message Complexity**

This section determines the worst case message complexity of centralized daemon for self stabilizing algorithms on spanning trees. The worst case can be defined as all nodes in the tree except the root being disturbed and losing SP.

A centralized daemon is defined as one in which only the root can decide which node makes the next move. For the nodes to re-establish SP and become stable, all nodes must eventually send a message to the root requesting permission to make a move and receive the necessary permission.

To ease analysis, the following two simplifying assumptions are made. Only one move is necessary to stabilize the node making the move. Nodes closer to the root are stabilized first.

Since the root is not perturbed, it retains information about its children. The root starts by sending a REQUEST message to each child. Each child will respond with a NEED message. The root then chooses one child and sends it a PERMISSION message, giving the node permission to make its move. This is repeated for each child.
The processing for an arbitrary node is described. A node receiving PERMISSION makes a move and returns to a stable state. The node then sends a STABLE message to all its neighbors except the neighbor from which it received PERMISSION. Nodes receiving STABLE examine their states. If they have already made moves, they return NO-NEED messages. If they need to make moves, they send NEEDs.

After a stable node receives messages from its neighbors, it checks to see if it has received NEEDs. If so, it sends a NEED toward the root. Otherwise it sends a NO-NEED. When these messages reach the root, it chooses one neighbor’s NEED and sends a PERMISSION. PERMISSION is sent down the tree until it reaches the node that sent the NEED. The node executes its privilege and moves into a stable state.

When all nodes are in a stable state, determined when the root receives NO-NEEDs from all its children, the root terminates the algorithm.

Stabilizing the tree using a centralized daemon requires $O(n^2)$ messages. This approach is the same used in (Ramarao & Venkatesan 1992) for finding and updating shortest path trees and provides the following result.

**Theorem 4.**—A centralized daemon for a self stabilizing algorithm on a tree has a message complexity of $O(n^2)$.

**CONCLUSIONS**

A self stabilizing algorithm for a shortest path spanning tree has been presented. Self stabilizing algorithms for tree structures can be very useful for maintaining the information necessary to route messages in a communication network.

**LITERATURE CITED**


AK at: akazmier@mail.uttyl.edu
PLANT CELL WALL DEGRADING ENZYMES PRODUCED BY THE PHYTOPATHOGENIC FUNGUS
SCLEROTIUM BATATICOLA

Jacobo Ortega
Biology Department, The University of Texas - Pan American,
Edinburg, Texas 78539.

Abstract.—The extracellular plant cell wall degrading enzymes of Sclerotium bataticola and the effect of different carbon sources on the production of these enzymes were investigated. Cellobiohydrolase and xylanase activities were detected in fluids collected from cultures containing xylan and sodium carboxymethyl cellulose (CMC) as carbon sources and enzyme inducers. Production of endoglucanase was induced by all carbon sources tested. The highest activities of endoglucanase and xylanase were measured in fluids collected from cultures containing xylan. Results of this study indicate that Sclerotium bataticola produces constitutively small amounts of endoglucanase.

Direct penetration of susceptible hosts by the infective hyphae of phytopathogenic fungi is facilitated by the production of cutinases (Agrios 1988), followed by softening or disintegration of host tissues by plant cell wall degrading enzymes produced by the pathogen (Kenaga 1974; Agrios 1988). Production of these enzymes is induced in many plant pathogenic fungi when these organisms are grown on media containing various sugar polymers (Cooper & Wood 1973; Pegg 1981; Ortega 1990).

Sclerotium bataticola Taub. is the sclerotial and mycelial stage of Macrophomina phaseolina (Tassi.) Goid. This pathogen attacks many field crop plants of economic importance. It causes charcoal rot of corn, cotton, sorghum, peanuts, soybeans and sugar beets (Nyvall 1989). Sclerotium bataticola also causes ashy stem blight of beans, root rot of chickpea, collar rot of coffee, and charcoal rot of potatoes (Cook 1978). The main objectives of this work were to determine the components of extracellular plant cell wall degrading enzymes of S. bataticola and to determine the effects of the carbon source on the production of these enzymes by the test fungus.

METHODS AND MATERIALS

Organism and culture conditions.—Stock cultures of S. bataticola were maintained on PDA slants (Difco, B13). The fungus was previously grown in 250-ml flasks with 125 ml of a medium containing: 0.2 g/l MgSO₄.7H₂O, 0.1 g/l Ca(NO₃)₂.4H₂O, 1 g/l Peptone, 2 g/l yeast
extract, and 20 g/l glucose in sodium citrate buffer at pH 5.0. After
four days growth at 26°C, 5.0 ml of mycelium inoculum was washed
twice in distilled water and then transferred to the cellulolytic growth
medium. The medium for the production of cellulases contained: 2.5 g/l
NH₄NO₃, 1.0 g/l K₂PO₄, 0.5 g/l MgSO₄, 0.5 g/l Ca(NO₃)₂·4H₂O, 0.72
mg/l Fe(NO₃)₃·9H₂O, 0.44 mg/l ZnSO₄·7H₂O, 2.0 mg/l MnSO₄·4H₂O,
0.40 mg/l ZnCl₂, and 10 g/l carbohydrate. The carbohydrates used as
carbon sources and enzyme inducers were: sodium carboxymethyl
cellulose (CMC, type 7HF, Aqualon Company), microcrystalline
cellulose and xylan (Sigma Chemical Company). The control cultures
had glucose as the sole carbon source. The pH of the growing medium
was adjusted to 5.0 with 0.1N KOH. Incubation of the cultures was
carried out for eight days in covered 250-ml flasks on an orbital shaker
at 80 rpm and 26°C.

Enzyme preparation and assays.—Samples of the culture fluids were
collected at intervals of 24 hours during the first four days and then after
seven and eight days of growth in the liquid medium. The culture fluids
were centrifuged (3850 x G for 20 minutes at 10°C) to obtain a clear
supernatant. The supernatant was subsequently used for the determina-
tion of extracellular enzyme activity. For simplification, the collected
supernatant is hereafter referred to as the enzyme. All tests were
replicated four times.

Cellobiohydrolase.—Cellobiohydrolase (1,4-B-D-glucan cellobiohy-
drolase, EC 3.2.1.91) activity was measured by combining in separate
test tubes 1.0 ml of enzyme with 25 mgs of microcrystalline cellulose
(type 50, Sigma Chemical Co.) in 1.0 ml of 0.05 M sodium citrate
buffer (pH 5.0) and incubating the reaction mixture for 120 minutes at
40°C. The tubes were stirred several times during incubation. After
centrifugation, the concentration of reducing sugar in the supernatant
was determined using the hydroxybenzoic acid hydrazide reagent (Lever
1972).

Endoglucanase.—Endoglucanase (CM-cellulase, carboxymethyl cel-
lulase, EC 3.2.1.4) activity was measured by combining 1.0 ml of
enzyme with 10 mgs of sodium carboxymethyl cellulose (type 7HF,
Aqualon Company.) in 2.0 ml of 0.05 M sodium citrate buffer, pH 5.0.
The reaction mixture was incubated at 40°C for 120 minutes. The
concentration of reducing sugar in the reaction mixture was determined
using the hydroxybenzoic acid hydrazide reagent (Lever 1972).
Table 1. Specific activities\(^1\) of cell wall degrading enzymes produced by *Sclerotium bataticola* grown for eight days in liquid medium with different carbon sources.

<table>
<thead>
<tr>
<th>Carbon source</th>
<th>Cellobiohydrolase</th>
<th>Endoglucanase</th>
<th>Xylanase</th>
<th>Extracellular protein (^2)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Microcrystalline cellulose</td>
<td>0.0*</td>
<td>4.87 ± 0.04</td>
<td>0.0*</td>
<td>0.78 ± 0.03</td>
</tr>
<tr>
<td>CMC</td>
<td>14.92 ± 0.19</td>
<td>39.44 ± 0.46</td>
<td>58.91 ± 1.30</td>
<td>0.32 ± 0.12</td>
</tr>
<tr>
<td>Xylan</td>
<td>15.51 ± 0.20</td>
<td>27.65 ± 0.40</td>
<td>54.65 ± 0.79</td>
<td>6.25 ± 0.23</td>
</tr>
<tr>
<td>Glucose</td>
<td>0.0*</td>
<td>0.0*</td>
<td>0.0*</td>
<td>0.32 ± 0.12</td>
</tr>
</tbody>
</table>

\(^1\) Micromoles of glucose, xylose or their reducing sugar equivalent/min/ml/mg of protein. Mean ± SD of four replications.

\(^2\) mg/ml.

* 0.0 no enzyme activity detected.

**Xylanase.**—Xylanase (EC 3.2.1.32) activity was measured by combining 10 mgs of xylan in 1.0 ml of 0.05 M sodium citrate buffer, pH 5.0, with 1.0 ml of enzyme. The reaction mixture was incubated at 40°C for 60 minutes. After centrifugation, the concentration of reducing sugars in the supernatant fluid were determined using the hydroxybenzoic acid hydrazide reagent (Lever 1972).

**Protein determination.**—Extracellular protein in the crude supernatant was determined with the BCA reagent (Pierce Chemical Company) using bovine serum albumin as a standard.

**Data analysis.**—The results were expressed as units of specific enzyme activity and represent means plus or minus the standard deviation of four replications. One unit of specific activity (Usp) was calculated as the amount of enzyme that liberated one micromole of glucose, xylose or its reducing sugar equivalent per minute per ml of enzyme per mg of extracellular protein under the conditions of the assay. Statistical analyses of experimental data were made using the Student’s *t*-test.

**RESULTS**

**Cellobiohydrolase.**—Production of cellobiohydrolase was induced in cultures that contained CMC and xylan. No cellobiohydrolase activity was detected in fluids collected from cultures that had microcrystalline cellulose or glucose as the sole carbon source (Table 1). Maximum cellobiohydrolase specific activity (82.50 Usp, Fig. 1c) was measured in fluids collected from cultures containing xylan one day after the
Figure 1. Production of cellobiohydrolase (■), endoglucanase (●) and xylanase (▲) by *S. bataticola* grown in liquid medium containing (a) microcrystalline cellulose, (b) CMC, (c) xylan and (d) glucose as the carbon source.

Inoculation of the liquid medium. This activity declined to 15.51 Usp measured in the fluids that were harvested after eight days of cultivation of the test fungus (Table 1). Activity of this enzyme was not detected in cultures containing CMC as the carbon source until the fungus had
grown for seven days in the liquid medium (Fig. 1b). After eight days of cultivation in the medium containing CMC, cellbiohydrolase activity was estimated in 14.92 Usp (Table 1).

Endoglucanase.—Production of endoglucanase by *S. bataticola* was induced in all the liquid cultures of this investigation (Fig. 1a, 1b, 1c and 1d). However, endoglucanase activity was not detected in fluids from cultures containing microcrystalline cellulose as the carbon source until the seventh day of growth in the liquid medium (Fig. 1a).

The activity of this enzyme in fluids from cultures containing CMC as the enzyme inducer was detected after the fungus had grown for three days in the medium (Fig. 1c). In these cultures, maximum endoglucanase activity (39.44 Usp) was determined after eight days of growth (Table 1).

*Sclerotium bataticola* was induced to produce endoglucanase in cultures containing xylan as the carbon source (Fig. 1c). The production of this enzyme began during or shortly after the first day of growth of the fungus. In cultures containing xylan, maximum endoglucanase production (78.41 Usp) was measured in fluids collected after three days of growth (Fig. 1c). However, endoglucanase activity declined to 27.51 Usp after eight days of growth in the medium containing xylan.

Production of endoglucanase in cultures containing glucose as the carbon source was, most probably, constitutive. Endoglucanase activity was detected in these cultures during the first four days of cultivation (Fig 1d). Maximum activity (22.51 Usp) of this enzyme in fluids from cultures with glucose as the enzyme inducer was detected after the second day of growth. However, endoglucanase activity could not be detected in these cultures after the seventh day of cultivation (Fig. 1d).

Xylanase.—Production of xylanase by the test fungus was induced in cultures containing CMC and xylan (Fig. 1b and 1c, respectively). Maximum production of this enzyme (343.18 Usp) was measured in fluids collected one day after inoculation from cultures that had xylan as carbon source (Fig. 1c). Xylanase activity declined steadily in fluids from cultures containing xylan from 343.18 Usp to 54.65 Usp measured in fluids collected after eight days of cultivation (Table 1). Xylanase activities in cultures containing CMC as carbon source were detected in fluids collected two days after inoculation (Fig. 1b). The activities of this enzyme increased from 12.36 to 58.91 Usp measured in fluids harvested after eight days of growth in the liquid medium (Table 1).
Microcrystalline cellulose or glucose did not induce the production of xylanase under the condition of this investigation (Table 1).

**Discussion**

Maximum production of cellobiohydrolase by the test fungus was measured in fluids from cultures containing xylan. Cellobiohydrolase activity in these cultures declined considerably (18.8%) during the course of this investigation (Fig. 1c). However, the highest amount of extracellular protein accumulated during eight days of cultivation of the fungus, was measured in the fluids of cultures containing xylan (Table 1). In studies of other plant pathogenic fungi, it was found that xylan used as a carbon source induced the production of cellobiohydrolase in liquid cultures of *Fusarium oxysporum* f. sp. *lycopersici* (cf. Ortega 1990) and *Exserohilum rostratum* (cf. Ortega 1993a).

No detectable cellobiohydrolase activity was found in culture fluids of *S. bataticola* grown in media containing microcrystalline cellulose as enzyme inducer (Table 1). However, it was earlier found that microcrystalline cellulose can induce the production of cellobiohydrolase in the plant pathogens *F. oxysporum* f. sp. *lycopersici* (cf. Ortega 1990), *Alternaria brassicae* (cf. Ortega 1992), *E. rostratum* (cf. Ortega 1993a), and *Curvularia senegalensis* (cf. Ortega 1993b). The absence of cellobiohydrolase activity in fluids collected from cultures containing glucose as the sole carbon source suggests that *S. bataticola* did not produce cellobiohydrolase constitutively under the conditions of this investigation. Previous studies of the plant pathogens *A. brassicae* (cf. Ortega 1992) and *E. rostratum* (cf. Ortega 1993a) revealed that these fungi produced constitutively small amounts of cellobiohydrolase.

The highest activity of endoglucanase was measured in fluids from cultures of *S. bataticola* containing xylan. In these cultures endoglucanase activity declined after the third day of growth (Fig. 1c). The induction of endoglucanase in cultures containing xylan as carbon source was reported in previous studies of the plant pathogens *F. oxysporum* f. sp. *lycopersici* (cf. Ortega 1990), *A. brassicae* (cf. Ortega 1992) and *E. rostratum* (cf. Ortega 1993a). Whereas the activity of endoglucanase evaluated in fluids collected from cultures containing CMC incremented during the duration of this investigation (Fig. 1b), the amount of total protein accumulated in the same cultures was only minimal (Table 1).

Production of endoglucanase in the control cultures having glucose as carbon source seems to indicate that the test fungus produced constitu-
tively a certain amount of endoglucanase during the first four days of growth in the liquid medium. The activity (21.03 Usp, Fig. 1d) of this enzyme measured in the fluids of the control cultures after the second day of growth was 26.8% of the maximum endoglucanase activity (78.41 Usp, Fig. 1c) evaluated in this investigation. Previous studies of the plant pathogens *F. oxysporum* f. sp. *lycopersici* (cf. Ortega 1990), *A. brassicaceae* (cf. Ortega 1992) and *E. rostratum* (cf. Ortega 1993a) revealed that these fungi can produce endoglucanase constitutively.

Maximum xylanase activity by *S. bataticola* was detected in fluids from cultures with xylan as carbon source and enzyme inducer (Fig. 1c). Whereas xylanase activity decreased in these cultures during the course of this investigation, the amount of total protein accumulated after eight days of growth was the highest measured in this investigation (Table 1).

It was reported before that xylan also induced xylanase secretion in liquid cultures of *F. oxysporum* f. sp. *lycopersici* (cf. Ortega 1990), *A. brassicaceae* (cf. Ortega 1992) and *E. rostratum* (cf. Ortega 1993a). No xylanase activities were detected in fluids collected from cultures containing microcrystalline cellulose or glucose as enzyme inducers (Fig. 1a and 1c respectively), corresponding with the small amounts of total protein measured in the fluids of cultures containing these carbon sources (Table 1). Most probably, the protein measured in fluids from cultures containing microcrystalline cellulose or glucose was not xylanase. However, it was reported before that microcrystalline cellulose induced the production of xylanase in the phytopathogens *F. oxysporum* f. sp. *lycopersici* (cf. Ortega 1990), *A. brassicaceae* (cf. Ortega 1992) and *E. rostratum* (cf. Ortega 1993a). Apparently *S. bataticola* did not synthesized xylanase in a constitutive manner under the conditions of this investigation. It has been shown that xylanase was produced constitutively by the phytopathogenic fungi *Rhizoctonia solani* (cf. Robson et al. 1989) and *E. rostratum* (cf. Ortega 1993a).

**Summary**

Secretion of cellobiohydrolase and xylanase was induced in liquid cultures of *S. bataticola* when CMC or xylan are used as sole sources of carbon and enzyme inducers. Whereas all carbon sources induced the production of endoglucanase and xylanase, the highest production of these enzymes was measured in the fluids collected from cultures containing xylan.
LITERATURE CITED


JO at: jortega@panam.edu
AN ASSAY FOR THE DETERMINATION OF A BINDING CONSTANT, $K_d$, FOR THE PHYSIOLOGICAL ELECTRON TRANSFER COMPLEX BETWEEN CYTOCHROME F AND PLASTOCYANIN

Kelly A. McKay and Michele R. Harris
Department of Chemistry, Stephen F. Austin State University
Nacogdoches, Texas 75962

Abstract.—This study reports the development of an assay for the determination of a binding constant, $K_d$, for the electron transfer complex between cytochrome f and plastocyanin. Preliminary results indicate a $K_d$ of 4.1 μM in 5 mM sodium phosphate - 0.1% SDS buffer at pH 7.

Photosynthesis is the process by which plants convert light energy into chemical energy in the form of ATP. The photosynthetic process occurs in the chloroplasts of plants through a variety of proteins which transfer electrons and pump protons to eventually produce ATP. Plastocyanin (PC) and cytochrome f (cyt f) are electron transfer proteins in the photosynthetic chain. PC is a small, soluble protein in the lumen of the thylakoid. Cyt f is part of the membrane-bound cytochrome b₆f complex. The molecular weights of cyt f and PC are 32 kD and 10.5 kD, respectively (Gray 1978). Cyt f is a part of the membrane bound cytochrome b₆f complex, and its role is to transfer an electron to PC. PC is a small, water soluble, blue copper protein located in the lumen of the thylakoid (Stryer 1995). The protein complex between cyt f and PC is believed to be stabilized by electrostatic interactions between a positively charged region on cyt f and a negatively charged area on PC (Harris 1994; Martinez et al. 1994).

To find a binding constant between these two proteins, an assay that was similar to one used by Davidson et al. (1993) was developed. The assay involves the mixing of the two proteins in a centrifuge concentrator, centrifuging the mixture briefly, and quantitating the proteins on each side of the concentrator’s membrane by visible spectroscopy, since both cyt f and PC have distinct visible spectra. PC has a characteristic peak at 598 nm that has an extinction coefficient of 4.9 mM⁻¹ and Cyt f has an extinction coefficient of 27.7 mM⁻¹ at 554 nm (Gray 1978). This assay has allowed for the preliminary determination of the $K_d$ for these two proteins, and with further study, the assay will also reveal information about the protein-protein interactions.
Methods and Materials

Plastocyanin purification.—Spinach was washed, de-stemmed, and homogenized in 50 mM Tris pH 8 and 0.2 M sucrose in a Warring blender. The homogenate was filtered through cheesecloth and centrifuged. The resulting pellet was resuspended in 10 mM Tris pH 8 and frozen. After thawing, the solution was centrifuged. The resulting supernatant was filtered and loaded onto a DEAE anion exchange column equilibrated with 50 mM Tris pH 8. The PC was eluted with a step gradient. PC eluted from the DEAE column with 50 mM Tris - 0.2 M NaCl and was further purified by gel filtration on a G-75 column equilibrated with 50 mM Tris. Purity was checked by UV-VIS spectroscopy by comparing the absorbance of the protein backbone at 280 nm to the visible absorbance at 598 nm.

Cytochrome f.—Spinach cyt f was purchased from the Sigma Chemical Company.

Binding constant assay.—The determination of the $K_d$ was done using a Centricon centrifuge concentrator purchased from Amicon with a molecular weight cutoff (MWCO) of 100 kD. A 30 kD MWCO concentrator did not allow any PC to pass through the membrane during the one minute centrifugation. Cyt f and PC were mixed at specific concentrations in 5 mM phosphate-0.1% SDS buffer and centrifuged at 1940 $X g$ (4,000 rpm) for 1 minute. The protein concentrations of cyt f and PC were then determined in the upper and lower chambers of the concentrators by visible spectroscopy (Hitachi model U-3000). As a control, cyt f and PC were centrifuged independently to determine the quantity of PC that passes through and how much cyt f was retained and concentrated by the Centricon concentrators.

It was assumed that the amount of PC passing through the concentrator’s membrane represented the free protein and that the amount of PC retained by the concentrator’s membrane was approximately equal to the bound PC in electrostatic complex with cyt f. The capacity of cyt f was determined by adding a known amount of cyt f taking into account the 1.2% concentrating effect the one minute centrifuging was found to have on the cyt f. The model used to describe the interaction between cyt f and PC was a ligand binding to a ligand at a single site model. This model can be mathematically described by the following equation (Davidson 1993):

$$\text{Bound PC} = \frac{\text{Capacity of cyt f} \times \text{Free PC}}{K_d + \text{Free PC}}$$
RESULTS

To solubilize enough membrane bound cyt f to make a stock solution of about 30 μM, the 5 mM phosphate buffer had to have 0.1% SDS incorporated into it. The SDS showed no effect on the visible portion of the spectra of PC. The 100 kD molecular weight cutoff membrane in the Centricon concentrator was found to concentrate cyt f by 1.2% and allow only 40% of the PC to pass through the membrane during the one minute centrifugation when the proteins were centrifuged independently as controls.

Cyt f and PC were mixed together in a Centricon concentrator so that their final concentrations were 12 μM and 15 μM, respectively in a total of 600 μL. After centrifugation, the concentration of PC that passed through the membrane was determined to be 6.6 μM according to its absorbance at 598 nm. 9.9 μM of PC was left in the top portion of the concentrator bound with cyt f according to the visible spectra of the mixture of PC and cyt f. The accuracy of the PC concentrations in the concentrator is questionable since the absorbances for these two concentrations are much less than the limits of accuracy of the instrument. Since it had already been determined that the concentrator concentrated cyt f by 1.2%, the concentration capacity of cyt f available to bind with PC was 14.4 μM. Solving equation (1) for $K_d$ gave a preliminary $K_d = 4.1 \mu M$ in 5 mM sodium phosphate - 0.1% SDS buffer at pH 7.

DISCUSSION & CONCLUSION

The $K_d$ for the interaction between cyt f and PC needs to be explored further. The interaction needs to be studied as a function of pH, ionic strength, and oxidation state of the proteins to better characterize the protein-protein interaction of cyt f and PC. Adjustments such as protein concentration, sample size, and centrifuge time and force are still needed; however, the development of this assay demonstrates the ability to measure the $K_d$ for this physiologically relevant protein complex.

The preliminary $K_d$ for the electrostatic interaction between cyt f and PC was determined to be 4.1 μM at 5 mM sodium phosphate - 0.1% SDS buffer at pH 7. This value is in close agreement to the value of 4.6 μM for the $K_d$ for the protein complex between methylamine dehydrogenase and amicyanin (Davidson 1993). Both the cyt f and PC complex and the methylamine dehydrogenase and amicyanin complex are natural physiological partners that are involved in electron transfer reactions. It is also interesting to note that both protein complexes are believed to be stabilized by electrostatic interactions.
ACKNOWLEDGMENTS

This work was supported by the Chemistry Department and a Welch Departmental Grant made to the Chemistry Department at SFASU.

LITERATURE CITED


MRH at: mharris@sfasu.edu
THE INFLUENCE OF HABITAT STRUCTURE
UPON DIVERSITY AND EVENNESS OF ABUNDANCE

Daniel M. Brooks
Department of Wildlife and Fisheries Sciences and
Texas Cooperative Wildlife Collections, Texas A&M University
College Station, Texas 77843

Abstract.—This study examined the relationship between habitat heterogeneity and species diversity in a transitional zone between temperate and tropical America. Additionally, the relationship between habitat heterogeneity and evenness of abundance (EA) was examined, as measured by both abundance and flock size. Sampling of avian community diversity, as well as flock size and abundance of three sympatric Neotropical species with different breeding strategies (Green Jay Cyanocorax yncas, Groove-billed Ani Crotophaga sulcirostris and Plain Chachalaca Ortalis vetula) took place along the Rio Grande River in southern Texas. Sampling occurred during nine months of an annual cycle, at four different habitats representing different degrees of heterogeneity. Diversity and habitat heterogeneity exhibited the typical positive relationship. The three species in this study varied in abundance at different sites due to different microhabitat preferences. Flock sizes of the three species became more similar with increasing habitat heterogeneity due to more microhabitats within a mosaic selected by the suite of species.

Diversity has proven difficult to study because it results from a number of interacting causal chains (Terborgh 1977). Several studies have found a positive relationship between structural complexity of habitats and species diversity (e.g., MacArthur & MacArthur 1961; Vuilleumier 1972; Tomoff 1974; Terborgh 1977; 1985; Terborgh & Faaborg 1980). Several of these studies have found that one can predict diversity by vegetative structure (i.e., foliage height profile) in temperate regions (e.g., MacArthur et al. 1962) but not in the tropics (Terborgh 1977). Roth (1976) found that there is a positive relationship between diversity and heterogeneity in south Texas, representing a transitional zone between temperate and tropical regions. The study herein will examine an additional test of this relationship in the south Texas transitional zone.

Terborgh (1985) notes that until recently the reasons underlying the association between diversity and structural complexity of habitat was poorly documented; studies failed to determine a cause and effect relationship. He further points out other factors contributing to diversity, including the roles of food resources and interspecific competition. It is important to develop new hypotheses accounting for diversity. This begins with testing field observations which may yield
alternative answers to old problems. Investigating attributes of differential abundance may provide insight into mechanisms which could help account for diversity. Evenness of abundance (hereafter referred to as EA) can be described as the presence of equal numbers of different individual species at the same site. The concept is similar to species evenness which is typically measured using all species in a community, whereas EA may be measured using individual species. Testing for a positive relationship between EA and habitat heterogeneity can be accomplished by examining the situation separately for actual abundance and flock size, both of which may be affected differently by habitat heterogeneity.

Specifically, this study addresses these questions:

1. What relationship exists between habitat heterogeneity and species diversity along the Rio Grande River?
2. What relationship exists between habitat heterogeneity and EA, as measured by abundance?
3. What relationship exists between habitat heterogeneity and EA, as measured by flock size?

STUDY SITE AND METHODS

Located in south Texas, the Bentsen-Rio Grande State Park (26°15'N, 98°30'W) is situated along the Rio Grande River, lying in a transitional zone between temperate and tropical America. The bird community in this region was described as early as 1924 (Friedmann 1925). The two dominant plant species at Bentsen-Rio Grande are sweet acacia (Acacia smallii) and honey mesquite (Prosopis glandulosa). The four sites surveyed during this study (the Campsite, Chaparral, Melon Patch and Rio Grande trails) were chosen to represent a gradient of habitat heterogeneity. The homogeneous Campsite Trail consists of a relatively closed, continuous canopy of Acacia in an advanced successional stage, lacking an understory. The Chaparral Trail was approximately 70% Mesquite scrubland and 30% stratified forest dominated by Acacia. Both the Melon Patch and Rio Grande trails were mosaics comprised of riparian woodland, open savannah, and brush habitats. Because the Melon Patch and Rio Grande trails represented the most diverse habitat mosaics, they were considered the most heterogeneous habitats for testing purposes.

The present study took place from July through November 1993, and March through June 1994. Each site was sampled during the first week
of each of these months, insuring that the samples were collected at monthly intervals (e.g., rather than the last week of one month and the first week of the following month). The three species chosen to measure EA were the Green Jay (*Cyanocorax yncas*), a cooperative helper-at-the-nest; the Groove-billed Ani (*Crotophaga sulcirostris*), a cooperative group breeder; and the Plain Chachalaca (*Ortalis vetula*), a monogamous breeder. These species have similar biogeographic distributional patterns, with the northern boundaries of their geographic distribution terminating in south Texas. They are all sub-tropical species characteristic of the transitional zone between temperate and tropical America. Additionally, these species were selected because they have different breeding strategies, avoiding bias of similar behavioral constraints. For example, these species flock differently and select different types of microhabitat in which to build their nests.

Data were collected by walking at a consistently slow pace along strip transects in the four different areas, recording number of birds/flock which could be accurately detected visually or auditorily using unlimited distance contacts (Ralph 1981). Surveys took place over the course of two days during the first week of each month sampled. The Campsite Trail was surveyed at daybreak, followed by surveys of the Chaparral and Melon Patch trails. Surveys of the Melon Patch and Rio Grande trails began approximately two hours prior to sunset. Differences between morning and evening did not appear to affect detectability because estimates of flock size and numbers obtained from the Melon Patch Trail were virtually indistinguishable. Select voucher slides were deposited in the Texas Photo-Record File at the Texas Cooperative Wildlife Collections, Texas A&M University (TPRF - TCWC, TAMU).

Diversity was compared using both species richness and the Shannon equitability index (*J*), where *J* = diversity at site *X* / maximum diversity for all sites. This *J* index represents evenness of allotment of individuals among species, ranging from 0 to 1.0 (Lloyd & Ghelardi 1964). Species richness is a community measure that is a significant component of species diversity. Each habitat was ranked to represent a gradient from least to most heterogeneous as follows: Campsite (1), Chaparral (2), Melon Patch (3), and Rio Grande (4). The role of habitat heterogeneity in determining diversity was tested using regression analysis with the computer program STATGRAPHICS (STSC 1986). A probability threshold of *P* = <0.05 would indicate a significant relationship. With the same computer program, analysis of variance (*ANOVA*) (or corresponding Kruskal-Wallis tests [*K-W*] if statistical assumptions were violated)
Table 1. Mean values for diversity, abundance and flock size.

<table>
<thead>
<tr>
<th></th>
<th>Melon Patch</th>
<th>Rio Grande</th>
<th>Chaparal</th>
<th>Campsite</th>
</tr>
</thead>
<tbody>
<tr>
<td>Diversity</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Species Richness</td>
<td>16.2</td>
<td>11.8</td>
<td>11.5</td>
<td>6.1</td>
</tr>
<tr>
<td>J Index</td>
<td>1.0</td>
<td>0.73</td>
<td>0.71</td>
<td>0.38</td>
</tr>
<tr>
<td>Abundance</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Chachalaca</td>
<td>6.1</td>
<td>1.8</td>
<td>2.6</td>
<td>10.3</td>
</tr>
<tr>
<td>Jay</td>
<td>8.1</td>
<td>4.2</td>
<td>7.3</td>
<td>3.6</td>
</tr>
<tr>
<td>Ani</td>
<td>6.2</td>
<td>3.5</td>
<td>0.5</td>
<td>0.5</td>
</tr>
<tr>
<td>Flock Size</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Chachalaca</td>
<td>1.5</td>
<td>1.4</td>
<td>1.5</td>
<td>3.4</td>
</tr>
<tr>
<td>Jay</td>
<td>1.6</td>
<td>1.2</td>
<td>2.1</td>
<td>1.1</td>
</tr>
<tr>
<td>Ani</td>
<td>1.8</td>
<td>1.4</td>
<td>0.4</td>
<td>0.4</td>
</tr>
</tbody>
</table>

was used to determine if abundance or flock sizes were significantly different at each habitat; non-significant results are interpreted as EA. For each parameter (diversity, abundance, and flock size), monthly means were obtained for each site (Table 1).

RESULTS

The most heterogeneous habitats support the most diverse avifaunas, as measured by both species richness (\( P = 0.04 \)) and the J index (\( P = 0.04 \)) (Figure 1). However, diversity at the Chaparal Trail almost rivals that of the Rio Grande Trail. Indeed, the Chaparal Trail is more heterogeneous than the Campsite Trail, but not as heterogeneous as the Rio Grande Trail.

Abundance and flock size did not vary significantly among the three species along the Melon Patch Trail or the Rio Grande Trail, indicative of EA in these more heterogeneous habitats. In contrast abundances differed significantly among the three species at the Chaparal Trail (\( K-W: P = 0.0002 \)) and the Campsite Trail (\( K-W: P = 0.007 \)). Similarly, flock sizes differed significantly among species at the Chaparal Trail (\( ANOVA: P = 0.02 \)) and the Campsite Trail (\( K-W: P = 0.005 \)).

DISCUSSION

Diversity.—The results of a positive relationship between avian diversity and increasingly complex habitats agree with previous findings of Roth (1976) in south Texas, and others (e.g., MacArthur et. al. 1962; Tomoff 1974; Terborgh 1977; 1985). However, other studies have reported the opposite relationship (e.g., Vuilleumier 1972; Terborgh &
Faaborg 1980). For example, Vuilleumier (1972) found diversity to increase in less diverse and more open beech forest rather than in more diverse and dense forests. Terborgh (1985) speculates the reasons for such findings may have to do with biogeographic isolation of areas where these studies took place (e.g., Patagonia [Vuilleumier 1972] and the West Indies [Terborgh & Faaborg 1980]).

Terborgh (1977) speculates that an increased abundance of resources in a complex environment like a tropical forest could allow a greater array of foraging specializations to achieve profitability, thus accounting for enhanced diversity. Seasonal availability of different resources in
this study may have caused fluctuations in diversity over the course of the year, although this study did not measure such resources explicitly. The most extreme example is in the case of the Melon Patch Trail where monthly diversity was minimal (4 species) during the coolest month of sampling (November) and reached its maximum (24 species) during one of the warmest months (June) when resources were more abundant.

**Abundance.**—Tomoff (1974) and Terborgh (1977) found positive relationships between habitat complexity and avian density. The three species in this study had varying densities at different sites due to different microhabitat preferences. One should note that this study did not measure density of the entire bird community at each site in this study. Chachalacas reach their peak density at the Campsite Trail. Jays approach their peak density at the Chaparal Trail. However, Anis were less abundant at the Chaparal and Campsite trails as they prefer grassland savannah and brush.

Certain “early colonizing” species adapted to live in specific habitats are represented in higher densities. This may prevent other species from inhabiting these areas through competition, and therefore limit diversity (Vuilleumier 1972). Thus, diversity should have an inverse relationship to the number of habitat specialists in a given area. This would be an interesting topic for future research.

**Flock size.**—Tomoff (1974) found habitat complexity positively correlated with breeding bird density in the Arizona desert. Flock sizes of the three species compared herein are more similar with increasing habitat heterogeneity. This likely reflects the increased number of microhabitats within a mosaic attracting a more diverse assemblage of species. For example, both the Melon Patch and Rio Grande trails offered habitat mosaics of woodland/forest and savannah/scrub preferred by all three species of birds.

**Reproductive strategy and EA.**—Avian breeding strategies are characterized primarily by monogamy, although different forms of cooperative breeding are increasingly documented in the literature (Heinsohn et al. 1990). Helpers-at-the-nest cooperation consists of juveniles or other adults, usually from previous cohorts, assisting breeding females or pairs and include species such as Green Jays (Alvarez 1975). Kin selection is the benefit rather than genetic contribution to the offspring.
Groove-billed Anis represent group-breeding in which several females lay in a nest which is cared for by a single male, or a social breeding group forms (Vehrencamp 1978). Maximizing reproductive output and increased protection against predators are the major benefits to group-breeding.

The Plain Chachalaca characterizes a monogamous species. Marion (1974) indicates that pair formation begins with birds in winter feeding flocks and monogamous bonds are formed and maintained until young are raised, possibly longer. Although monogamy is the norm for members of the family Cracidae, exceptions occur such as the yellow-knobbed curassow \((\textit{Crax daubentoni})\) in Venezuela (Strahl et al. in press).

Average flock size would appear to vary from one reproductive strategy to the next. This may not always be the case as mongamous species often form familial flocks during the non-breeding season, while group nesters only nest during a "snapshot" of time in a given year. As group nesters Anis form larger flocks during the breeding season; thus, fewer breeding flocks should be encountered in less desirable habitats such as forest or woodland. This, in turn, makes flock size more similar to those of the other two species, which do not form groups when breeding. Similarly because Chachalacas often have larger broods than the other two species, their numbers and flock sizes increase dramatically.

Group size and composition may have important consequences for the survival and fecundity of organisms (Pulliam & Caraco 1984). Seasonal variation in food availability influences flock size of certain parrots (Pizo et al. 1995). A major factor attributing to this is different seasonal patterns in the American tropics. This emphasizes the important role seasonality plays in determining flock size.

**ACKNOWLEDGMENTS**

I am grateful to Jeffrey A. Back, Bret Augenstein and Margie Cohen for aiding in data collection. Roxanne Lerma and other staff members at Bentsen-Rio Grande State Park provided stimulating conversation about the Rio Grande bird community. Thanks to Keith Arnold and an anonymous reviewer for providing helpful comments on this manuscript.
Literature Cited

Alvarez, H. 1975. The social system of the green jay in Colombia. Living Bird, 14:5-44.


DMB at: Ecotropix@aol.com
NEW FISH HOSTS FOR NINE FRESHWATER MUSSELS
(BIVALVIA: UNIONIDAE) IN TEXAS

Robert G. Howells
Texas Parks and Wildlife Department, Heart of the Hills Research Station
HC07, Box 62, Ingram, Texas 78025

Abstract.—Fish hosts of the glochidial larval stages of nine species of mussels are reported from Texas. These include two species of *Lampsilis* and one species each of *Pyganodon*, *Utterbackia*, *Anodonta*, *Arcidens*, *Tritogonia*, *Quadrula* and *Cyrtonaia*. 

Freshwater mussels (family Unionidae) have recently been recognized as the most-rapidly declining faunal group in North America (Williams et al. 1993). Many species support significant commercial and sport fisheries and are important members of aquatic ecosystems. Unlike marine bivalve mollusks, unionids have a parasitic larval stage (glochidium) which requires specific fish hosts prior to transformation to the juvenile stage. Host fishes required by many unionid species are unknown yet critical to the management and protection of this resource. Fishery management practices, habitat alterations, and other factors may have direct impacts on continued successful reproduction of freshwater mussels or indirectly through impacts on required host fishes.

Beginning in 1992, the Texas Parks and Wildlife Department’s (TPWD) Heart of the Hills Research Station (HOH) staff began statewide surveys of freshwater mussel populations in Texas and investigations into many aspects of unionid biology.

METHODS AND MATERIALS

Gravid females obtained during field surveys were returned to HOH for subsequent examination. Where fish hosts were unknown or utilization of additional local species was possible, female mussels were opened by cutting anterior and posterior adductor muscles. Gills containing glochidia in marsupia were excised and their contents examined under a dissecting microscope. When actively-moving glochidia were found, they were removed from gill marsupia and placed in a 20-liter container of spring water. Potential host fishes were then placed in this container and water was aerated for 30-60 minutes to allow glochidia time to locate hosts and attach. Test fishes were obtained from areas where mussels do not occur to avoid possible host-immunity problems suggested for previously-infected hosts (Reuling
Thereafter, fishes were placed in aerated, 40-liter aquaria. Approximately 24-48 hours after infection, fishes were examined under a dissecting microscope for signs of encysted glochidia. Infected fishes were subsequently returned to aquaria. Tank bottoms were siphoned every 2-3 days and material obtained was examined microscopically for the presence of recently-transformed juvenile unionids.

**RESULTS AND DISCUSSION**

New hosts were identified for nine species of unionids as follows:

*Pyganodon grandis* (giant floater).—This species of bivalve has been commonly assigned to the genus *Anodonta* (see Howells et al. 1996:36). At least 37 fish species have been reported as hosts for this unionid (Hoggarth 1992; Watters 1994) which ranges widely throughout the Mississippi River valley and southwest into Texas. Additionally, Rio Grande cichlid (*Cichlasoma cyanoguttatum*) was found to be an acceptable host in this study. Transformation occurred 19 days after attachment at 17°C. Glochidia encysted on fins.

*Utterbackia imbecillis* (paper pondshell).—This species of bivalve has been commonly assigned to the genus *Anodonta* (see Howells et al. 1996:39). This species has been reported as one of only three North American unionids which may be capable of transforming to the juvenile stage without a fish host (Howard 1915). However, at least 12 fish species have also been confirmed as suitable hosts (Hoggarth 1992; Watters 1994). Glochidia observed during this study encysted on the fins and body of greenthroat darter (*Etheostoma lepidum*) and transformed in 9-12 days at 17°C. Glochidia which failed to attach to one of the test fishes died within 24 hours. No transformation without a host was observed.

*Anodonta suborbiculata* (flat floater).—Until recently, no hosts for this species were known. Barnhart et al. (In Press) reported flat floater utilized golden shiner (*Notemigonus crysoleucas*), warmouth (*Lepomis gulosus*), white crappie (*Pomoxis annularis*), and largemouth bass (*Micropterus salmoides*) as hosts. During this study, glochidia attached to fins of longear sunfish (*L. megalotis*), green sunfish (*L. cyanellus*), and channel catfish (*Ictalurus punctatus*) and transformed after 31 days at 18°C. Adults which produced these glochidia were obtained from B. A. Steinhagen Reservoir (Neches River drainage) in December 1993 and differed from typical flat floaters by being darker in color, more inflated, less deep bodied, and having higher beaks. Whether these
represent a similar undescribed species or a local ecophenotype of flat floater is as yet undetermined.

*Lampsilis bracteata* (Texas fatmucket).—No hosts were previously reported for this very rare, endemic unionid. Glochidia observed during this study encysted on gills of bluegill (*L. macrochirus*) and green sunfishes (*L. cyaneellus*). Transformation occurred in 21 days at 24°C. No glochidia were observed to encyst on longear sunfish, channel catfish, blacktail shiner (*Cyprinella venusta*), or goldfish (*Carassius auratus*).

*Lampsilis hydiana* (Louisiana fatmucket).—No hosts were previously known for this unionid. Glochidia observed during this study encysted on gills of green sunfish, channel catfish, and blue catfish (*I. furcatus*). Transformation occurred in 37 days at 18°C. A single glochidium attached to a gray redhorse (*Moxostoma congestum*), but it was rejected several days later.

*Ardicentos confragosus* (rock-pocketbook).—Five fish species have been reported as hosts for this mussel (Hoggarth 1992; Watters 1994). In this study, successful glochidial encystment occurred on channel catfish gills with transformation in 36 days at 18°C. Additionally, very light infestations (three glochidia on two test fish) occurred on green sunfish; however, glochidia were absent from these fish after 31 days and no juvenile mussels were recovered from the test tank. Although limited numbers of potential juveniles may have precluded ready detection following transformation, green sunfish is probably only a marginal host species at best. No encystment occurred on largemouth bass in this study.

*Tritogonia verrucosa* (pistolgrip).—No hosts have been reported for this unionid. Glochidia observed in this study successfully encysted on flathead catfish (*Pylodictis olivaris*) gills. One transformed juvenile mussel was found in 24 days, one at 26 days, and many at 31 days at 20°C. Channel catfish and redear sunfish (*Lepomis microlophus*) harbored no encysted glochidia 48 hours after the initial exposure.

*Quadrula nobilis* (gulf mapleleaf).—This mussel has previously been assigned to *Quadrula quadrala* (mapleleaf) or considered as a subspecies of pistolgrip (see Howells et al. 1996:125). Glochidia observed during this study encysted on gills of flathead and channel catfishes and began transformation in 44 days at 20°C.
Cyrtonaias tampicoensis (Tampico pearlymussel).—No hosts have previously been reported for this species. Glochidia in this study attached to gills of longnose gar (Lepisosteus osseus) and transformed in 14 days at 18°C. Other fish species to which glochidia attached but failed to transform included bluegill, redear sunfish, warmouth, redbreast sunfish (Lepomis auritus), longear sunfish, green sunfish, largemouth bass, channel catfish, and gray redhorse.

Identification of these fish host-mussel relationships enhances knowledge of the reproductive biology of these unionids. This may be particularly important for species like Texas fatmucket which appears to have been lost from its range throughout central Texas and may now be confined to a single small stream in the upper Colorado River drainage (Howells et al. In Press). Maintaining a healthy longnose gar population in this stream may be critical to the continued survival of the remaining Texas fatmuckets. Additional information on hosts for unionids in Texas is presented in Howells et al. (1996).

LITERATURE CITED


RGH at: ams@xtc.com
GENERAL NOTE

NOTEWORTHY RECORDS OF MAMMALS
FROM FANNIN COUNTY, TEXAS

Frederick B. Stangl, Jr. and Theresa J. McDonough
Department of Biology, Midwestern State University
Wichita Falls, Texas 76308

Compared to other regions of the state, the eastern third of Texas has received little attention by mammalogists, and few parts of the area have yet to be systematically surveyed for mammals. Fannin County provides a case-in-point. Situated on the Red River boundary with Oklahoma, the county is located east of the most recent treatments of north-central Texas mammals (Dalquest & Horner 1984) and west of the area considered by McCarley's (1959) report on east Texas mammals. The geographic scope of Schmidly's (1983) coverage of east Texas mammals includes Fannin County, but only a single voucher specimen from the county is listed, the fox squirrel (Sciurus niger). Aside from a specimen of Peromyscus leucopus reported by Stangl & Baker (1984), the authors are unaware of additional works since that time that include voucher records of mammals for the county.

Field parties from Midwestern State University (MWSU) recently collected small mammals from two Fannin County localities during April 1993 and November 1996. In addition to specimens of S. niger and P. leucopus from these localities, seven other species were taken. Each of the seven represented county records, and two of these (P. gossypinus and O. palustris) help define the northern range of these taxa in Texas. All specimens were deposited in the Collection of Recent Mammals at Midwestern State University (MWSU).

Sylvilagus floridanus.—The eastern cottontail is common throughout the county. Several were observed during the evenings at Bonham State Park along the margins of woodland. A single adult male (MWSU 20993) was collected.

Reithrodontomys fulvescens.—An adult male specimen (MWSU 19259) of the fulvous harvest mouse was taken from 5.5 mi NW of Honeygrove in a stand of bunchgrass. Suitable grassland habitat for this species is widespread in the county. Wilkins (1995) found this harvest mouse common to the immediate south in Hunt County.
*Peromyscus gossypinus.*—Seven specimens (MWSU 19270, 19271, 19274-19277, 19288) of the cotton mouse were trapped 5.5 mi NW of Honeygrove in wooded situations adjacent to the grass-lands where *R. fulvescens* was taken. Two others (MWSU 19272, 19273) were taken from a similarly wooded area 2.4 mi N of Coffee Mill Lake. These animals represent a marginal record from along the western boundary of the species in Texas.

*Peromyscus maniculatus.*—A single deer mouse (MWSU 19288) was trapped 5.5 mi NW of Honeygrove in association with the fulvous harvest mouse. Wilkins (1995) also recorded the species from adjacent Hunt County, where it was most commonly taken from along a wooded draw.

*Neotoma floridana.*—The eastern woodrat was found by Wilkins (1995) to be common in nearby Hunt County, and it is probably common in wooded situations throughout Fannin County. A single specimen (MWSU 20557) was collected 6 mi S of Telephone.

*Sigmodon hispidus.*—The hispid cotton rat is probably the single most common species of mammal in the county. Two specimens (MWSU 20994, 20995) were collected from grassy parks in Bonham State Park, and three (MWSU 19266-19268) were trapped from a similar area 5.5 mi NW of Honeygrove.

*Oryzomys palustris.*—An adult male specimen (MWSU 19269) of the marsh rice rat was trapped in a runway through lush vegetation bordering a drainage ditch 5.5 mi NW of Honeygrove. This represents a northwestern marginal record of the marsh rat in the state. Schmidly (1983) lists very few specimens of the marsh rat from the northeastern quarter of Texas, and the animal is reported to be uncommon across the northwestern parts of its range in Oklahoma (Stangl et al. 1992). It was only recently reported just to the northeast of Fannin County in Love County, Oklahoma (Gettinger 1991); unfortunately, none of those live-caught animals were prepared as voucher specimens.

*Additional comments.*—There are several species for which voucher specimens were not obtained, and yet some noteworthy observations can be made. A search was made for the runs of the eastern mole (*Scalopus aquaticus*) and gophers (*Geomys*); none were found. The latter case may be significant, for Fannin County is mapped by Davis & Schmidly (1994) as a hiatus between *G. breviceps* to the east and *G. bursarius* to the west.
Two typical components of the eastern Texas woodlands, the southern flying squirrel (Glaucomys volans) and swamp rabbit (Sylvilagus aquaticus), occur today in the county, according to local residents and the Bonham State Park staff, although attempts to procure specimens failed. Another eastern form, the gray squirrel (Sciurus carolinensis), apparently occurred in small numbers in Fannin County as recently as 20 years ago. While still common farther south and east in the state, this squirrel’s range appears to be contracting in Texas as it is in Oklahoma (Stangl et al. 1992).

ACKNOWLEDGMENTS

Collections were made under permits granted by the Texas Parks and Wildlife Department. We thank Duane Lucia, regional biologist for the department, for his hospitality and assistance in the field. Clyde Jones and an anonymous reviewer are acknowledged for their contributions to an earlier draft of this manuscript.

LITERATURE CITED


FBS at: stanglf@nexus.mwsu.edu
Plan Now for the 101th Annual Meeting of the Texas Academy of Science

March 5 - 7, 1998
University of Texas at Tyler

Program Chair
Dovalee Dorsett
Department of Information Systems
Baylor University
P. O. Box 98005
Waco, Texas 76798-8005
Ph. 254/710-2258
FAX 254/710-1091
E-mail: dovalee_dorsett@baylor.edu

Local Host
Don Killebrew
Department of Biology
University of Texas at Tyler
3900 University Boulevard
Tyler, Texas 75799
Ph. 903/566-7252
FAX 903/566-7189
E-mail: don_killebrew@mail.uttyl.edu

Future Academy Meetings
1999-Texas Lutheran University
2000-Texas A&M University-Corpus Christi
2001-Stephen F. Austin State University
IN RECOGNITION OF THEIR ADDITIONAL SUPPORT OF
THE TEXAS ACADEMY OF SCIENCE DURING 1997

Patron Members
Don W. Killebrew
Ned E. Strenth

Sustaining Members
Dovalee Dorsett
Deborah D. Hettinger

Supporting Members
Frances Bryan Edens
Donald E. Harper, Jr.
Donivan Porterfield
William F. Reynolds
Margaret S. Stevens
MEMBERSHIP.—Any person or members of any group engaged in scientific work or interested in the promotion of science are eligible for membership in The Texas Academy of Science. Dues for regular members are $30.00 annually; supporting members, $60.00; sustaining members, $100.00; patron members, $150.00; associate (student) members, $15.00; family members, $35.00; affiliate members, $5.00; emeritus members, $10.00; corporate members, $250.00 annually. Library subscription rate is $50.00 annually.

Application for Membership
(please print or type)

Name__________________________________________

Last First Middle

Mailing Address______________________________________________________________

City________________ State_____________ Zip_________

Type of Membership__________________________________________________________

Send Application Form and Check or Money Order to:

Dr. Brad C. Henry
TAS Executive Secretary
Department of Biology
University of Texas-Pan American
Edinburg, Texas 78539

Please photocopy this Application Form
THE TEXAS ACADEMY OF SCIENCE, 1997-98

OFFICERS

President: Ronald S. King, University of Texas at Tyler
President Elect: Dovalee Dorsett, Baylor University
Vice-President: James W. Westgate, Lamar University
Immediate Past President: Kenneth L. Dickson, University of North Texas
Executive Secretary: Brad C. Henry, University of Texas-Pan American
Corresponding Secretary: Deborah D. Hettinger, Texas Lutheran University
Manuscript Editor: Jack D. McCullough, Stephen F. Austin State University
Managing Editor: Ned E. Strenth, Angelo State University
Treasurer: Michael J. Carlo, Angelo State University
AAAS Council Representative: Sandra S. West, Southwest Texas State University

DIRECTORS

1995  Thomas Atchison, Stephen F. Austin State University
      Charles H. Swift, Hutchinson Junior High School in Lubbock
1996  Robert D. Owen, Texas Tech University
      Andrew J. Tirpak, Jr., Texas A&M University at Galveston
1997  Olufisayo Jejelowo, Texas Southern University
      Orlan L. Ihms, TU Electric of Dallas

SECTIONAL CHAIRPERSONS

Anthropology: Jeff D. Leach, Centro de Investigaciones Arqueologicas
Biological Science: David Marsh, Angelo State University
Botany: Allan Nelson, Texas A&M University-Kingsville
Chemistry: Delphia F. Harris, University of the Incarnate Word
Computer Science: John A. Ward, Brooke Army Medical Center
Conservation and Management: Michael F. Small, Texas A&M University-Kingsville
Environmental Science: Irene Perry, Sam Houston State University
Freshwater and Marine Science: Cynthia Gorham-Test, Environmental Protection Agency
Geography: David R. Hoffpauir, Sam Houston State University
Geology: Betsy Torrez, Sam Houston State University
Mathematics: Ben Sultenfuss, Stephen F. Austin State University
Physics: Cyrus D. Cantrell, University of Texas at Dallas
Science Education: Suzette Thorp Johnson, Kealing Jr. High in Austin
Systematics and Evolutionary Biology: Jim Collins, Kilgore College
Terrestrial Ecology: Monte Thies, Sam Houston State University

COUNSELORS

Collegiate Academy: Jim Mills, St. Edward's University
Junior Academy: Kathy Mittag, University of Texas at San Antonio
      Vince Schielack, Texas A&M University
GENERAL INFORMATION

MEMBERSHIP.—Any person or member of any group engaged in scientific work or interested in the promotion of science is eligible for membership in The Texas Academy of Science. For more information, please access the Academy’s homepage at:

http://www.uttyl.edu/~tas/taswhat.htm

Dues for regular members are $30.00 annually; supporting members, $60.00; sustaining members, $100.00; patron members, $150.00; associate (student) members, $15.00; family members, $35.00; affiliate members, $5.00; emeritus members, $10.00; corporate members, $250.00 annually. Library subscription rate is $50.00 annually.

The Texas Journal of Science is a quarterly publication of The Texas Academy of Science and is sent to most members and all subscribers. Payment of dues, changes of address and inquiries regarding missing or back issues should be sent to:

Dr. Brad C. Henry
Department of Biology
The University of Texas-Pan American
Edinburg, Texas 78539
E-mail: bradhenry@panam.edu

AFFILIATED ORGANIZATIONS
American Association for the Advancement of Science,
Texas Council of Elementary Science
Texas Section, American Association of Physics Teachers
Texas Section, Mathematical Association of America
Texas Section, National Association of Geology Teachers
Texas Society of Mammalogists

The Texas Journal of Science (ISSN 0040-4403) is published quarterly at Lubbock, Texas, U.S.A. Periodicals postage paid at San Angelo, Texas and additional mailing offices. POSTMASTER: Send address changes, and returned copies to The Texas Journal of Science, Box 43151, Lubbock, Texas 79409-3151, U.S.A. The known office of publication for The Texas Journal of Science and The Texas Academy of Science is P. O. Box 10986, ASU Station, San Angelo, Texas 76909, U.S.A.; Dr. Michael J. Carlo, Treasurer.
CONTENTS

Seedling Survival, Growth and Mortality of Juniperus ashei (Cupressaceae) in the Edwards Plateau Region of Central Texas.  
By J. T. Jackson and O. W. Van Auken ................................. 267

Water Quality of the San Marcos River.  
By Alan W. Groeger, Patrick F. Brown, Todd E. Tietjen and Travis C. Kelsey ... 279

Permutations and Change Ringing.  
By David R. Cecil ............................................................. 295

The Time from Sunrise to Sunset.  
By Stewart C. Welsh .......................................................... 303

Complete Structural Determination of 1,2-Benz-8-(Alanyl)-3-Phenoxazone by NMR Techniques (HSQC & HMBC).  
By K. G. Bhansali, S. G. Milton and F. Matloubimoghaddam ............ 315

Selective Activation of Stress Proteins in the Muscle of the Parasitic Worm Ascaris suum from Pig Intestine.  
By Sheng-Hao Chao, Manus J. Donahue and Ruthann A. Masaracchia .... 319

Occurrence of Infectious Bacteria in Captive-reared Kemp’s Ridley (Lepidochelys kempi) and Loggerhead (Caretta caretta) Sea Turtles.  
By Bradley A. Robertson and Andrea C. Cannon .......................... 331

Prevalence of Cuterebrid (Diptera: Cuterebridae) Parasitism among Black-tailed Jackrabbits in Southern Texas.  
By D. Keith Crenshaw and Scott E. Henke ................................ 335

Distribution of Multiple Oil Tolerant and Oil Degrading Bacteria around a Site of Natural Crude Oil Seepage.  
Robert S. Stewart, Jr., Christopher Emmons, Dana Porfirio and Robert J. Wiggers .................................................. 339

GENERAL NOTES

Noteworthy Records of Mammals from Stonewall County, Texas.  
By Michael W. Ruhl and Frederick B. Stangl, Jr. .......................... 345

Observations of Winter Interactions between a Red-headed Woodpecker (Melanerpes erythrocephalus) and Golden-fronted Woodpeckers (M. aurifrons).  
By Michael S. Husak ................................................................ 348

Index to Volume 49 (Subject, Authors & Reviewers) ....................... 351

Recognition of Member Support ............................................. 357

Annual Meeting Notice for 1998 ............................................. 358

Postal Notice ........................................................................ 359
THE TEXAS JOURNAL OF SCIENCE
EDITORIAL STAFF

Manuscript Editor:
Jack D. McCullough, Stephen F. Austin State University
Managing Editor:
Ned E. Strenth, Angelo State University
Associate General Editor:
Michael J. Carlo, Angelo State University
Associate Editor for Botany:
Robert I. Lonard, The University of Texas-Pan American
Associate Editor for Chemistry:
John R. Villareal, The University of Texas-Pan American
Associate Editor for Geology:
M. John Kocurko, Midwestern State University
Associate Editor for Mathematics and Statistics:
E. Donice McCune, Stephen F. Austin State University
Associate Editor for Physics:
Charles W. Myles, Texas Tech University

Manuscripts intended for publication in the Journal should be submitted in TRIPLICATE to:
Dr. Jack D. McCullough
TJS Manuscript Editor
Department of Biology - Box 13003
Stephen F. Austin State University
Nacogdoches, Texas 75962

Scholarly papers in any field of science, technology, or science education will be considered for publication in The Texas Journal of Science. Instructions to authors are published one or more times each year in the Journal on a space-available basis, and also are available from the Manuscript Editor at the above address.

The Texas Journal of Science is published quarterly in February, May, August and November for $30 per year (regular membership) by THE TEXAS ACADEMY OF SCIENCE. Periodical postage rates (ISSN 0040-4403) paid at Lubbock, Texas. Postmaster: Send address changes, and returned copies to The Texas Journal of Science, PrinTech, Box 43151, Lubbock, Texas 79409-3151, U.S.A.
SEEDLING SURVIVAL, GROWTH AND MORTALITY OF JUNIPERUS ASHEI (CUPRESSACEAE) IN THE EDWARDS PLATEAU REGION OF CENTRAL TEXAS

J. T. Jackson and O. W. Van Auken

Division of Life Sciences, The University of Texas at San Antonio
San Antonio, Texas 78249

Abstract.—This study examined the survival, growth and mortality of various spatial cohorts of seedlings of Juniperus ashei. The greatest mortality occurred during the hot, dry summer months. In addition, a large number of J. ashei seedlings with reduced growth was found beneath the canopy of mature J. ashei trees. These seedlings appear to serve as a seedling bank, providing a source of recruitment of new individuals into the population with the death of the overstory trees. Higher seedling growth rates were found at the edge of established woodlands, suggesting that edge habitats may be best for growth beyond the seedling stage. No seedlings survived in the associated grasslands. Thus, J. ashei woodlands appear to be expanding more by way of the growth of new individuals at the edges of established woodlands, rather than from new individual plants establishing in associated grasslands.

Juniperus woodlands are widely distributed throughout North America (Wells 1965; Gould 1969; Blackburn & Tueller 1970; Little 1971; Baskin & Baskin 1986). Despite the dominance of the Juniperus spp. in these woodlands, their regeneration and expansion are poorly understood. Juniperus ashei is the dominant woody plant in the majority of the woodland communities of the Edwards Plateau in central Texas. Several studies (Bray 1904; Foster 1917; Smeins 1980) have suggested that it has expanded into areas that were historically grasslands. However, the demography of J. ashei is essentially unknown. In central Texas, Juniperus ashei Buchholz. (Ashe juniper) appears to be the most common Juniperus species, although J. virginiana is found in many areas of east and northeast Texas and J. deppeanna, J. monosperma and J. pinchotti are found in the Big Bend region and parts of northwest Texas (Correll & Johnston 1970).

Juniperus ashei occurs primarily on the thin, dry soils of the Edwards Plateau region of central Texas (Correll & Johnston 1970). However, the species ranges from southern Missouri and northern Arkansas south through central Texas with isolated populations in northern Mexico (Little 1971). Juniperus ashei is one of the dominant plants in the majority of the woodland communities across the Edwards Plateau region (Correll & Johnston 1970; Van Auken et al. 1979; Gehlbach 1988; Smeins & Merrill 1988). The regeneration and expansion of the
Juniperus woodlands on the Edwards Plateau of central Texas seem to involve many of the same factors that are important for their eastern and western counterparts. In particular, soil moisture, shading, fire frequency, herbivory, competition and mycorrhizal symbiosis have been shown to play important roles (McClean 1985; Blomquist 1990; Smeins et al. 1994; Terletsky & Van Auken 1996; Bush & Van Auken in press).

In order to understand the regeneration dynamics of a woodland system, a large number of individuals must be followed through time by marking and continually tracking the members of the population. This type of demographic study has been used to show population trends for Juniperus monosperma in northern Arizona (Johnsen 1962), Juniperus occidentalis in southern Idaho (Burkhardt & Tisdale 1976) and J. virginiana in eastern Nebraska (Schmidt & Stubbendieck 1993).

Prior to European settlement, the distribution of Juniperus ashei is thought to have been limited by fires to canyons, ravines and limestone outcroppings (Bray 1904; Foster 1917; Smeins 1980). With settlement came an increase in the number of domestic herbivores, a decrease in the amount of light fluffy fuel and a decrease in fire frequency. As a result of these changes came an increase in the density of J. ashei in many areas thought to have been grasslands (Bray 1904; Foster 1917; Smeins 1980). Juniperus ashei has been described as invading central Texas grasslands (Smeins 1980; McClean 1985; Blomquist 1990; Smeins et al. 1994); however, it may be more accurately described as expanding into these grasslands from associated woodlands. The characteristics that allow J. ashei to replace existing grasses are poorly understood but relative growth rates were highest at higher irradiances in grassland soils (McClean 1985), and J. ashei is drought tolerant (Fonteyn et al. 1985).

In spite of the importance of this species in central Texas, there have been few published studies of J. ashei seedling establishment or distribution (Van Auken 1993). Higher densities of J. ashei seedlings were found under mature J. ashei, Quercus fusiformis and Prosopis glandulosa canopies than in adjacent grasslands, thus, the distribution is not random (Yancy 1982; Blomquist 1990; Chavez-Ramirez 1992). Similar patterns have been shown for J. pinchotii, J. occidentalis and J. monosperma (Johnsen 1962; Burkhardt & Tisdale 1976; McPherson et al. 1988).

The environmental conditions required for germination and initial establishment may not be the same conditions required for growth of
mature individuals. *Juniperus ashei* seedlings may have adaptations to low light levels; however continued survival and growth probably depends on subsequent exposure to increased amounts of radiant energy (McClean 1985). This would suggest the necessity of tree-fall gaps to assure survival to maturity for these low light seedlings, which is similar to other woody forest species (Ghent 1958; Harper 1977). Just as seeds require the precise conditions of a safe site to germinate, seedlings may require specific conditions to move beyond the seedling stage into the mature community stage (Harper 1977).

It is hypothesized that the low light, low temperature, higher moisture environment found under the canopy of the mature woodlands may be the preferred site for germination and initial establishment, while the more extreme conditions found at the edge of the canopy, in the associated grasslands, or in canopy gaps are less favorable for germination and initial establishment but are more favorable for continued growth beyond the seedling stage. The first purpose of this study was to determine the time of mortality of *J. ashei* seedlings in the field. The second purpose was to estimate the survival of various size seedlings. Finally, the third purpose was to determine survival and growth rates of seedlings of various spatial cohorts.

**Study Site**

This study was conducted in Eisenhower Park, in northern Bexar County, Texas, approximately 5 km east of the University of Texas at San Antonio campus (98°36'W and 29°48'N). The park is on the southern edge of the Edwards Plateau near the Balconies Escarpment. It is representative of the region and includes small, open grasslands and *Juniperus/Quercus* woodlands. Mean annual precipitation for the study site is 78.69 cm with peaks in May (10.72 cm) and September (8.66 cm); however, monthly precipitation is highly variable with very little reported during June and July, especially during the study years. The low monthly mean temperature is 9.6°C in January and the high monthly mean temperature is 29.4°C in July (National Weather Service personnel, pers. comm.).

The vegetation type found in the study area is predominantly a *Quercus fusiformis* (live oak) / *Juniperus ashei* (Ashe juniper) woodland. Other woody species present in the woodlands include *Quercus texana* (Spanish oak), *Celtis laevigata* (hackberry), *Diospyros texana* (Texas persimmon), *Berberis trifoliata* (agarita) and *Rhus virens* (evergreen sumac) (Correll & Johnston 1970; Van Auken et al. 1979; 1980; 1981).
These woodlands are interspersed with small grasslands with *Aristida longiseta* (red three-awn), *Bouteloua curtipendula* (side oats gramma), other C₄ grasses and forbs (Gould 1975; Terletzky & Van Auken 1996).

**METHODS AND MATERIALS**

Two hundred and fifty 1 m² quadrats were established to measure mortality and growth across four microhabitats. Quadrats were established by driving a 30.5 cm nail into the ground at each of four corners of a 1 by 10 m area, which was divided into ten 1 by 1 m contiguous quadrats. One hundred quadrats were established in a grassland microhabitat at least 5 m from the associated woodland canopy. One hundred quadrats were established beneath the *Q. fusiformis / J. ashei* canopy at least 3 m from the edge of the associated grassland. Twenty-five quadrats were established just inside the canopy edge with the outside edge being the canopy drip line and 25 were established just outside the canopy edge with the inside edge being the canopy drip line. These edge quadrats were 0.5 by 2 m, with the long axis being parallel to the drip line.

In January 1994, all *Juniperus ashei* seedlings present in all quadrats were censused. Individuals were determined to be alive or dead. A seedling was considered alive if it had any green tissue present. Live individuals were tagged with 31.8 mm diameter, 1.4 mm thick, round, consecutively numbered, aluminum tags. A sixty mm finishing nail was used to secure each tag to the ground as near the base of the seedling as possible. Each month, for 21 months, all individuals were censused for survival. Seedlings that were missing for three consecutive census dates were classified as dead. After a seedling was classified as dead, it was removed from the quadrat.

Mortality totals were determined for the four spatial microhabitats and compared using a $X^2$ test. A general linear model of the percent survival on size class (0.1 mm) of basal diameter was fit to the data to examine the relationship of survival to size (SAS Institute 1982).

In January 1994, at the beginning of the study, basal diameter, height and the number of branches were measured for all seedlings present in all quadrats. In September 1995, at the end of the study, basal diameter, height and the number of branches were again measured. The growth rates / year of the *J. ashei* seedlings present were calculated. These rates were analyzed using ANOVAs comparing growth rates in each habitat.
Results

In January 1994, 993 *J. ashei* seedlings were present. Three hundred and thirteen (31.5%) had died prior to the study, while 680 (68.5%) were alive in January 1994. Of the number found alive initially, 253 (37.2%) died by the end of the study. Mortality was greatest in the summer months with 103 deaths in July 1994 (Fig. 1). In September of 1994, after one growing season, 535 seedlings (78.7%) were still alive and 427 (62.8%) survived two growing seasons to September 1995.

To understand the population dynamics of *J. ashei* seedlings, survival over two years was examined in relation to basal diameter (Fig. 2A). The basal diameter size distribution of the 680 *J. ashei* seedlings that were alive initially included 401 (59%) seedlings in the 0.45 to 0.75 mm size classes. There was a significant difference in the survival through two growing seasons between basal diameter size classes of the seedlings ($X^2 = 18.58$, df = 8, $P < 0.0001$), with larger seedlings having a greater probability of survival.

During the study, survival increased with increased basal diameter (Fig. 2B). The 0.35 mm size class only had 37% survival after two summers, while 76% of the 0.85 mm size class, 73% of the 0.95 mm size class, and 85% of the >1 mm size class survived through two summers. The linear relationship between basal diameter and percent survival after two summers was also significant ($r^2 = 0.95$, $P < 0.001$).

The January 1994 measurements of the basal diameters for the dead seedlings were compared to the September 1995 measurements of the basal diameters for the live seedlings (Fig. 2C). The mean basal diameter of the dead seedlings was 0.57 mm (SD = 0.67), and was
Figure 2. *Juniperus ashei* seedling survival and mortality by basal diameter size classes. (A) Number of live and dead seedlings after two growing seasons. (B) Percentage of each size class surviving two growing seasons. (C) Number of live and dead seedlings using measurements from January 1994 for the dead seedlings and September 1995 for the live seedlings. Size classes are 0.1 mm in basal diameter and labels are medians for each class.
Figure 3. Percent survival of *J. ashei* seedlings in four microhabitats after two growing seasons.

significantly different from the mean basal diameter for the live seedlings which was 1.35 mm (SD = 1.74; *P* < 0.001). There appear to be two sets of distributions, with 87% of the dead seedlings having basal diameters of 0.6 mm or less and 84% of the live seedlings having basal diameters of 0.6 mm or greater.

The spatial distribution of the *J. ashei* seedlings across the four microhabitats was highly skewed with a density of 0.11 seedlings / m² (1.1%) found in the grassland microhabitat, 1.00 seedlings / m² (2.6%) in each of the two edge microhabitats, and 9.31 seedlings / m² (93.7%) in the woodland microhabitat. The percent of these seedlings surviving the duration of the study also varied across microhabitats. Of the 11 grassland seedlings there were no survivors, while in the outside edge there was 16% survival (4/25), in the inside edge there was 32% survival (8/25), and in the woodland canopy microhabitat there was 45% survival (422/931) (Fig. 3).

Growth rates of *J. ashei* seedlings for basal diameter, height and number of branches were calculated. Because of the low number of individuals from the edge cohorts, these microhabitat measurements were pooled in the calculation of growth rates. There were no survivors from the grasslands, so comparisons with grasslands could not be made. Mean basal diameter growth rate from January 1994 to September 1995 was 1.01 mm / year for the edge habitat while it was 0.07 mm / year for the canopy microhabitat (Table 1). Increase in mean height was 139.77 mm / year for the edge habitat and only 9.50 mm / year for the
Table 1. Mean growth rates (SD) for basal diameter, height, and new branches in edge and woodland canopy microhabitats for J. ashei seedlings that survived from January 1994 to September 1995. (Edge N = 12, Canopy N = 422)

<table>
<thead>
<tr>
<th>Variable</th>
<th>Mean Growth Rate (SD)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Edge</td>
</tr>
<tr>
<td>Basal Diameter</td>
<td>1.01 (1.30)</td>
</tr>
<tr>
<td>(mm / yr)</td>
<td></td>
</tr>
<tr>
<td>Height</td>
<td>139.77 (169.12)</td>
</tr>
<tr>
<td>(mm / yr)</td>
<td></td>
</tr>
<tr>
<td>Branches</td>
<td>182 (222)</td>
</tr>
<tr>
<td>(new branches / yr)</td>
<td></td>
</tr>
</tbody>
</table>

Canopy habitat. Mean increase in number of branches was 182 branches / year for the edge habitat and 3 branches / year for the canopy habitat. The mean growth rate of the seedlings was significantly higher in the edge microhabitat than in the associated canopy microhabitat for basal diameter ($P < 0.001$), height ($P < 0.001$), and number of branches ($P < 0.001$).

**DISCUSSION**

The regeneration of a species is a function of its germination and survival strategy (Harper 1977; Mack & Pyke 1984). Seeds of a plant will respond to conditions that promote germination. These conditions should be followed by an additional set of conditions that are favorable for seedling survival, growth and reproduction (Fenner 1985). *Juniperus* woodlands throughout western North America are reported to have expanded in recent years (Johnsen 1962; Blackburn & Tueller 1970; Burkhardt & Tisdale 1976). The expansion of a population would indicate the establishment and growth of individuals in neighboring areas not previously inhabited (Holthuijzen et al. 1987). The possible causes for the expansion of western *Juniperus* woodlands include domestic herbivory, fire suppression, climatic change or a combination of these factors (Johnsen 1962; Blackburn & Tueller 1970; Burkhardt & Tisdale 1976; Smiens 1980; McPherson et al. 1988).

In the present study, seedling survival and growth were investigated to better understand the replacement and expansion dynamics of *J. ashei* populations. Most mortalities occurred during the hot and dry months, consistent with other species of *Juniperus* (Johnsen 1962; Burkhardt & Tisdale 1976). Low survival was found for the smallest size classes of seedlings and survival increased with increasing seedling size. This appears to be consistent with findings for *J. monosperma* where
seedlings germinating earlier in the season had increased survival over those that germinated later (Johnsen 1962), and with findings for other woody plant species (Streng et al. 1989; Jones et al. 1994). The highest growth rates were found for *J. ashei* seedlings in the edge microhabitats. This has not previously been reported, although high irradiance is a known requirement for the growth of *Juniperus* seedlings (Johnsen 1962; Burkhardt & Tisdale 1976; McClean 1985).

Environmental conditions such as temperature, soil moisture and irradiance, should be less extreme beneath the canopy of an adult tree or shrub as compared to the associated open areas (Johnsen 1962; Turner et al. 1966; Burkhardt & Tisdale 1976; Harper 1977; McPherson et al. 1988). All of the *J. ashei* seedlings in the grassland microhabitat died, and the greatest survival was found to be beneath the associated woodland canopy. Thus avoiding the deleterious conditions present in open habitats appears to be key to the success of new *J. ashei* seedlings, suggesting an intolerance of the conditions present in the interspaces between these canopies. These data are similar to the reports of poor survival for *J. monosperma* and *J. occidentalis* in open areas with increased survival beneath associated canopies (Johnsen 1962; Burkhardt & Tisdale 1976).

When the growth of the seedlings was examined, the variation was quite high. The apparent cause of this heterogeneity in growth was the location of the individual seedling in relation to the canopy. Individual seedlings at the edge of the canopy tended to be larger in shoot size than individuals from below the canopy. *Juniperus ashei* seedlings have been reported to have greater root/shoot ratios at low irradiance levels than in high irradiance levels (McClean 1985). The relationship between lack of canopy cover and growth of *Juniperus* seedlings shoots is alluded to in other reports that suggest growth beyond the seedling stage is dependent upon the removal of the shading canopy (Johnsen 1962; Burkhardt & Tisdale 1976). This suggests that overstory mortality and subsequent replacement from seedlings below is important for the maintenance of the population within established woodlands.

The cause of seedling mortality was not determined; however, few seedlings were physically removed by herbivores or lost (personal observation). Mortalities were highest during the hottest and driest months, which would suggest that desiccation was a contributing factor. Interference from neighboring plants, especially the overstory trees, did not increase mortality since survival was higher under the canopy than in the associated grasslands. Shading by larger woody plants probably
suppressed growth as individuals present under these canopies showed little size change over the 21 month study.

The large number of small seedlings present under the canopy can be interpreted as evidence of a woodland regeneration strategy (Harper 1977). The growth of seedlings beneath the canopy was suppressed, but their mortality was lower than among those in the canopy edge or grassland microhabitats. Seedlings under the canopy survive, but the environmental conditions required for growth beyond the seedling stage, i.e. intense sunlight levels, are not present and growth is reduced. This produces a seedling bank, a large number of suppressed seedlings waiting to be released after a disturbance or gap formation (Ghent 1958; Harper 1977). These seedlings could represent a safeguard against biotic and abiotic factors that result in the loss of the larger adult members of the population (Harper 1977).

*Juniperus ashei* seedlings found at the edge of mature *J. ashei* canopies may allow expansion of the woodland into the adjacent grassland since they were larger and grew faster in height and number of branches than the associated canopy shaded seedlings. Growth of these edge individuals could result in an increase in the area of the woodland and a concomitant decrease in the area of the associated grassland. This supports some reports that *J. ashei* woodlands are expanding (Smeins 1980; Van Auken 1993) and suggests a mechanism for this expansion.

**ACKNOWLEDGMENTS**

The authors thank the College of Sciences and Engineering, University of Texas at San Antonio for a small grant to J. T. Jackson for partial financial support of this research. We also thank J. K. Bush and V. Veit for helpful suggestions and manuscript reviews, and the personnel at the San Antonio Parks and Recreation Department for permission to use the grounds at Eisenhower Park.

**LITERATURE CITED**


OWV at: oauken@utsa.edu
Abstract.—The San Marcos River exhibits a distinct pattern of changing chemical and physical characteristics as it runs its 133 km course to the confluence with the Guadalupe River. This evolution of water quality includes a shift from a primary influence of groundwater to a more runoff-dominated river ecosystem, anthropogenic influences of point and nonpoint pollution, and change in character as the river flows through different physiographic regions. The river is of a constant nature and has very high water quality in its headwaters, however it becomes a more variable, turbid lowland river closer to its confluence with the Guadalupe River.

The San Marcos River emerges from a series of 200 closely-spaced openings forming a spring outfall with the second highest discharge in Texas (Brune 1981). This artesian system is fed by the San Antonio portion of the Edwards Aquifer, a 290 km long, crescent-shaped limestone aquifer running along the southern and eastern edge of the Edwards Plateau (Abbott & Woodruff 1986). The headwater stretch of the river is known for its relatively constant temperature and flow (Hannan & Dorris 1970). The springs and upper river contains a very productive submerged macrophyte community, and harbors many endemic or range-restricted organisms. These include the federally listed endangered or threatened species Zizania texana (Texas wild rice), Eurycea nana (San Marcos salamander), Etheostoma fonticola (fountain darter), and Gambusia georgei (San Marcos gambusia). The constancy of the environment has also allowed for the invasion of a number of exotic species that have a significant influence on the system.

This river is a truly unique ecosystem within the state, and the purpose of this study was to characterize important chemical and physical aspects of the river from its origin to its confluence with the Guadalupe River. This effort included sampling at 14 sites along the entire length of the river, and additional sampling in the upper river to more closely examine nutrient loading and limitation within this stretch.

Study Sites

Sites were sampled from the headwaters and along the entire length of the river (133 river km) to its confluence with the Guadalupe River.
Figure 1. Sampling site locations on the San Marcos and Blanco rivers.

(Fig. 1). All river distances were taken directly from Texas Parks and Wildlife (Table A2 in TPWD 1994b) or interpolated from this source with USGS maps, and were measured from the headwater springs to the confluence. Two headwater sites were located at an artesian well behind the Freeman Aquatic Biology Building on the Southwest Texas State University campus (site 1) and in Spring Lake near the largest spring (site 2). Site 3 was 0.5 river km downstream of the springs at the Old Fish Hatchery Building in City Park. Site 4 was about 100 m downstream of the outfall of the A.E. Wood State Fish Hatchery (river km 3.5). Site 5 was 500 m below the outfall of the San Marcos Sewage Treatment Plant (SMSTP, river km 4.8). The Blanco River enters the San Marcos River 7.2 km downstream from the springs, and site 6 was at the Caldwell County Road 266 crossing (also known as Westerfield Crossing) (river km 9.5). Site 7 was at the Highway 1979 crossing just south of Martindale (river km 18), and site 8 was at the Highway 1977 crossing east of Staples (river km 27). Site 9 was at the State Route 20 crossing just south of Fentress (river km 42), and site 10 was at the Caldwell County Road 119 crossing (river km 54). Site 11 was at the U.S. Highway 90 crossing west of Luling (river km 64), and site 12 was
at the U.S. Highway 80 crossing in Luling (river km 74), which is also near the USGS Luling gauging station. Site 13 was at the Highway 2091 crossing in Palmetto State Park (river km 97), and site 14 was at the Highway 2091 crossing directly west of Gonzales (river km 125), 8 river km above the San Marcos River confluence with the Guadalupe River. There was also a site on the Blanco River (site BR) located at the Old Martindale Road crossing (County Road 295) above the confluence with the San Marcos River.

Two additional sites were used for diel monitoring and nutrient limitation experiments. These included Thompson’s Island (TI), located between sites 3 and 4 (just upstream from the Country Road 299 crossing, at river km 3.4), and Cummins Dam (CD), a site between sites 5 and 6 just upstream from the dam (downstream of the confluence with the Blanco River, at river km 8.7).

**METHODS**

The 14 sites along the river were measured on seven dates: 27 March 1992, 22 July 1992, 16 November 1992, 31 January 1993, 16 April 1993, 12 September 1993, and 10 October 1994. Temperature, pH, dissolved oxygen and specific conductivity were measured with a Hydrolab Surveyor II that was calibrated daily (Hydrolab 1985). Alkalinity was measured according to Wetzel & Likens (1991). Turbidity was measured with a HF Instruments model DRT turbidimeter. Nutrient analyses were carried out on an Alpkem RFA 300 autoanalyzer, and were based on the methods described by Strickland & Parsons (1972).

On October 10 and 11, 1994 sampling over a diel period was done at five sites (3, TI, 5, CD, and BR) in the upper river region in which all the variables described above were measured at 3 hr intervals.

In February, 1995 an experiment was carried out to determine the limiting nutrients in the upper river regions. Unglazed bathroom tiles (2.54 by 1.27 cm) were placed at sites TI and 5 to measure periphyton colonization rates through chlorophyll \(a\) accumulation upstream and downstream of the SMSTP. The tiles were suspended at a depth which 75\% of the incident light at each site would penetrate to, and were left in the river for 14 d. Simultaneously, water samples were collected at each site for a nutrient limitation bioassay with the alga *Selenastrum capricornutum* (USEPA 1971). Samples were apportioned into 1 L cubitainers, and the appropriate nutrient additions were made. The treatments were control (no nutrient additions), +P (a \(K_2PO_4\) solution
was added to a final enrichment of 50 μg P L⁻¹, +N (a NH₄Cl solution was added to 100 μg N L⁻¹ final enrichment), and +M (metals, 100 μL of the micronutrient solution of Woods Hole MBL algal growth media (Nichols 1973) was added per cubitainer). Four combination treatments (nitrogen and phosphorus, +NP; nitrogen and metals, +NM; phosphorus and metals, +PM; and all three in combination, +NPM) at the same enrichments above were also included in this experiment. The metal solution included EDTA, iron, copper, zinc, cobalt, manganese, and molybdenum. All treatments were done in triplicate at both sites except for the control treatments, which had six replicates, and the cubitainers were incubated in 24 hr light (60 μE m⁻² s⁻¹) and gently shaken on a shaker table for 14 d. Response to nutrients was quantified by change in chlorophyll a content within the cubitainers. Chlorophyll a was determined in DMSO-acetone extracts (Burnison 1980).

Data from the U.S. Geological Survey (USGS Water Resources data reports, USGS 1969-93) were compiled from three stations to provide more specific chemical characteristics and flow data of the waters of the San Marcos and Blanco rivers. Data were pooled from three wells and a spring (USGS local identifiers LR-67-01-801, LR-67-01-806, LR-67-09-105, and LR-67-09-111) in San Marcos which were very similar in chemical composition to the San Marcos Springs (Groeger & Gustafson 1994) to represent the ionic content of the river headwaters. Data were from USGS water years 1978-87, 1989-91, and 1993. A USGS site (USGS # 08172000) at Luling (corresponding to site 12 of this study, drainage basin area of 2170 km²) was used to represent a site indicative of a greatly increased terrestrial influence (USGS 1969-93). The Blanco River USGS site (USGS # 08171000, drainage basin area of 919 km²) was in Wimberley, and data from USGS water years 1974-76, 1979, and 1988-93 were used.

**Results**

**Temperature.**—Variation in temperature of the San Marcos River was slight in the headwaters region (Fig. 2A). The range at site 3 during this study was 21.1-22.5°C, which closely corresponded to an earlier study (Hannan & Dorris 1970) at a nearby series of sites in which mean monthly temperatures ranged from 21.0-23.3°C over a 16 month period. Variation in water temperature increased at successive sites downstream from the artesian well, and this variation was much greater downstream of the confluence with the Blanco River (Fig. 2A). At site 14, the last sampling point before the confluence with the Guadalupe River, the
Figure 2. Temperature (A), pH (B), and specific conductance (C) on seven dates at sites along the San Marcos River. The solid line is the median value at each site. The vertical dotted line is the confluence with the Blanco River.

temperature ranged from 11.9-27.3°C. The USGS temperature data collected near site 12 (corresponding to the data in Table 1) ranged from 6-30°C (n = 161).
Table 1. Summary of USGS data, representing the chemical composition of the headwaters and a downstream site (Luling, TX) of the San Marcos River, and the Blanco River. Data are the median, mean, first to third quartile distribution (1-3 Q), range, and total number of samples (n). Sp. Cond. = specific conductance; Alk. = alkalinity.

<table>
<thead>
<tr>
<th>Location</th>
<th>Sp. Cond. (µS/cm)</th>
<th>pH</th>
<th>Ca²⁺ (meq/L)</th>
<th>Mg²⁺ (meq/L)</th>
<th>Na⁺ (meq/L)</th>
<th>K⁺ (meq/L)</th>
<th>Alk. (meq/L)</th>
<th>Cl⁻ (meq/L)</th>
<th>SO₄²⁻ (meq/L)</th>
<th>Si (mmol/L)</th>
</tr>
</thead>
<tbody>
<tr>
<td>San Marcos Springs</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Median</td>
<td>598</td>
<td>7.0</td>
<td>4.49</td>
<td>1.40</td>
<td>0.52</td>
<td>0.04</td>
<td>5.20</td>
<td>0.56</td>
<td>0.54</td>
<td>0.20</td>
</tr>
<tr>
<td>Mean</td>
<td>596</td>
<td>7.0</td>
<td>4.43</td>
<td>1.43</td>
<td>0.53</td>
<td>0.04</td>
<td>5.19</td>
<td>0.58</td>
<td>0.55</td>
<td>0.19</td>
</tr>
<tr>
<td>1-3 Q</td>
<td>581-617</td>
<td>6.9-7.1</td>
<td>4.24-4.59</td>
<td>1.34-1.48</td>
<td>0.48-0.60</td>
<td>0.03-0.04</td>
<td>5.08-5.25</td>
<td>0.51-0.65</td>
<td>0.50-0.60</td>
<td>0.18-0.20</td>
</tr>
<tr>
<td>Range</td>
<td>506-638</td>
<td>6.5-7.3</td>
<td>3.84-4.89</td>
<td>1.23-1.73</td>
<td>0.38-0.70</td>
<td>0.03-0.05</td>
<td>5.00-5.41</td>
<td>0.42-0.82</td>
<td>0.37-0.75</td>
<td>0.02-0.30</td>
</tr>
<tr>
<td>n</td>
<td>59</td>
<td>58</td>
<td>56</td>
<td>56</td>
<td>56</td>
<td>54</td>
<td>56</td>
<td>56</td>
<td>56</td>
<td>56</td>
</tr>
<tr>
<td>Blanco River</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Median</td>
<td>459</td>
<td>7.8</td>
<td>3.29</td>
<td>1.40</td>
<td>0.35</td>
<td>0.03</td>
<td>4.15</td>
<td>0.37</td>
<td>0.47</td>
<td>0.15</td>
</tr>
<tr>
<td>Mean</td>
<td>466</td>
<td>7.8</td>
<td>3.25</td>
<td>1.37</td>
<td>0.35</td>
<td>0.03</td>
<td>4.09</td>
<td>0.37</td>
<td>0.50</td>
<td>0.15</td>
</tr>
<tr>
<td>1-3 Q</td>
<td>444-491</td>
<td>7.6-7.9</td>
<td>2.97-3.54</td>
<td>1.23-1.48</td>
<td>0.33-0.37</td>
<td>0.03-0.04</td>
<td>3.84-4.42</td>
<td>0.34-0.39</td>
<td>0.40-0.62</td>
<td>0.14-0.17</td>
</tr>
<tr>
<td>Range</td>
<td>420-592</td>
<td>7.3-8.3</td>
<td>2.64-3.79</td>
<td>1.07-1.56</td>
<td>0.27-0.39</td>
<td>0.01-0.05</td>
<td>3.40-4.72</td>
<td>0.31-0.51</td>
<td>0.27-0.94</td>
<td>0.02-0.20</td>
</tr>
<tr>
<td>n</td>
<td>40</td>
<td>40</td>
<td>40</td>
<td>40</td>
<td>40</td>
<td>40</td>
<td>40</td>
<td>40</td>
<td>40</td>
<td>40</td>
</tr>
<tr>
<td>San Marcos River</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Median</td>
<td>578</td>
<td>8.0</td>
<td>3.84</td>
<td>1.48</td>
<td>0.87</td>
<td>0.05</td>
<td>4.60</td>
<td>0.96</td>
<td>0.60</td>
<td>0.18</td>
</tr>
<tr>
<td>Mean</td>
<td>570</td>
<td>8.0</td>
<td>3.67</td>
<td>1.47</td>
<td>0.87</td>
<td>0.05</td>
<td>4.36</td>
<td>0.95</td>
<td>0.63</td>
<td>0.18</td>
</tr>
<tr>
<td>1-3 Q</td>
<td>536-609</td>
<td>7.8-8.2</td>
<td>3.54-4.04</td>
<td>1.40-1.56</td>
<td>0.70-1.00</td>
<td>0.04-0.05</td>
<td>4.20-4.80</td>
<td>0.73-1.10</td>
<td>0.56-0.67</td>
<td>0.16-0.20</td>
</tr>
<tr>
<td>Range</td>
<td>125-835</td>
<td>7.1-8.6</td>
<td>0.85-4.59</td>
<td>0.21-5.10</td>
<td>0.17-1.57</td>
<td>0.03-0.13</td>
<td>0.86-5.18</td>
<td>0.34-3.36</td>
<td>0.13-1.21</td>
<td>0.01-0.40</td>
</tr>
<tr>
<td>n</td>
<td>180</td>
<td>142</td>
<td>179</td>
<td>179</td>
<td>143</td>
<td>134</td>
<td>179</td>
<td>179</td>
<td>179</td>
<td>179</td>
</tr>
</tbody>
</table>
Figure 3. Relationship between dissolved oxygen and temperature in the San Marcos River at 14 sites. The solid and dotted curves represent 100% (± 20%) oxygen saturation concentration at an atmospheric pressure of 760 mm Hg at sea level. The unfilled squares represent sites 1 and 2, the artesian well and Spring Lake, respectively. The filled symbols represent the other 12 sites.

**pH.**—The pH in the artesian well and Spring Lake (sites 1 and 2) was much lower than other sites, indicating that aquifer CO$_2$ concentrations were higher than those in equilibration with the atmosphere. The pH increased rapidly downstream of site 2 (Fig. 2B). Downstream of the confluence with the Blanco River pH values were relatively constant and corresponded to those expected in a limestone-dominated drainage.

**Dissolved oxygen.**—Dissolved oxygen concentrations within the San Marcos River were within 20% of the temperature-dependent saturation concentration (Fig. 3) except for sites 1 and 2. Water is vigorously mixed as it leaves Spring Lake, either over a spillway or a very steep rapids, greatly increasing the rate at which dissolved gasses approach an atmospheric equilibrium concentration (Hannan & Dorris 1970).

**Specific conductance and alkalinity.**—Specific conductance was relatively constant in the upper river, though there was a distinct increase downstream of the SMSTP (site 5, Fig. 2C). Specific conductance was lower and much more variable downstream of the confluence with the Blanco River. Alkalinity, which was highly
correlated with specific conductance \( r = 0.79, n = 114 \), exhibited a very similar pattern to that of specific conductance (data not shown) except alkalinity did not exhibit a corresponding increase below the SMSTP.

**Turbidity.**—The river, known for its clear headwaters, becomes increasingly turbid downstream (Fig. 4), a characteristic of the river obvious to the casual observer. Both the State Fish Hatchery and SMSTP were apparently responsible for increased turbidity in the upper river, though construction and suburban and agricultural land practices in the upper river’s drainage probably contribute also. The Blanco River can have dramatic effects on turbidity in the San Marcos River during high flow periods (Fig. 4), but is not particularly turbid during normal flows (median turbidity at the USGS station on the Blanco River was 1.9 NTU \( n = 40 \)).

**Nutrient concentrations.**—Nutrient concentrations in the water emerging from the aquifer tend to be relatively constant. Soluble reactive phosphorus (SRP) usually ranges from approximately 5-15 \( \mu g \) P L\(^{-1} \) and total phosphorus (TP) approximately 15-30 \( \mu g \) P L\(^{-1} \) (Fig. 5A). Nitrate ranged from about 1500-1700 \( \mu g \) NO\(_3^-\)+NO\(_2^-\)N L\(^{-1} \) (Fig. 5B), and ammonium 1-30 \( \mu g \) NH\(_4^+\)N L\(^{-1} \) (Fig. 5C). In the upper river SRP and TP concentrations were relatively constant until they were greatly
Figure 5. Phosphorus (A), nitrate-N (B), and ammonium-N (C) concentrations on seven dates at sites along the San Marcos River. The vertical dotted line is the confluence with the Blanco River. In A, the points represent SRP concentrations and the solid line is the SRP median concentration. The dotted horizontal line is the median concentration of total phosphorus.

enriched by the SMSTP, and were reduced below the confluence with the Blanco River. Nitrate also increased downstream of the SMSTP,
though much less dramatically than SRP, and tended to decrease downstream to <1000 μg L⁻¹. Ammonium concentrations increased both downstream of the State Fish Hatchery and SMSTP, and decreased further downstream (Fig. 5C).

Ions.—The water emerging from the San Marcos Springs was enriched in all the major ions, except magnesium and possibly potassium, relative to the Blanco River (Table 1). The San Marcos River at Luling has a lower specific conductance relative to the water coming from the springs (Table 1), which can mostly be attributed to a
loss in calcium and alkalinity. Conversely, sodium and chloride increased over the same stretch of river. At all three USGS sites, calcium accounts for over 62% of the equivalent charge of cations and alkalinity accounts for 75% or more of the anions (Table 1).

**Diel.**—On the upper river, above the SMSTP, dissolved oxygen concentrations varied on a diel cycle (Fig. 6A) driven primarily by macrophyte photosynthesis and respiration (Hannan & Dorris 1970). This diel cycle was dampened below the SMSTP (site 5), apparently because effluent released from the plant was always close to atmospheric saturation. Nutrient concentrations at the SMSTP site were pulsed during the day, apparently corresponding to releases from the plant. SRP (Fig. 6B), NH$_4$-N, TP, and NO$_3$-N (data not shown) all increased from 0600 to about 2400 hrs, and then concentrations decreased, with a distinct peak about 1800 to 2200. Both at upstream sites and in the Blanco River there was no discernible diel pattern of nutrient fluctuation.

**Algal biomass.**—Tiles incubated in the river downstream of the SMSTP accumulated significantly more algal biomass, 20.0 ± 4.5 μg chlorophyll a cm$^2$ (mean ± 95% confidence interval), than those at the upstream site, 5.8 ± 0.9 μg chlorophyll a cm$^2$. The bioassay experiment clearly showed that algal biomass responded only to the addition of phosphorus in water from the upstream site (Fig. 7). All treatments that included a phosphorus addition yielded about 100 μg chlorophyll a L$^{-1}$ after 14 d, and there was no additional increase with any nutrient in addition to phosphorus. All other treatments yielded < 10 μg chlorophyll a L$^{-1}$, including the control. Water from downstream of the SMSTP supported a much higher growth of algae (control = 46.4 μg chlorophyll a L$^{-1}$), and the only significant increase over the control was due to the addition of both nitrogen and phosphorus (99 μg chlorophyll a L$^{-1}$). The addition of metals inhibited algal growth in the downstream waters.

**DISCUSSION**

The chemical and physical quality of the San Marcos River evolves spatially and temporally as it flows from spring source to its confluence with the Guadalupe River. The changes in quality may be sudden or gradual, and the causes are both natural and anthropogenic. The first change is the exposure of aquifer water, which has typically been isolated from the atmosphere for a number of years (< 20 years, Guyton et al. 1979), to the atmosphere. Due to respiratory activity as the water percolates into and through the aquifer, high CO$_2$ concentra-
Figure 7. Final chlorophyll \( a \) concentrations for the nutrient limitation bioassay on samples collected upstream and downstream of the San Marcos sewage treatment plant. Error bars represent ± 95% confidence intervals.

(Continued)

tions (and resulting low pH) and depressed dissolved oxygen concentrations result, a common feature of groundwater ecosystems (Chapelle 1993). The low pH within the aquifer allows for more rapid chemical weathering and higher capacity for these ground waters to carry ions, particularly calcium and alkalinity. This accounts for the San Marcos River carrying higher ionic concentrations than the surface streams.
which feed it on the Edwards Plateau. The Blanco River (Table 1), which is one of the source rivers for the aquifer, is quite similar in its ionic chemistry to the other rivers that recharge the aquifer (Groeger & Gustafson 1994). Physical mixing processes allow the river waters to quickly reach atmospheric equilibrium with O₂ and CO₂, particularly as they leave Spring Lake. The damming of the river to form Spring Lake has created a very productive ecosystem, and metabolic processes of macrophyte communities within the lake and upper river have a great effect on certain parameters, such as the diel variation in O₂ and CO₂ and reduction of NO₃-N concentrations (Fig. 5).

At the confluence with the Blanco River, the variability of physical and chemical characteristics increased dramatically. This variability was most pronounced during storm events (22 July 1992 and 10 October 1994), with the highest turbidity and lowest specific conductance occurring shortly after large storms within the Blanco drainage basin. The Blanco River has a drainage basin of 1070 km² and therefore when these two rivers flow together, the terrestrial influence that is typical for rivers (e.g. diel light and temperature cycles, storm events, seasonality) begins to have a much larger effect on the spring-fed San Marcos River. Specific conductance downstream of the confluence reflected the lower concentration of ions in the Blanco River relative to the headwaters of the San Marcos River. The change in water chemistry in the San Marcos River downstream of this point can be partially attributed to the dilution effect of the Blanco River (Table 1). The long-term mean discharge from the San Marcos Springs (4.67 m³ s⁻¹, 1957-91) and from the Blanco River at Kyle (4.19 m³ s⁻¹, 1957-91) account for 42 and 38% of the mean discharge in the San Marcos River at Lulling (11.07 m³ s⁻¹, 1940-92). Nutrients tended to be low in the Blanco River, and were generally diluted downstream of the confluence.

The SMSTP was a major point source of nutrients in the upper river. SRP, TP, NH₄, and NO₃ all increased at this point. Both nutrient data and bioassay results suggest the river upstream of the SMSTP was strongly phosphorus-limited. At site 3, nutrient ratios (atomic) of dissolved inorganic nitrogen (NO₃+NO₂-N + NH₄-N) to SRP were 411:1, and for dissolved inorganic nitrogen to TP was 60:1. Other data (USGS provisional data) suggests these ratios are a regular feature of this stretch of the river. Normally, ratios > 10:1 or 20:1 are thought to be the point at which phosphorus becomes limiting (Sakamoto 1966; Forsberg et al. 1978), and the ratios reported here are very high relative to other phosphorus-limited ecosystems (Grimm & Fisher 1986; Hecky
The addition of phosphorus to the upper river greatly increases the capacity for algal growth. The State Fish Hatchery increased NH$_4^+$ in the river, and at least occasionally released high quantities of algae (and therefore TP) downstream, as they empty their ponds (TPWD 1994a). The increase in specific conductance below the SMSTP was due mostly to elevated concentrations of sodium and chloride in the treated sewage (USGS provisional data), as has been commonly associated with increased loading of domestic sewage in other systems (Feth 1981; Smith et al. 1987).

Increase in turbidity over the length of the river is probably due to both natural causes, as the river flows through the Blackland Prairie and Post Oak Belt physiographic zones, and land use patterns. Land use along a 1 mile corridor on either side of the river consists of 44% pasture and 18% cropland (Pulich et al. 1994). These types of land uses are often responsible for increases in suspended sediments (Gregory & Walling 1973). One of the apparent consequences of increased turbidity was a shift away from a macrophyte-dominated community in the lower river, but the increased variability in flow and changing bottom substrates may also be very important in this change. Sodium and chloride concentrations, and to a lesser extent sulfate, were higher at the Luling site due to oil field activity in Caldwell and Guadalupe counties, though these concentrations have been decreasing since the late 1960's with deep-well injection of brine and decreased oil pumping (Rawson 1968).

The San Marcos River suffers the same fate that other rivers draining the southcentral Texas Cretaceous limestone. Nutrients in these rivers are greatly increased by sewage inputs from population centers along the eastern edge of Edwards Plateau region corresponding to the Interstate 35 corridor. These include the San Gabriel River and the city of Georgetown, the Colorado River and Austin, and the Guadalupe River and New Braunfels. The city of San Marcos has concluded, along with the Texas Natural Resources Conservation Commission, that the city will reduce phosphorus concentrations in sewage effluent from a proposed upgrade of their plant down to 1 mg TP L$^{-1}$. This should cause a significant increase in the water quality of the river.

Acknowledgments

Dr. Bobby Whiteside contributed significantly to this project. We would like to thank Texas Parks and Wildlife Department, U.S.
Environmental Protection Agency, and the San Marcos River Foundation for partial funding of this research.

**Literature Cited**


Pulich, W. Jr., S. Perry & D. German. 1994. Habitat and land use inventory and change detection analysis of the San Marcos River Corridor, p. 11-33 IN The San Marcos River: A case study, Texas Parks and Wildlife Department, Austin, Texas.


TPWD. 1994a. Biological assessment for the A.E. Wood State Fish Hatchery. Texas Parks and Wildlife Department, Austin, TX, 100 pp.

AWG at: ag11@swt.edu
PERMUTATIONS AND CHANGE RINGING

David R. Cecil
Department of Mathematics
Texas A&M University-Kingsville
Kingsville, Texas 78363

Abstract.—Computers have long used permutations in ordering/sorting routines. Now permutations are using computers. The connection is change ringing. The mark ordering algorithm techniques of the 1960s, used to generate permutations for computer usage, are similar to an early method of change ringing known as Plain Bob. Now computers are instrumental in solving a 350 year-old problem concerned with generating all possible permutations on a set of seven bells subject to certain restraints. This paper describes various methods of generating permutations in change ringing, gives algebraic formulations for some of them and ends with a discussion of the centuries old problem mentioned above.

ENGLISH CHANGE-RINGING

There are more than 5000 churches with belltowers in England today. Canada and the USA have a total of 35. The most famous one in the United States is Old North Church in Philadelphia (Paul Revere was a bell ringer there and thus had access to the tower). Texas has two working belltowers for English change ringing, one in Houston (St. Thomas Episcopal Church, eight bells, 7-0-7, 1971) and one in Abilene (Church of the Heavenly Rest, six bells, 6-1-5, 1982). Bell weights are expressed in hundred-weights (cwt), where 1cwt = 112 lbs., quarter hundred-weights (=28 lbs.) and pounds, with an expression such as "6-1-5" referring to the heaviest bell in a tower. In Abilene the heaviest weighs 705 lbs. (6*112 + 1*28 + 5 = 705).

English change ringing consists of ringing n tuned bells (4 ≤ n ≤ 12 with 8 quite common, in which case the bells are tuned to the notes of an octave such as C to the next lowest C) in a steady rhythm so that the bells ring some subset of the group of all possible permutations of n. There are n! possible changes or permutations on n bells. Each tone row is the result of applying a permutation and consists of ringing each of the n bells exactly once. There is usually a one-beat pause at the end of every second row. An extent on n bells consists of ringing n! + 1 changes beginning and ending with the bells in the row 123...n and with no other change repeated. Bell 1 is called the Treble and is the lightest bell in a tower. The weights get progressively heavier as one goes from bell 1 to bell n with the heaviest bell called the Tenor.
The twenty-four possible changes on a set of four bells can be rung in less than a minute. Ringing all 5040 changes on seven bells takes about three hours and is called a peal. An extent on nine bells would take about eight to nine days of continuous ringing.

**RULES FOR RINGING METHODS**

1. Each composition begins and ends in rounds (the row 123...n), meaning that the bells are rung progressively downward in tone.

2. Each bell sounds exactly once in each tone row.

3. No bell may change its order of ringing by more than one position up or down from one row to the next (bells are swung through a full circle, which allows precise timing but restricts the movement of the bells within the pattern; hence the only possible changes consist of transpositions of pairs of adjacent bells). As many pairs of bells as possible should change from row to row so as to produce variety.

4. No row is repeated within a composition (the ringing is said to be true).

5. No bell may lie still (strike in the same position) for more than two successive changes (this rule is relaxed occasionally).

Ringers rely on any symmetries of a composition to memorize it; no music or other visual aids are available when they ring. Compositions are rung continuously and by the same ringer for each bell (or ringers for very heavy bells).

**SOME TERMINOLOGY**

The notations used by bell-ringers and the corresponding permutations are given below. Multiplications of permutations are to be performed right to left, while the bell-ringers notation is considered as operating from left to right so, for example, xb means change x is rung first then change b follows.

On an even number n of bells: \( x = (12)(34)(56)\ldots(n-1,n) \), \( x \) means all adjacent bells are crossed; \( 1n = 1 = n = (23)(45)(67)\ldots(n-2,n-1) = b \);
12 = (34)(56)(78)···(n-1,n) = c and 14 = (23)(56)(78)··· = d, with xb
= (1246···753) = (1246···, n-2, n, n-1, n-3,···753). So on 4 bells, known
as minimus, 14 = (23) = b means that the bells in places 1 and 4 are
fixed, denoted simply by 1 or 4, while the bells in internal places 3 and
4 interchange places.

On an odd number n of bells: x = n = (12)(34)(56)···(n-2,n-1), x
means the nth place is fixed; 1 = (23)(45)(67)···(n-1,n) = b; 12n =
(34)(56)(78)···(n-2,n-1) = c and 14n = (23)(56)(78)··· = d, with xb =
(1246···753) = (1246···, n-3, n-1, n, n-2,···753). Thus for doubles (5
bells) x = 5 = (12)(34); 1 = (23)(45) = b; 125 = (34) = c and 145 =
(23) = d.

For any number of bells xb = (1246···753) and (xb)n-1 = (1357···642),
the inverse of xb. Also (xb)n-1 x equals (23)(45)(67)···(n-2,n-1) for n
even, and equals (23)(45)(67)···(n-1,n) for n odd.

The Simplest Group to Ring

Plain Hunt (or plain course, or the hunting group H) produces 2n
different changes. It is the dihedral group Dn of order 2n with I = (1) =
(xb)n = x2 = (b)2. With an even number n of bells plain hunt is
denoted by (x.1n)n and can be described by “all pairs change,” then
“central pairs change,” then “all pairs change,” etc. until rounds is
repeated. On an odd number n of bells the representation is (n.1)n with
corresponding description “back bell stays fixed and all other pairs
change,” then “front bell stays fixed and all other pairs change,” then
“back fixed ···,” etc. To a bell-ringer Plain Hunt Minimus is written as
x14x14x14x14 while Plain Hunt Doubles is 5.1.5.1.5.1.5.1.5.1.

In Plain Hunt the treble moves, or courses, row to row from position
1 to 2 ··· to n, repeats once at n (makes places at n), then moves to n-1,
then to n-2, ··· to 1 at which time the bell makes places in 1 and the
process is repeated. In going from position 1 to position n (or hunting
up from the front to the back as it is called), the treble strikes slower
(more bells, n of them, strike in between) than when it is going
(hunting) down from n to 1. All n of the bells plain hunt, each bell
beginning at a different position; the order being given by the
permutation (xb)n-1, with (from rounds) the odd numbered bells hunting
up and the even numbered ones hunting down.
Table 1. Plain Bob Minimus.

<table>
<thead>
<tr>
<th>Lead 1</th>
<th>Lead 2</th>
<th>Lead 3</th>
</tr>
</thead>
<tbody>
<tr>
<td>x</td>
<td>1234</td>
<td>1342</td>
</tr>
<tr>
<td>2143</td>
<td>x</td>
<td>3214</td>
</tr>
<tr>
<td>2413</td>
<td>12(34)</td>
<td>2314</td>
</tr>
<tr>
<td>4231</td>
<td>xb</td>
<td>4213</td>
</tr>
<tr>
<td>4321</td>
<td>14(23)</td>
<td>2413</td>
</tr>
<tr>
<td>3412</td>
<td>(xb)^2</td>
<td>4132</td>
</tr>
<tr>
<td>3142</td>
<td>(xb)</td>
<td>14(34)</td>
</tr>
<tr>
<td>1324</td>
<td>(xb)^3</td>
<td>1412</td>
</tr>
<tr>
<td>1342</td>
<td>bc</td>
<td>1423</td>
</tr>
</tbody>
</table>

What happens to bell 2 in any lead happens to bell 3 in the following lead.

What happens to bell 3 in any lead happens to bell 4 in the following lead.

What happens to bell 4 in any lead happens to bell 2 in the following lead.

The row 3124 means the 3rd heaviest bell is rung 1st, followed by the treble with the tenor last.

Only when n is three does Plain Hunt produce all possible n! changes.

A Plain lead P is defined to be \((xb)^{n-1}xc = (3579...8642)\). This is \((3579..., n-3, n-1, n, n-2, ...8642)\) for n even and \((3579..., n-2, n, n-1, n-3, ...8642)\) for n odd. In doubles \(P = (xb)^4xc = (3542)\) with the bells in 13524 while in minor (6 bells) \(P = (35642)\) with the bells in positions 135264.

**INCREASING THE NUMBER OF PERMUTATIONS**

The Plain Bob method builds on Plain Hunt but inserts the "dodge" c to obtain the \((2n)^{th}\) row (instead of ringing another change of 1 = b which would return the bells to rounds). This dodge is performed a total of n-1 times (the results of which appear in rows \(k*(2n)\) for \(k = 1,2,...,n-1\)) so the pattern finally does repeat after \(2n^*(n-1)\) changes. Plain Bob may be described as \(P^{n-1} = ((xb)^{n-1}xc)^{n-1}\). The main feature of Plain Bob is the continued plain hunting of the treble. The rest of the bells (called the working bells) ring the same pattern, but starting at different lead ends, with the coursing order being 2468...753 (given by the permutation P). This means that, in the second lead, bell 2 does what bell 4 did in the first lead, etc. For four bells the pattern can be described as “lead (two blows always), hunt up, two blows behind, dodge 3-4 down, hunt down, lead, hunt up, dodge 3-4 up, two blows behind, hunt down, lead and make seconds”.

Exploring Plain Bob Minimus note that \( \text{PPP} = ((xb)^3xc)^3 \) with three repetitions of the sequence \( x14x14x14x12 \). This rings all \( 4! \) elements of \( S_4 \), the symmetric group on 4 symbols. If \( \mathcal{H} \) is the 8 element hunting group with \( I = (x14)^4 \), and \( \mathcal{B} \) the group \{I, bc, (bc)^2 \}, then all but the last row of the three columns (Table 1) give the coset decomposition \( S_4 = \mathcal{H} + bc \mathcal{H} + (bc)^2 \mathcal{H} \), while the first eight rows (Table 1) (of three elements each) represent the partition \( S_4 = \mathcal{B} + \mathcal{B} x + \cdots + \mathcal{B} (xb)^3x \).

The purpose of bobs and singles is to alter the coursing order, so as to introduce rows not present in a plain course.

A bob is formed (CCCBr 1995a) by moving places (e.g. fourth’s place, rather than second’s place, is made at lead-end) or by the addition or removal of non-adjacent places (e.g. at the lead-end in the plain course of a method, second’s, fifth’s and eight’s place may be made, and the bob removes the first two of these). The change \( d \) is such an example, where \( d = 145 = (23) \) in doubles and, in minor, \( d = 14 = (23)(56) \). In most even-bell methods the bob involves one bell making fourth’s. A bob always rearranges the positions of an odd number of bells.

A Bob lead, denoted by \( B \), is defined as \((xb)^{n-1}xd = (579\ldots n\ldots 64)\). In minor \( B = (xb)^5xd = (564) \) with the bells in 123564 while in triples (seven bells) \( B = (xb)^6xd = (5764) \) with the bells in 1235746. The method Call Bob has the representation \( (P^n-2 B)^3 = [((x.1n)^{n-1} x.12.)^{n-2} (x.1n)^{n-1} x.14]^3 \) giving \( 3(2n(n-1)) \) different changes when \( n \) is at least 5. In doubles \( (PPP)^3 = (253)^3 \) give the full extent of \( 5! \) changes.

A single is formed (CCCBr 1995a) by the addition of pairs of adjacent places to the places of the plain lead or the bobbed lead. An example is \( 1234 = (56) \) in minor, or \( (56)(78)\ldots \) for \( n \) bells. In most even-bell methods a single involves making third’s and fourth’s. A single always rearranges the positions of an even number of bells in the coursing order. The letter \( S \) denotes a single lead, which is defined as \( (xb)^{n-1}x(56)(78)\ldots = (23)(579\ldots 64) \). In minor \( S = (xb)^5x(56) = (23)(564) \) with the bells in positions 132564 and in major (eight bells) \( S = (xb)^7x(56)(78) = (23)(57864) \), bells in 13257486.

In any of the plain leads \( P \) of Plain Bob a bob or a single can be called instead of performing the \( c \) change of the \( P \) lead. The method known as Call Single is obtained if a single \( S \) is inserted in place of the
bob B in Call Bob on n bells (forming \((P^{n-2} S)^3\)). When n is equal to six the 180 changes \((P^4 B)^3\) of Call Bob Minor can be doubled to 360 with the operation \((P^4 B)^2 (P^4 S)(P^4 B)^2 (P^4 S)\).

The values for P, B and S vary with methods that are not single plain hunt.

**The Standard Four**

The four procedures that many ringers learn first are Plain Bob, Grandsire, Kent and Stedman. With some knowledge of Plain Bob, the remaining three can be briefly explored.

In Double Hunt methods two bells (one of them being the treble) plain hunt. In the Grandsire method (best suited for an odd number of bells) the other plain hunt bell is the second. Grandsire Doubles has a plain course of three cosets (of 10 changes each) for a total of 30 changes. The notation is given by \(P^3 = (W.5.1)^3\), where \(W = 3.1(5.1)^3\). This begins with the \(3 = (12)(45)\) change since this is an easy one for ringers to remember when to perform the 3 change again (namely when the treble returns to the lead). With the hunting group \(\mathcal{R}\) having \(I = (1.5)^3\) this plain course coset form is \(\mathcal{R} + (354) \mathcal{R} + (354)^2 \mathcal{R}\). In order to ring all \(5! = 120\) changes necessary to obtain \(S_5\) the formula \(((PB)^2 PS)^2\) is used. Here \(B = W.3.1\) is the bobbed lead and \(S = W.3.123\) is the single lead. Some other ways to obtain \(S_5\) are \((PS (PB)^2)^2\) and \((SPSB)^3\). For \(n\) odd and at least 5 it is known that there is no extent for Grandsire using only plain and bob leads (White 1987).

In Treble Dodging methods the treble dodges while hunting, that is it moves row to row in the order 1,2,1,2, 3,4,3,4, ..., n-1,n,n-1,n, n,n-1,n,n-1, ..., 4,3,4,3, 2,1,2,1 at which time the process is repeated. In treble dodging methods (almost always performed using an even number of bells) a lead is a group of \(4n\) changes commencing when the treble appears in position 1 and ending the third time the treble is in that same position. Kent Treble Bob Minor with notation \((Y16Y^*16)^5\), where \(Y = 34x34(16x12x)^2\) and \(Y^*\) is \(Y\) reversed, has five leads each with 24 changes for a total of 120 changes. As with any treble bob method no internal places are made as the treble passes from one dodging position to another. Further analysis of Kent Treble Bob Minor is available (White 1993).
In Stedman’s Principle (rung on an odd number of bells) there is no fixed (plain hunting) bell as has been the case in the methods discussed above. All the bells are working bells. One formula for Stedman’s Doubles is \{[(3.1)^2 3.5 (1.3)^2 1.5]^4 (3.1)^2 3.5 (1.3)^2 1.125]\}^2 (White 1996). This generates all 120 possible changes. A collection of 82 Stedman Triple methods was compiled in mid 1994 (CCCBr 1995b). Stedman Triples uses alternating groups of slow and quick sixes with a slow six being 3.1.3.1.3.1 and a quick six being 1.3.1.3.1.3 (Griffiths 1994). Each row of six is connected to the next row of six by any one of three kinds of changes; a plain 7 = (12)(34)(56), a bob 5 = (12)(34)(67), or a single 567 = (12)(34). Stedman’s Triples has rounds as the fourth row of a quick six for the beginning group, as for example starting with 3215476, 3124567, 1325476, 1234567, 2135476 and 2314567. The next group of six (a slow one) would begin with either 3241657 (as the result of a plain), or with 3241576 (resulting from a bob) or with 3241567 (the result of a single).

The centuries old problem in bell ringing was whether it was possible to ring an extent of all 7! possible changes without using singles? The first affirmative answer (Wyld 1994) used 705 bobs. A number of other solutions appeared in rapid succession with the current minimum number of bobs needed with no singles being 438 (Johnson 1995). The quest continues and can be followed in The Ringing World weekly journal.

**LITERATURE CITED**


Knuth, Donald E. 1973. The art of computer programming/volume 3 sorting and searching. Addison-Wesley, Reading, Massachusetts, xii+725pp.+foldout.


DRC at: D-Cecil@tamuk.edu
THE TIME FROM SUNRISE TO SUNSET

Stewart C. Welsh

Department of Mathematics, Southwest Texas State University
San Marcos, Texas 78666

Abstract.—An approximation is obtained for the length of time that the upper rim of the sun remains above the horizon on a given day of the year at a given latitude. Only basic methods of plane trigonometry and analytic geometry are employed in these arguments.

This contribution was motivated by articles by Penning (1990) and Wagon (1990). The primary objective is to inspire undergraduate calculus and analytic geometry students by applying the basic theory, together with some basic plane trigonometry, to a real life problem: On a given day of the year and at a given latitude, for how many hours will the top rim of the sun be visible?

This problem has, of course, been solved to a great degree of accuracy and its solution may be found in any text on astronomy (i.e. Montenbruck 1991 and Smart 1977). To understand these solutions one is required to know basic astronomical nomenclature such as declination, hour angle, zenith angle, etc. and to have some knowledge of spherical trigonometry. Most students lack this knowledge.

The objective of this exercise is to derive a formula for the number of hours from sunrise to sunset on a given day of the year and at a given latitude using only basic plane trigonometry and some simple formulae from analytic geometry. No knowledge of astronomy is assumed. The material is well within the grasp of the average undergraduate student who has completed a class in analytic geometry.

The author has used portions of this material for projects in trigonometry classes by applying the techniques to the special cases outlined in the section on exercise problems. The response from students was extremely encouraging.

MAIN DERIVATION

A simple Copernican model.—The formula shall be derived from a greatly simplified model. First, the earth is treated as a perfect sphere that rotates on its axis once every twenty-four hours, during which time the change in the earth’s position relative to the sun is neglected. It is assumed that the earth moves at uniform speed in a circular orbit with the sun at its center, making one complete revolution every 365 days.
Figure 1. Representation of the counterclockwise circular orbit of the earth around the sun as seen from above the z-axis. This orbit lies in the xy plane. Vector $\mathbf{n}$ denotes the projection, onto the xy plane, of the radius vector $\mathbf{N}$ through the North Pole $N$ (Figure 2). The rays of light from the sun are parallel to the y-axis, and the x-axis is chosen so that we have a right-handed coordinate system. Angle $\alpha$ denotes the position of the earth counterclockwise relative to the Spring equinox.

A Cartesian coordinate system will be used with the z-axis normal to the plane of the earth’s orbit, so that when viewed from the positive z-axis, the earth moves counterclockwise around its orbit. The direction of the z-axis is called the zenith (Figure 1). The earth’s axis is not parallel to the zenith, and this is the primary cause of the variation in the length of day during a year. The angle between the zenith and the vector $\mathbf{N}$ from the center of the earth to the North Pole is taken to be $23.5^\circ$. The equinoxes are the days when the projection $\mathbf{n}$ of $\mathbf{N}$ onto the xy plane is tangent to the earth’s orbit, and the solstices are the days when $\mathbf{n}$ and the orbit are perpendicular.

Figure 2 shows, as projected onto the yz plane, the earth’s attitude relative to the sun’s rays on the summer solstice. The sun is so far away that we may treat its rays as being parallel. The great circle on the earth’s surface that is orthogonal to the sun’s rays is known as the
Figure 2. The earth-sun configuration at the Summer solstice as projected onto the yz plane. The axis of the earth cuts through the North Pole N and is slanted at 23.5° from the z-axis. We assume, due to the great distance from the sun to the earth, that the rays of the sun are parallel when they strike the earth with each ray parallel to the y-axis. The projection onto the yz plane of both the circle of latitude at \( \theta_l \) (see Fig. 4) and the equator are also shown.

circle of illumination which is formed by the intersection of the earth with the xz plane. Because of atmospheric refraction of the sun’s rays, however, the sun is actually visible from beyond the circle of illumination. The earth’s atmosphere bends the sun’s rays towards the earth in such a way that, according to the book of Smart (1977), the upper rim of the sun is visible to an observer 0.833° beyond the circle of illumination (Figure 3). Of this, 0.567° is the average refraction contribution and an additional 0.266° allows for the half-diameter of the sun’s disk, since sunrise and sunset are determined by the upper rim of the sun, rather than the sun’s center, crossing the horizon. One can see qualitatively from Figures 1 and 2 that in the northern hemisphere the day will be longest on the summer solstice and shortest on the winter solstice.

An earth-centered coordinate system.—As mentioned above, the z-axis of our Cartesian coordinate system is taken to be orthogonal to the plane of the earth’s orbit. It is convenient to let the coordinate system move with the earth, with the origin being the center of the earth and the
Figure 3. If $M$ represents either the point of sunrise or sunset, then the great circle shown here is defined to contain the $y$-axis and the point $M$ and is, therefore, perpendicular to the $xz$ plane. The intersection of the earth and the $xz$ plane defines the circle of illumination which is represented by the vertical axis through the origin $O$. Since $M$ lies at an angular elevation of $0.833^\circ$ beyond the circle of illumination, we must have $y = \sin 0.833$ at $M$

positive $y$-axis always pointing in the direction from sun to earth. The direction of the $x$-axis is then determined by the condition that the coordinate system be right-handed. Thus, the zenith direction remains fixed, relative to the sun, but the $x$ and $y$ axes turn at the rate of one revolution per year (Figure 1).

The position of the earth at any time is specified by the angle $\alpha$ of the radius vector from sun to earth, which we will measure counterclockwise from the Spring equinox, with $-180^\circ < \alpha \leq 180^\circ$ as in Figure 1. From Figures 1 and 2, one can see that for $0^\circ < \alpha < 180^\circ$ the vector $n$ has a negative $y$-component (and the days will be longer than on the equinoxes), while for $-180^\circ < \alpha < 0^\circ$ this vector has a positive $y$-component (and the days are shorter than on the equinoxes).

To become more familiar with this annually turning coordinate system, one should determine the coordinates $(x_i, y_i, z_i)$ of the North Pole as functions of the angle $\alpha$. Without loss of generality one may take the radius of the earth to be unity, then the surface of the earth is the sphere $x^2 + y^2 + z^2 = 1$. From Figure 2, it is clear that $z_i = \cos 23.5$ and the
projection \( n \), onto the \( xy \)-plane, of the vector \( N \) from the center of the earth to the North Pole has length \( r = \sin 23.5 \). Since the direction of \( n \) remains fixed relative to the \( z \)-axis throughout the year as the \( xy \) axes turn, the vector \( n \) will appear to turn clockwise through one revolution per year relative to the \( xy \) axes. From Figure 1, the components of \( n \) relative to the \( xy \) coordinate system are seen to be \((r \cos(-\alpha), r \sin(-\alpha)) = (r \cos \alpha, -r \sin \alpha)\), since the angle \( \alpha \) is measured counterclockwise from the Spring equinox where \( n \) lies along the positive \( x \)-axis. Thus, the coordinates of the North Pole, the components of the vector \( N \), are:

\[
x_1 = r \cos \alpha = \sin 23.5 \cos \alpha,
\]

\[
y_1 = -r \sin \alpha = -\sin 23.5 \sin \alpha,
\]

and

\[
z_1 = \cos 23.5.
\]

One can now turn to the main problem: Calculating the length of the day at a given latitude \( \theta_L \) in the northern hemisphere when the earth’s position is represented by a specified angle \( \alpha \). Recall that the latitude of any point in the northern hemisphere is the angle \( \theta_L \) measured north from the equator. The points with a given latitude \( \theta_L \) form a circle of radius \( \cos \theta_L \) on the surface of the earth called the circle of latitude \( \theta_L \), or the parallel of latitude (Figure 4). This circle is formed by the intersection of the \( x^2 + y^2 + z^2 = 1 \) and the plane \( P \) (say) which is parallel to the equator at a distance of \( \theta_L \).

The vector \( H \) from the origin to the center \( H \) of the circle of latitude \( \theta_L \) satisfies \(( |H| / |N| ) = \sin \theta_L \), so \( H = N \sin \theta_L \) as may be seen from Figure 4. Since the components of the vector \( N \) in our \( xyz \) coordinate system have been found above, one sees that

\[
H = (\sin 23.5 \cos \alpha \sin \theta_L, -\sin 23.5 \sin \alpha \sin \theta_L, \cos^2 23.5 \sin \theta_L).
\]

Knowing a point \( H \) on the plane \( P \) and a normal vector \( N \), one can write down the equation of \( P \) in the form,

\[
x \sin 23.5 \cos \alpha - y \sin 23.5 \sin \alpha + z \cos 23.5 = \sin \theta_L \sin^2 23.5 \cos^2 \alpha + \sin \theta_L \sin^2 23.5 \sin^2 \alpha
\]

\[
+ \sin \theta_L \cos^2 23.5,
\]

which simplifies to,

\[
x \sin 23.5 \cos \alpha - y \sin 23.5 \sin \alpha + z \cos 23.5 - \sin \theta_L = 0. \quad (1)
\]
In Figure 5, we show the circle of latitude $\theta_L$ with the sun's rays impinging on it when the earth's position is specified by the angle $\alpha$, and we indicate the two points $S$ and $T$ where the plane $y = \sin 0.833$ intersects with this circle. These points lie $0.833^\circ$ beyond the circle of illumination (which is the great circle obtained by the intersection of the earth with the $xz$ plane) and, thus, it is daybreak at $T$ and sunset at $S$, since the earth turns counterclockwise when viewed from above the North Pole. The main task is to find the coordinates of these two points, since the length of the day at latitude $\theta_L$ is then the time required for the earth to turn on its axis through the arc from $T$ to $S$.

Since points $T$ and $S$ lie in the intersection of the sphere $x^2 + y^2 + z^2 = 1$ and the plane $y = \sin 0.833$, then the $x$ and $z$ coordinates of $T$ and $S$ are related by the equation,

$$z^2 = \cos^2 0.833 - x^2.$$
Figure 5. The projection onto the the $xy$ plane of the circle of latitude at $\theta_L$ as viewed from above the $z$-axis. We indicate the direction of the sun's rays when the earth is specified by a counterclockwise angle $\alpha$ measured relative to the Spring equinox. $T$ and $S$ denote sunrise, respectively, sunset, since the earth turns counterclockwise in its orbit as viewed from the zenith. From Fig. 3, it is seen that at points $T$ and $S$ we must have $y = \sin 0.833$.

$T$ and $S$ also lie on the plane $P$ described by Eq. (1), so one has,

$$\pm \cos 23.5 \sqrt{\cos^2 0.833 - x^2} = -x \sin 23.5 \cos \alpha + \sin 0.833 \sin 23.5 \sin \alpha + \sin \theta_L.$$  \hspace{1cm} (2)

Writing,

$$T_1 = \sin 0.833 \sin 23.5 \sin \alpha + \sin \theta_L,$$
Figure 6. The intersection of the earth and the plane $P$ produces the circle of latitude at $\theta_t$, which has its center at $H$ and radius equal to $\cos \theta_t$. We depict this circle as viewed from above the North Pole. Points $T$ and $S$ represent sunrise, respectively, sunset; while $T$ and $S$ denote the position vectors of, respectively, sunrise and sunset relative to the origin, $H$, of the $x'$, $y'$ axes. The angle $\phi$ swept out from $T$ to $S$ determines the time taken from sunrise to sunset as $D = (\phi/360)24 = (\phi/15)$ hours.

and squaring both sides of Eq. (2) produces a quadratic equation in $x$ which has the solution,

$$x = \frac{T_1 \sin 23.5 \cos \alpha}{\cos^2 23.5 + \sin^2 23.5 \cos^2 \alpha}$$

$$\pm \frac{\cos 23.5 \sqrt{\cos^2 0.833(\cos^2 23.5 + \sin^2 23.5 \cos^2 \alpha) - T_1^2}}{(\cos^2 23.5 + \sin^2 23.5 \cos^2 \alpha)}$$

(3)

It is clear from Figure 5 that the $x$-coordinate of the point $T$ is obtained
from Eq. (3) by choosing the negative sign, while $S$ corresponds to taking the positive sign. Note that, if the expression inside the radical in Eq. (3) becomes negative, then for these values of $\alpha$ and $\theta_L$ there is no sunrise, or there is no sunset. These considerations are made below under Exercise Problems.

Using the $x$ and $y$ coordinates of $T$ and $S$, one could now calculate the time taken from sunrise to sunset. For the moment, denote the coordinates of $T$ and $S$ by $(x_T, y_T, z_T)$ and $(x_S, y_S, z_S)$, respectively. It is more convenient at this juncture to choose the point $H$ as the origin and to determine the coordinates of $T$ and $S$, $(x'_T, y'_T, 0)$, respectively, $(x'_S, y'_S, 0)$ (say), relative to a new right-handed coordinate system $x'y'z'$ where $x'$ and $y'$ lie in the plane $P$ containing the circle of latitude $\theta_L$ as shown in Figure 6, and $z'$ is parallel to $N$. Since the earth rotates on its own axis once every twenty-four hours, the time taken from sunrise to sunset is given by $D = 24\phi/360 = (\phi/15)$ hours, where $\phi$ is the angle swept out by the radius vector of the circle of latitude as it rotates from position $HT$ to $HS$ as in Figure 6.

Denoting the vectors $HT$ and $HS$ by, respectively, $T$ and $S$, one can determine $\phi$ by means of the dot and vector products. First one has,

$$\cos \phi = \frac{T \cdot S}{|T||S|} = \frac{T \cdot S}{\cos^2 \theta_L} = \frac{x_T x'_S + y_T y'_S}{\cos^2 \theta_L}. \quad (4)$$

Also,

$$T \times S = |T||S| \sin \phi \left(\frac{N}{|N|}\right)$$

$$= \cos^2 \theta_L \sin \phi \left(\frac{N}{|N|}\right). \quad (5)$$

So, Eq. (5) yields,

$$\sin \phi = \frac{(x'_T y'_S - y'_T x'_S)}{\cos^2 \theta_L}. \quad (6)$$

Thus, Eqs. (4) and (6) enable us to uniquely specify $\phi$ in the interval $[0^\circ, 360^\circ)$. If the situation arises that $\cos \phi = 1$ and $\sin \phi = 0$, then it will always be clear from the date and latitude under consideration whether $\phi$ is to be taken as $0^\circ$ or $360^\circ$.

The next task is, therefore, to choose judiciously the $x'y'$ axes to lie in the plane $P$ with origin at $H$. 
The translations,
\[ \hat{x} = x - \sin 23.5 \cos \alpha \sin \theta_L, \]
\[ \hat{y} = y + \sin 23.5 \sin \alpha \sin \theta_L, \]
and
\[ \hat{z} = z - \cos 23.5 \sin \theta_L, \]
define new axes \( \hat{x}\hat{y}\hat{z} \) with origin at the point \( H \) (Figure 5). Rotating the \( \hat{x}\hat{y} \) axes clockwise, in the \( \hat{x}\hat{y} \) plane, through an angle \( \alpha \) produces yet another set of axes \( \bar{x}, \bar{y} \) and \( \bar{z} \) (say) for which \( \bar{x} \) is parallel to \( n \) (Figure 5). Clearly, these new axes satisfy the equations,
\[ \bar{x} = \hat{x}\cos \alpha - \hat{y}\sin \alpha \]
and
\[ \bar{y} = \hat{x}\sin \alpha + \hat{y}\cos \alpha. \]

Finally, one rotates the \( \bar{x}\bar{z} \) axes clockwise, in the \( \bar{x}\bar{z} \) plane, through 23.5° to obtain the desired \( x'y'z' \) axes where: \( y' = \bar{y}, y' = (\sec 23.5)\bar{x} \)
and \( z' \) is parallel to the vector \( N \) so that the coordinate system is right-handed. It is easy to see from Figures 4 and 5 that axes \( x' \) and \( y' \) do indeed lie in the plane \( P \). This sequence of translations and rotations of axes produces the following sets of coordinates, for the points \( T \) and \( S \) relative to the \( x'y' \):
\[ x' = \sec 23.5 \left[ x_i \cos \alpha - \sin 0.833 \sin \alpha - \sin 23.5 \sin \theta_L \right] \]  
(7)
and
\[ y' = x_i \sin \alpha + \sin 0.833 \cos \alpha, \]  
(8)
for \( i = T \) and \( S \).

Now, the only unknown quantity remaining is the value of \( \alpha \). Since the earth orbits the sun in 365 days and there are 360° in one complete orbit, determined by \( \phi \) in the interval -180° < \( \alpha \) ≤ 180°, then \( \alpha \) is approximately the number of days from the Spring equinox to the date on which one wishes to calculate \( D \), with the proviso that \( \alpha \) is positive for dates closer to the summer solstice than the winter solstice and negative otherwise. Note that due to the actual elliptical orbit of the earth around the sun, the time taken for the earth to move around the sun from the Spring equinox to the Autumn equinox is about 184 days (92 days for both Spring and Summer), while Autumn to Spring takes only about 181 days (91 days for Autumn and 90 days for Winter). So,
if one is interested in a particular date which falls \( d \) days from the Spring equinox with \( d \) taken positive if the date lies in the period from Spring to Autumn and negative otherwise, then,

\[
\alpha = \begin{cases} 
\frac{90d}{92}, & \text{if } 0 \leq d \leq 92; \\
90 + \frac{(d - 92)90}{92}, & \text{if } 92 < d \leq 184; \\
d, & \text{if } -90 \leq d < 0; \\
\frac{90(d + 90)}{91} - 90, & \text{if } -181 < d < -90;
\end{cases}
\]  

To summarize the procedure for finding the length of time \( D \) from sunrise to sunset: Calculate \( \alpha \) from Eq. (9), for the date under consideration. Determine the \( x' \) and \( y' \) coordinates of the points \( T \) and \( S \) using Eqs. (7) and (8) in conjunction with Eq. (3), where the negative sign is taken for \( T \), the positive sign, for \( S \) and \( y_T = y_S = \sin 0.833 \). Finally, evaluate \( \phi \) from Eqs. (4) and (6) and obtain, \( D = (\phi/15) \) hours.

Note that the formula for the time from sunrise to sunset, derived in this exercise, is accurate to within about four minutes. The reader will find a table of observed sunrise and sunset times in Smith (1991).

For a rigorous account of how astronomers have successfully tackled the problem of calculating sunrise and sunset times to a great degree of accuracy, see Montenbruck (1991) and Smart (1977).

**Exercise Problems**

There are four convenient special cases for this formula; namely, the equinoxes and the solstices. As an exercise, the reader is urged to confirm the following results.

The Solstices.

(a) Summer:

Set \( a = 90^\circ \). Then, for \( 0 \leq \theta_L \leq 65.67^\circ \),

\[
D = \frac{1}{15} \left[ 360 - \cos^{-1}\left(2(\tan \theta_L \tan 23.5 + \sec 23.5 \sec \theta_L \sin 0.833)^2 - 1\right) \right]
\]

\[
= \frac{1}{15} \left[ 360 - 2 \cos^{-1}(\tan \theta_L \tan 23.5 + \sec 23.5 \sec \theta_L \sin 0.833) \right].
\]
Note that, if \( \theta_L > 65.67^\circ \), then the sun is visible for the entire day, i.e., there is no sunset and \( D = 24 \) hours.

(b) Winter:

Set \( \alpha = -90^\circ \). Then,

\[
D = \frac{2}{15} \cos^{-1}(\tan \theta_L \tan 23.5 - \sec 23.5 \sec \theta_L \sin 0.833),
\]

is valid in the interval \( 0^\circ \leq \theta_L \leq 67.33^\circ \). For \( \theta_L > 67.33^\circ \), the sun is below the horizon for the entire day and \( D = 0 \) hours.

The Equinoxes.

Spring and Autumn:

Set \( \alpha = 0^\circ \) or \( \alpha = 180^\circ \). Then,

\[
D = \frac{1}{15} \left[ 360 - \cos^{-1}(2 \sec^2 \theta_L \sin^2 0.833 - 1) \right]
\]

\[
= \frac{1}{15} \left[ 360 - 2 \cos^{-1}(\sec \theta_L \sin 0.833) \right]
\]

\[
= \frac{1}{15} \left[ 180 + 2 \sin^{-1}(\sec \theta_L \sin 0.833) \right].
\]

For any latitude with \( \theta_L \geq 89.167^\circ \), there is no sunset and \( D = 24 \) hours.

**LITERATURE CITED**


SCW at: sw03@swt.edu
COMPLETE STRUCTURAL DETERMINATION OF 1,2-BENZO-8-(ALANYL)-3-PHENOXAZONE BY NMR TECHNIQUES (HSQC & HMBC)

K. G. Bhansali, S. G. Milton and F. Matloubimoghaddam*
College of Pharmacy and Health Sciences, Texas Southern University
Houston, Texas 77004 and *Department of Chemistry, Sharif University of Technology, Tehran, Iran

Abstract.—The structure of 1,2-Benzo-8-(Alanyl)-3-Phenoxazone was determined by use of heteronuclear single quantum coherence (HSQC) and heteronuclear multiple bond coherence (HMBC). Both HSQC and HMBC experiments optimize direct and long range H' - C'^ connections respectively rather than C'^-H' connections. In this study HMBC experiments allows the assignment of quaternary carbons C-3 and C-17 with protons that are two and three bonds away (\( ^{3}J_{C-H} \)). The HSQC experiments show the direct H' - C'^ connections for C-15, C-16, C-4, C-6, C-11, C-14 and C-9 by using C'^ satellites in proton spectrum to acquire correlation. This study confirms the attachment of alanyl group at C-8 and the position of C-3 in the form of C = O of BLP.

It has been shown that 1-nitroso-2-naphthol qualitatively and quantitatively reacts with various phenolic compounds in the presence of HNO\(_3\) (Bhansali 1971). In order to study the mechanism of reaction, nitroso naphthol was reacted with tyramine and 1,2-Benzo-8-(2-aminoethyl)-3-phenoxazone (BAP) was produced. This compound was characterized by one and two-dimensional NMR spectroscopy and mass spectrometry (Donaldson & Lenon 1979). BAP is an analog of actinomycin D and is a very potent antitumor agent which is also very toxic for human use. Moreover, BAP was selected by the National Cancer Institute (NCI) of Bethesda, Maryland, for screening against HIV activity during its drug development program. Similarly, the reaction of nitroso naphthol with tyrosine produced 1,2-Benzo-8-(alanyl)-3-phenoxazone, (BLP) and was characterized by one and two-dimensional NMR spectroscopy and mass spectrometry (Bhansali & Kook 1993). This compound was screened against various cell lines of prostate cancer and HIV activity by the National Cancer Institute in its drug development laboratories and has shown very promising results. Further, this compound received a patent by the U.S. Patent Office in 1994.

Moreover, heteronuclear single quantum coherence (HSQC) and heteronuclear multiple bond coherence (HMBC) experiments are quite useful in sequencing carbon atoms through proton determination especially for the end parts of the molecule. Because of the usefulness of this compound, it is considered of importance to confirm its absolute configuration by HSQC and HMBC experiments.
Figure 1. HSQC contour plot of 1,2-benzo-8-alanyl-3-phenoxazone nitrate.

Table 1. \(^1\text{H}-^{13}\text{C}\) - NMR (HSQC) Data of BLP

<table>
<thead>
<tr>
<th>Position</th>
<th>(^1\text{H}(^3\text{J Hz}))</th>
<th>(^{13}\text{C})</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td></td>
<td>130.8</td>
</tr>
<tr>
<td>1a</td>
<td></td>
<td>147.1</td>
</tr>
<tr>
<td>2</td>
<td></td>
<td>132.1</td>
</tr>
<tr>
<td>3</td>
<td></td>
<td>182.9</td>
</tr>
<tr>
<td>4</td>
<td>6.43</td>
<td></td>
</tr>
<tr>
<td>4a</td>
<td></td>
<td>106.6</td>
</tr>
<tr>
<td>6</td>
<td>7.45</td>
<td></td>
</tr>
<tr>
<td>6a</td>
<td></td>
<td>143.0</td>
</tr>
<tr>
<td>7</td>
<td>7.48</td>
<td></td>
</tr>
<tr>
<td>8</td>
<td></td>
<td>133.3</td>
</tr>
<tr>
<td>9</td>
<td>7.78</td>
<td></td>
</tr>
<tr>
<td>9a</td>
<td></td>
<td>130.5</td>
</tr>
<tr>
<td>11</td>
<td>8.59 (1.3, 1.7, 7.9)</td>
<td>124.3</td>
</tr>
<tr>
<td>12</td>
<td>7.88 (1.3, 7.9, 9.1)</td>
<td>132.2</td>
</tr>
<tr>
<td>13</td>
<td>7.81 (7.2, 9.1)</td>
<td>132.5</td>
</tr>
<tr>
<td>14</td>
<td>8.15 (1.3, 2.3, 7.2)</td>
<td>125.4</td>
</tr>
<tr>
<td>15</td>
<td>3.16, 3.22 (4.5, 6.32, 8.0)</td>
<td>35.1</td>
</tr>
<tr>
<td>16</td>
<td>4.33 (4.5, 6.2)</td>
<td>53.1</td>
</tr>
<tr>
<td>17</td>
<td></td>
<td>170.5</td>
</tr>
</tbody>
</table>
Figure 2. HMBC contour plot of 1,2-Benz-8-alanyl-3-Phenoxazone Nitrate.

Table 2. NMR (HMBC) Data of BLP

<table>
<thead>
<tr>
<th>H</th>
<th>C</th>
</tr>
</thead>
<tbody>
<tr>
<td>14</td>
<td>C-3, C-12</td>
</tr>
<tr>
<td>15</td>
<td>C-17, C-16, C-8</td>
</tr>
<tr>
<td>6</td>
<td>C-9a</td>
</tr>
<tr>
<td>7</td>
<td>C-6a, C-15</td>
</tr>
<tr>
<td>9</td>
<td>C-6a, C-15</td>
</tr>
<tr>
<td>11</td>
<td>C-1a, C-13</td>
</tr>
<tr>
<td>4</td>
<td>C-2</td>
</tr>
<tr>
<td>13</td>
<td>C-11</td>
</tr>
</tbody>
</table>

Methods and Materials

BLP was run in DMSO-d$_6$ on the BrukerAMX500 HMBC and HSQC experiments were used to determine the complete structure of BLP. The former is the long-range $^1$H-$^{13}$C experiment which allows the assignment of quaternary carbons with protons which are two or three bonds away (2,3 J C-H), while by HSQC experiment the direct $^1$H-$^{13}$C connections were obtained by using $^{13}$C satellites in proton spectrum to acquire correlation.
RESULTS AND DISCUSSION

All carbons and protons can be assigned by HSQC (Figure 1, Table 1). The HMBC experiment demonstrates that the H-14 (Figure 2, Table 2) has long range coupling with C-3 carbonyl group (182.9 ppm) and C-12 (132.2 ppm), on the other hand, H-4 could be related via long-range correlation to C-2 (132.1 ppm), this confirms the position of C-3 carbonyl. For confirmation of the position of the substituent at C-8, the HMBC experiment also shows clearly the long-range correlations of the beta proton H-15 (3.2 ppm) of the amino acid part of the molecule with the carboxyl group of the amino acid C-17 (170.5 ppm), and the C-16 (52 ppm), and C-8 (135 ppm). This does not make the assignment of the peak at 135 ppm to C-8, because it still could be the C-7 of the other isomer. But protons H-7 (7.48 ppm) and H-9 (7.76 ppm) shows ($^3J_{C-H}$) correlation to C-6a (143.0 ppm) which pins down the assignment making it the 8-isomer. This in conjunction with the correlation of C-8 with H-15 (2.96 ppm) completes the match.

The present data generated by HMQC and HMBC experiments support the previous data on characterization of 1,2-Benzo-8-(2-aminoethyl)-3-phenoxazone by $^1$H-NMR, $^1$H-COSY, J resolved 2D and 13C $^1$H heteronuclear correlation experiments. Further, this study concludes the complete structural determination of the compound.

ACKNOWLEDGMENTS

This study was supported by a grant from Research Centers in Minority Institutions (RCMI) Grant No. 2G12RR03045-06.

LITERATURE CITED


SELECTIVE ACTIVATION OF STRESS PROTEINS IN THE MUSCLE OF THE PARASITIC WORM ASCARIS SUUM FROM PIG INTESTINE

Sheng-Hao Chao, Manus J. Donahue and Ruthann A. Masaracchia
Department of Biological Sciences, University of North Texas
Denton, Texas 76203-5220

Abstract.—The major tissues of Ascaris suum contain the stress proteins (HSP) corresponding to the HSP70 and HSP90 family. Western blot analysis determined that in muscle, intestine and reproductive tract, the HSP70 family was the most abundant stress protein. Two forms of immunoreactive HSP70 proteins were detected. The concentrations of HSP72 protein were 1.9, 2.3, and 0.76 pg/mg protein in intestine, muscle and reproductive tract, respectively. Constitutive levels of the HSP52 protein, which was also detected with the HSP70 antibody, were 0.80, 5.8, and 0.34 pg/mg in intestine, muscle and reproductive tract, respectively. Further studies on the HSP70 proteins in muscle revealed that the HSP72 protein is a cytoplasmic protein whereas the HSP52 was equally distributed in the soluble and particulate fraction of the muscle. In contrast, both proteins appeared to be cytoplasmic in intestine and reproductive tract. Parasites maintained ex vivo at 37°C or 40°C showed a 2-fold increase in both HSP72 and HSP52, consistent with results in other organisms which suggest that parasites mount only a modest heat stress response. By contrast, maintenance of Ascaris suum, an essentially anaerobic organism, in an oxygen atmosphere resulted in a 4-fold increase in HSP52, but no change in HSP72 levels. Collectively, the data suggest that the parasite Ascaris suum responds to selective stresses which may occur in its micro environment.

The stress protein family (HSP) was first observed in response to heat shock of Drosophila, but numerous studies since that time have established the universality of this response (Lindquist 1986). The major HSP protein families are highly conserved in prokaryotes and eukaryotes with respect to both structures and functions (Schlesinger 1990; Ang et al. 1991; Hendrick & Hartl 1993). The major HSP proteins, HSP70, occur in both cytoplasm and organelles where they bind to nascent or damaged unfolded proteins. Although these proteins are induced by a variety of environmental stresses, they also play an essential role in normal protein folding and cellular trafficking. By contrast, the HSP60 or groEl family of stress proteins are found only in bacteria or bacteria-derived organelles (mitochondria and chloroplasts). These proteins direct folding and oligomerization of proteins transported into these organelles although additional “housekeeping” functions have been proposed for these proteins. The functions of the HSP90/htpG and HSP27 families are less well understood. Deletion of the htpG gene in bacteria produces no detectable phenotypes, whereas deletion of the genes in yeast is lethal. In mammals, the HSP90 proteins are abundant
in normal cells and mediate a variety of regulatory events, of which steroid receptor activation is the best documented. HSP27 occurs in most cells, albeit at low concentrations, and is induced by heat shock or toxic chemicals. Other functions which have been associated with this protein include growth, differentiation and neoplastic transformation (Zhou et al. 1993).

In contrast to the acute heat shock response, some organisms which are persistently exposed to thermal variations develop thermal tolerance (Subjeck & Shyy 1986). In organisms with acquired thermotolerance, the HSP proteins are expressed at high constitutive level which in some cases is not further elevated after acute thermal stress. Studies of parasites which have developmental stages in both poikilotherm and homeotherms have suggested that thermal tolerance may be a common property of many parasitic organisms. Brandau et al. (1995) demonstrated that in two Leishmania strains (L. major and L. donovani) high constitutive levels of HSP70 and HSP83 were observed and neither of these proteins were induced by acute heat stress. In Tritrichomonas mobilensis, a mammalian parasite, and Tritrichomonas augusta, an amphibian trichomonad, considerably different thermotolerance was observed (Bozner 1996). Thermotolerance for HSP70 induction exhibited only a 4°C range in T. mobilensis, whereas T. augusta tolerates a 13°C cultivation range. De Carvalho et al. (1994) failed to detect a classical heat treatment response in Trypanosoma cruzi maintained in a 48 hr culture. Studies of HSP70 mRNA turnover in this study, as well as in the work of Brandau et al. (1995) suggest that regulation of HSP induction may occur primarily at post-transcriptional level in these parasites.

Members of the nematode genus Ascaris are predominantly parasitic. Since Ascaris species are adapted to a spectrum of hosts, the public health and agricultural impact of this intestinal parasite is world wide. Ascaris lumbricoides is the most prevalent human parasite world wide, ranging from semi-tropical climates in the southern United States to most of Asia, Latin America and Africa (Bundy 1994; Long-Qi et al. 1995). Ascaris suum infects virtually all domestic swine, at significant expense to the agricultural industry. In the free living larval state of A. suum development, oxygen is required and a mitochondrial cytochrome system similar to that of the mammalian host has been described (Saruta et al. 1995). However, oxygen is toxic to the adult parasite which resides in the mainly anaerobic environment of the host small intestine. There is no functional tricarboxylic acid cycle in these organisms and unsaturated organic acids are used as terminal electron acceptors (Saruta et al.
1995). Since Ascaris is biochemically more complex than the parasites in which the stress response has been studied, this study investigated the HSP family in Ascaris suum with particular emphasis on the response of the organism to oxygen toxicity.

**MATERIALS AND METHODS**

**Specimen acquisition.**—Specimens of Ascaris suum were collected within 30 min after slaughter in a local abattoir. For some experiments animals were removed immediately from the pig small intestine and the parasite intestine, muscle and reproductive tract were dissected out and frozen in liquid nitrogen. For ex vivo (organisms removed from the host and maintained in a synthetic laboratory environment) experiments, intestine were transported to the laboratory before animals were removed. Adult female parasites that measured 20 - 30 cm in length were used in all experiments.

**Ex vivo maintenance.**—Ascaris suum were maintained in A. suum saline at 37°C in the presence of 95% N₂ - 5% CO₂ (Donahue et al. 1982). Three to five worms were suspended in 500 ml media for the designated time intervals. In experiments designed to test the effects of oxygen, the media were gassed with 80% N₂ - 20%O₂. Under anaerobic conditions the worms can be maintained 3 - 4 days ex vivo without detectable loss of viability (Donahue et al. 1981a).

**Tissue preparation.**—Specimens were dissected longitudinally and intestine, muscle and reproductive tract were immediately frozen in liquid nitrogen and stored at -80°C until analyzed. The frozen tissues were weighed and immersed in 3 vol of ice-cold 20 mM Tris-Cl, pH 7.5, 5 mM EDTA, 5 mM EGTA, 2 mM dithiothreitol, 0.1 mM phenylmethylsulfonyl fluoride, 6 mM benzamidine, and 2 μM leupeptin. All subsequent tissue preparation was conducted at 4°C. The tissues were homogenized in a precooled polytron for 30 sec and the resulting homogenate was centrifuged at 3000 g for 20 min. The resulting supernatant (LSS) was removed from the pellet (LSP) and centrifuged at 103,000 g for 30 min. The resulting supernatant (HSS) was frozen in 30 μl aliquots at -80°C. Protein concentrations were determined by the Coomassie dye binding method. The protein concentration of the LSP was estimated by subtracting the total protein concentration of the HSS from the total protein concentration of the LSS.

**HSP analysis.**—Frozen HSS was thawed in SDS PAGE sample buffer and analyzed by SDS PAGE on 12% polyacrylamide gels. Resolved proteins were transferred to PVDF membranes and stored in phosphate buffered saline, pH 7.3 (PBS). Membranes were blocked with 3% dry
skim milk containing 0.1% Tween 20 in PBS. Membranes were probed with anti-HSP antibodies at a dilution of 1:2000. Anti-HSP70, anti-HSP60, and anti-HSP90 were obtained from StressGen (Victoria, B.C., Canada). Each of these antibodies is directed towards a universally conserved sequence in the respective HSP. In addition, the HSP70 reacts with both cognate and induced HSP70. Anti-HSP27 was generously provided by Dr. John Strahler of the University of Michigan (Bitar et al. 1991). Washed blots were probed with appropriate secondary antibodies (1:5000) conjugated with alkaline phosphatase (BioRad, Richmond, CA), and immunocomplexes were detected with chemiluminescent substrate (CSPD) according to the manufacturers instructions (Tropix, New Bedford, MA). The developed films were quantitated by video densitometry. Authentic HSP70, HSP60 and HSP90 were purchased from StressGen (Victoria, B.C., Canada). Authentic HSP27 was generously provided by Dr. Jacques Landry of the Université Laval (Zhou et al. 1993). Prestained molecular weight standards were purchased from BioRad (Richmond, CA).

RESULTS

Occurrence of Ascaris suum HSP.—HSP70 and HSP90 were readily detected by their respective antibodies in Western blots of HSS obtained from A. suum muscle and intestine (Figure 1). In both tissues, two forms of the HSP70 were detected. The heavier isoform appeared as a 72 kD protein and the smaller HSP70 isoform was 52 kD. These proteins will be referred to as HSP72 and HSP52 although both are homologous with the HSP70 as shown by the antibody reactivity. The HSP90 antibody detected a 90 kD protein in both tissues although twice as much sample was required to reliably detect this HSP. Several smaller proteins at lesser concentrations were also detected with the anti-HSP90 antibody; these proteins were not further investigated. HSP72, HSP52, and HSP90 could also be detected in reproductive tract although the immunoreactivity observed in these tissues were less than that in muscle and intestine.

Extract from intestine, muscle and reproductive tract was also analyzed with HSP60 and HSP27 antibodies. HSP60 could not be reliably detected in any tissue examined even when the sample concentration was increased to ~0.5 mg/gel lane. HSP27 was detected in muscle and intestine with amounts of sample comparable to that required for detection of HSP90.

Authentic HSP70 was analyzed as described for the tissue samples using concentrations of protein ranging from 50 - 150 ng/lane. Immunoreactive bands were quantitated by video densitometry and a
Figure 1. Occurrence of HSP in _Ascaris suum_ tissues. Worms were killed immediately after transport to the laboratory and HSS prepared from intestine (lane A) or muscle (lane B) as described in Methods. Proteins were analyzed by 12% SDS PAGE, transferred to PVDF, and probed with anti-HSP70 antibody (left panel) or anti-HSP90 antibody (right panel). Soluble intestine protein was 440 μg/lane and soluble muscle protein was 220 μg/lane.

standard curve was constructed. Extract was diluted so that the densitometry tracings of the immunoreactive bands fell within the standard curve and the amount of HSP72 and HSP52 was estimated. By this method, the amount of HSP72 and HSP52 in muscle was estimated to be 2.3 μg/mg soluble protein and 5.8 μg/mg soluble protein, respectively. In contrast, in intestine the amount of HSP72 and HSP52 was estimated to be 1.9 μg/mg and 0.80 μg/ml, respectively. In reproductive tissue, the levels of HSP72 and HSP52 were 0.76 μg/ml and 0.34 μg/mg, respectively.

HSP occur as both soluble proteins and proteins associated with particulate fractions. Since the HSP70 was the most prevalent HSP among those investigated, the distribution of HSP70 isoforms in the insoluble fraction obtained from low speed centrifugation (LSP) and the soluble fraction obtained from high speed centrifugation (HSS) was compared. The LSP was resuspended in SDS sample buffer to give a protein concentration approximately twice that determined for the HSS. Samples from both fractions of intestine, muscle and reproductive tract were analyzed for HSP70 as previously described. Results are shown in Figure 2. Virtually all of the HSP72 and HSP52 in intestine and reproductive tract was found in the soluble fraction. However, in muscle the distribution of HSP70 isoforms was significantly different.
Similar to intestine and reproductive tract, the HSP72 was found primarily in the soluble protein fraction, whereas HSP52 clearly occurred in both the soluble and particulate fractions. When the results are corrected for volume differences, the data suggest that ~20% of the muscle HSP52 is associated with the particulate fraction.

**Heat Shock HSP70 induction in muscle.**—Since the most abundant parasite stress protein is the HSP70 isoforms in muscle, the induction of these proteins was further investigated. A major concern was that removal of the parasite from the host might be sufficient to induce stress protein synthesis. The pigs are killed in a controlled temperature environment of ~20°C and intestines are obtained within 30 min after slaughter and within 5 min after removal from the animal. No difference in the relative distribution of HSP72 and HSP52 or the total amounts of these proteins could be detected when tissues which were dissected immediately from the worms at the slaughter house were compared to tissues obtained after transport to the laboratory in the intestine (Figure 3). In both samples, the amount of HSP72 was approximately twice the concentration of HSP52 in intestine, and the amount HSP72 was approximately half the amount of HSP52 in muscle. The relative amounts of HSP70 isoforms in the two tissues was unchanged in tissues obtained at the slaughter house as compared to those obtained after transport. On the basis of these results, no significant induction of HSP70 isoforms appears to occur in the time interval between removal of the parasite from the host and transport to the laboratory.

Induction of HSP70 isoforms in the *ex vivo* incubations was investigated at 37°C and 40°C. Worms were dissected at the beginning of the
Figure 3. Induction of HSP70 in fresh and transported *Ascaris suum* intestine and muscle. *Ascaris suum* intestine (lanes A and B) and muscle (lanes C and D) were dissected out at the slaughter house within 30 min of host killing (lanes A and C) or after transport to the laboratory in the pig intestine (lanes B and D). HSS proteins were analyzed for HSP70 as described in Figure 1 (left panel).

incubation (0 hr) and at 2 hr intervals up to 6 hr. Analysis of muscle extracts prepared from parasites incubated at 40°C (Figure 4) or 37°C (Figure 5) showed an increase in both HSP72 and HSP52 with time. At 40°C, the amount of HSP72 increased 1.3 fold and HSP52 increased 1.7 fold in the first 2 hr. After 4 hr, both HSP72 and HSP52 values were increased by ~2 fold and no further increase was observed after a total incubation time of 6 hr.

At 37°C, induction of HSP72 followed a comparable time course and after 6 hr the stress protein level was increased 2 fold. At 37°C, no induction was observed until the 4 hr time point at which time the increase was 1.2 fold. After 6 hr HSP52 was increased 2.4 fold. This is in contrast to some mammalian and fruitfly systems in which a 100-fold increase in HSP70 is observed in a comparable time frame (Lindquist 1986). Since the increase in HSP72 and HSP52 was not different at 37°C and 40°C, the induction may be the result of *ex vivo* incubation as opposed to temperature shock.

*Oxygen-induced induction of HSP70 in muscle.*—Adult parasites
Figure 4. Induction of HSP70 in *Ascaris suum* muscle incubated at 40°C. *Ascaris suum* muscle was dissected from animals immediately after transport to the laboratory (lane A) and after 2 hr (lane B), 4 hr (lane C), or 6 hr (lane D) incubation of the worms at 40°C in the presence of 95% N₂-5% CO₂ as described in Methods. HSS was prepared from muscle and analyzed as described in Figure 1 with anti-HSP70 antibody. All samples contain 220 µg total protein.

normally inhabit the small intestine where the oxygen content is than 0.5%. Consistent with this microaerophilic environment, in the *ex vivo* incubation the animals survive less than 24 hr in the presence of atmospheric oxygen. To test the hypothesis that oxygen might induce a stress protein response before apoptosis is initiated, parasites were incubated at 37°C in the presence of an oxygen-free atmosphere and in a 20% oxygen atmosphere. HSP70 in muscle extracts was analyzed and results are shown in Figure 5. HSP52 was increased 3.8 fold in the presence of oxygen as opposed to 2.4 fold in the presence of nitrogen. In the first 4 hr of *ex vivo* incubation, a modest change in HSP52 was observed in the presence of nitrogen (<1.2 fold) or oxygen (1.5 fold). However, in the final 2 hr incubation, the amount of HSP52 increased 2 fold in the presence of nitrogen and 2.6 fold in the presence of oxygen (Figure 6). The total increase in HSP52 was 3.8 fold in the presence of oxygen and 2.4 fold in the presence of nitrogen. These data suggest that the time frame required for HSP52 induction is 4 - 6 hr. In contrast, no difference in the amount in HSP72 was observed in the presence or
CHAO, DONAHUE & MASARACCHIA
327

Figure 5. Induction of HSP70 in *Ascaris suum* muscle incubated in the presence and absence of O₂. *Ascaris suum* muscle was dissected from animals immediately after transport to the laboratory (lane A) or after 2 hr (lanes B and C), 4 hr (lanes D and E), or 6 hr (lanes F and G) incubation of the intact worms at 37°C in the absence (lanes B, D and F) or presence (lanes C, E, and G) of O₂ as described in Methods. HSS was prepared and analyzed with anti-HSP70 antibody as described in Figure 1.

absence of oxygen in the time frame investigated.

**DISCUSSION**

Similar to other studies with parasitic organisms, the HSP70 isoforms are constitutively expressed at a relatively high level in adult *Ascaris suum* tissues. The proteins were most abundant in muscle and least abundant in reproductive tract with intestine containing an intermediate concentration. No HSP70 could be detected in the cuticle/hypodermis, the fourth major tissue of the organism, although the possibility that HSP70 was present, but below levels of detection, cannot be excluded. In muscle, the major *A. suum* tissue, the HSP70 isoforms constitute approximately 0.8% of the soluble protein and 0.16% of the particulate protein. These estimates are obtained from a standard curve constructed with authentic bovine HSP70. Since the antibody used to detect the protein is a monoclonal antibody directed toward a unique conserved domain of the HSP70 protein, the reactivity of both HSP72 and HSP52 with this antibody identifies the parasite proteins as HSP70 proteins. In addition, since the antibody is specific for this domain, it is likely that the reactivity of the *A. suum* proteins and other HSP70 proteins with the monoclonal antibody would be comparable. Therefore, it is concluded
that this is a reasonably reliable estimate of HSP70 expression in the parasite.

Since two other studies on parasitic organisms have suggested that induction of stress proteins in these species may occur by a post-translational mechanism which could be very rapid (De Carvalho et al. 1994; Brandau et al. 1995), the induction of the HSP70 proteins in the time interval between killing of the host and dissection of the tissues was investigated. During the 30 min interval in question, the host intestines do not change temperature significantly since they are held in the carcass of the host. After removal of the host intestine, the parasites were obtained and dissected within 10 min. Analysis of HSP70 in these tissues and those obtained after transport to the laboratory showed no significant difference in HSP72 or HSP52 levels. Since induction would be predicted to continue through this time interval, the data suggest that the high level of HSP70 proteins is indeed constitutive synthesis, and not induction.

The occurrence of two forms of the HSP70 proteins was unexpected. Even though the tissues were homogenized in a cocktail of protease inhibitors, the possibility that the lower molecular weight form was a product of HSP72 proteolysis was considered. Several observations suggest
that HSP52 is not a product of HSP72. First, the distribution of HSP72 and HSP52 are not comparable in the various tissues. HSP52 is the predominant HSP70 isoform in muscle, but in intestine and reproductive tract, HSP72 is the predominant isoform. This argues against proteolysis since the intestine contains higher protease activity than the other two tissues. Second, induction of HSP70 synthesis in the presence of oxygen occurred selectively in the HSP52 isoform whereas both HSP72 and HSP52 were induced by ex vivo incubation. Finally, the ratio of HSP72/HSP52 observed in all tissues studied was remarkably constant and independent of the time between host sacrifice and tissue dissection. This suggests that anomalous degradation of the proteins was not occurring during this time. Collectively, the data suggest that both HSP72 and HSP52 are distinct isoforms of the HSP70 family.

The presence of particularly abundant HSP70 isoforms in A. suum muscle is consistent with the central role this tissue plays in the organism’s metabolism. Since the parasite is free swimming and does not attach to the intestinal wall, muscle activity is continually required to counteract the flushing effect of host peristalsis. Muscle ATP is primarily derived from glucose since the tissue lacks a functional tricarboxylic acid cycle (Saruta et al. 1995). The source of glucose in host nonfeeding intervals is glycogen and the relatively sophisticated regulation of glycogen synthesis and mobilization has been studied extensively in this laboratory (Donahue et al. 1981a; 1981b; 1981c; 1982; Ghosh et al. 1989). In the laboratory, worms survive stresses, including starvation up to 60 hr, without noticeably compromises in vitality. The single exception to this apparent adaptation to stress is the toxicity of oxygen.

In other organisms multiple forms of the HSP70 proteins are observed (Hendrick & Hartl 1993). These isoforms correspond to genes which are constitutively expressed and genes which are selectively induced by unique stimuli. The selective induction of HSP52 with oxygen suggests that the HSP72 and HSP52 genes are independently regulated in this comparatively simple organism. Since elevated temperature failed to induce HSP70, but oxygen stress did selectively increase one HSP70 isoform, A. suum may be another example of an organism which is thermal tolerant, but retains the potential to respond to other environmental stresses. Further studies are in progress to define the stress response in this parasite more extensively.

ACKNOWLEDGMENTS

This work was supported in part by a grant to RAM from the University of North Texas Organized Research Fund. We gratefully acknowledge the technical assistance of Ms. Donna Ritchey.
Literature Cited


RAM at: ruthannm@facstaff.cas.unt.edu
Abstract.—Specimens of Kemp’s ridley and loggerhead sea turtles which died during captive rearing (1984 to 1996) were subjected to complete necropsy. Seven different bacterial strains were isolated and identified from Kemp’s ridleys and three strains from loggerheads. *Salmonella* spp., *Aeromonas* spp. and *Pseudomonas* spp. were found in both species.

The National Marine Fisheries Service (NMFS) Galveston Laboratory has reared Kemp’s ridley (*Lepidochelys kempii*) and loggerhead (*Caretta caretta*) sea turtles in captivity from 1978 to the present (Fontaine et al. 1985; Caillouet 1987). Kemp’s ridley hatchlings were received from Rancho Nuevo, Tamaulipas, Mexico or Padre Island National Seashore, Corpus Christi, Texas and were reared until release into the Gulf of Mexico (Caillouet et al. 1995). Loggerhead hatchlings were received from Clearwater Marine Science Center in Clearwater, Florida or Mote Marine Laboratory in Sarasota, Florida and were reared for turtle excluder device (TED) certification trials and released into the Gulf of Mexico. From 1978 to 1983, Galveston Laboratory personnel isolated bacteria from sick turtles and necropsied turtles that died in captivity, and the bacteria identified were reported elsewhere (Clary & Leong 1984; Leong et al. 1989).

This study was undertaken to compile data on the occurrence of infectious bacteria from necropsied Kemp’s ridleys and loggerheads of the 1984-1996 year-classes. The data were gathered to identify potentially pathogenic bacteria for biologists and veterinarians rearing and treating sea turtles in captivity.

**METHODS AND MATERIALS**

From 1984 through 1996, 16,042 specimens of Kemp’s ridley hatchlings were received alive at the NMFS Galveston Laboratory. Of these, 938 (5.8%) died; 116 specimens of these were necropsied. From 1987 through 1996, 1,447 specimens of loggerhead hatchlings were also
Table 1. Incidence of seven bacteria strains in 116 specimens of Kemp’s ridley and 32 loggerhead turtles necropsied and four rectal swabs taken from sick loggerheads were analyzed at the Texas Veterinary Medical Diagnostic Laboratory.

<table>
<thead>
<tr>
<th>Bacteria</th>
<th>Kemp’s ridley (N=116)</th>
<th>Loggerhead (N=36)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Number</td>
<td>%</td>
</tr>
<tr>
<td>Salmonella spp.</td>
<td>48</td>
<td>41.3</td>
</tr>
<tr>
<td>Aeromonas spp.</td>
<td>13</td>
<td>11.2</td>
</tr>
<tr>
<td>Citrobacter spp.</td>
<td>9</td>
<td>7.8</td>
</tr>
<tr>
<td>Proteus spp.</td>
<td>8</td>
<td>6.9</td>
</tr>
<tr>
<td>Escherichia spp.</td>
<td>7</td>
<td>6.0</td>
</tr>
<tr>
<td>Pseudomonas spp.</td>
<td>7</td>
<td>6.0</td>
</tr>
<tr>
<td>Enterococcus spp.</td>
<td>2</td>
<td>1.7</td>
</tr>
</tbody>
</table>

received. Of these, 117 (8.8%) died; 32 specimens of these were necropsied and four sick turtles were examined by rectal swab. Specimens were sent to the Texas Veterinary Medical Diagnostic Laboratory (TVMDL) in College Station, Texas for complete necropsy. Additional turtles that died were not necropsied, either because they had undergone postmortem decomposition or were fixed in formalin for other purposes. Healthy turtles were not sampled for the presence of bacterial infections.

RESULTS AND DISCUSSION

The most common bacterial isolates from Kemp’s ridleys were *Salmonella* spp. (41.3%; Table 1). An outbreak of *Salmonella* spp. in the 1987 year-class of Kemp’s ridleys accounted for most of this occurrence. These bacteria were found in turtles as young as three to nine days post hatch and as old as 10-12 months. *Salmonella* spp. were found in the yolk sacs and intestines in younger animals and in intestines of older animals. The second most frequent isolates from Kemp’s ridleys were *Aeromonas* spp. (11.2%). The intestine was the source of most of the bacterial isolates from Kemp’s ridley, followed by the yolk sac, body cavity and lung. No infectious bacteria were isolated from 18.2% of the necropsied Kemp’s ridleys.

The bacteria most frequently isolated from loggerheads were *Aeromonas* spp. (19.4%; Table 1). *Salmonella* spp. had the second highest occurrence in loggerheads (8.3%). The intestine and rectal swabs accounted for most of the bacterial isolates from loggerheads. No infectious bacteria were isolated from 66.7% of the loggerheads.
The bacteria isolated and reported here are potentially pathogenic to all sea turtles. The outbreak of *Salmonella* spp. infections in the 1987 year-class Kemp’s ridleys suggests a detrimental effect of pathogenic organisms on a captive population. *Aeromonas* spp. were reported by Sinderman (1977) as being common in marine waters and might be pathogenic to animals living under environmental stress. Pasquale et al. (1994) isolated *Aeromonas hydrophila* in turtles (*Pseudemis scripta*) that had a 95% mortality rate. Other researchers (Stickney et al. 1973; Leong et al. 1989) isolated *Aeromonas* spp., *Proteus* spp., *Pseudomonas* spp. and *Citrobacter* spp. from Kemp’s ridley and loggerhead hatchlings.

Most of the sea turtle pathology research done at the NMFS Galveston Laboratory took place during the early years of the Kemp’s ridley head-start experiment from 1977 to 1983 (Clary & Leong 1984; Leong et al. 1989). Improvement of sea turtle husbandry techniques over the years raised the survival rates after 1983 (Clary & Leong 1984; Fontaine et al. 1985). Since no attempts were made to isolate bacteria from healthy turtles, one cannot conclude from this data that the bacteria isolated was in fact the cause of death. To verify pathogenic bacteria, healthy turtles will need to be tested for the presence of microorganisms.

Diagnosing infected turtles and isolating the bacteria are critical for proper treatment of individuals, and to prevent disease outbreaks in captive populations. Even with improved husbandry practices, sea turtles reared in captivity are still subject to bacterial infections. However, the high survival rates in sea turtles reared in captivity at the Galveston Laboratory suggest that bacterial infections were not a major problem.

**LITERATURE CITED**


BAR at: brobtson@aol.com
PREVALENCE OF CUTEREBRID (DIPTERA: CUTEREBRIDAE)
PARASITISM AMONG BLACK-TAILED JACKRABBITS
IN SOUTHERN TEXAS

D. Keith Crenshaw and Scott E. Henke
Campus Box 218, Caesar Kleberg Wildlife Research Institute
Texas A&M University-Kingsville
Kingsville, Texas 78363

Abstract.—Twenty-two of 80 (27.5%) adult black-tailed jackrabbits (Lepus californicus) examined in southern Texas from March to July of 1996 were infected with Cuterebra sp. larvae. The number of larvae per jackrabbit ranged from 0 to 3 with a mean abundance of 0.5 ± 0.1 (SE) larvae per jackrabbit. More females (45.2%) were infected than males (7.9%) and prevalence of infection was greater (P < 0.001) in gravid females (60%) than non-gravid females (23.5%). Locality of infection on the host included the genital, flank and shoulder regions.

Black-tailed jackrabbit, Lepus californicus, populations have declined in abundance during the last decade in southern Texas. Reasons for jackrabbit declines are unknown; however, speculations have included Lyme disease (Burgess & Windberg 1989), loss of grassland habitat due to invasion of shrublands (Medlin 1974), and competition with domestic livestock for forage (Currie & Goodwin 1966; Johnson 1979). One often overlooked reason for population declines is parasitism.

Bot flies, Cuterebra sp., are myiasis-producing parasites that typically infect rodents and lagomorphs (Davidson & Nettles 1988). Pathologic effects of cuterebrid larvae include lowered body weight (Geis 1957), reproductive efficiency (Sealander 1961), and bone marrow fat content (Pelton 1968), increased leukocyte count (Bennett 1973; Geis 1957), anemia (Bennett 1973; Sealander 1961), enlarged lymph nodes (Childs & Cosgrove 1966), and increased host mortality (Philip et al. 1955). This paper reports the prevalence of Cuterebra sp. parasitism in a wild population of black-tailed jackrabbits in southern Texas.

METHODS

Eighty adult black-tailed jackrabbits were collected near Carrizo Springs (28°17' N, 100°15' W) in southern Texas from March through July of 1996. The area is characterized as a semi-arid grassland and mesquite, Prosopis glandulosa, shrubland that receives an average of 54 cm of annual precipitation (Stevens & Arriaga 1985). Temperatures ranged from 11 to 37°C during the study period. Jackrabbits were shot with a .22 caliber rifle, sexed, classified as juveniles or adults according to eye lens weight.
Table 1. *Cuterebra* sp. infection of 38 male and 42 female black-tailed jackrabbits collected in southern Texas during March through July, 1996. The terms prevalence, abundance, and intensity follow the definition of Margolis et al. (1982).

<table>
<thead>
<tr>
<th>Cuterebra infection</th>
<th>Male</th>
<th>Female</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Prevalence</td>
<td>3/38 (7.9%)</td>
<td>19/42 (45.2%)</td>
<td>22/80 (27.5%)</td>
</tr>
<tr>
<td>Relative Abundance</td>
<td>0.18</td>
<td>0.83</td>
<td>0.52</td>
</tr>
<tr>
<td>Range</td>
<td>0 - 3</td>
<td>0 - 3</td>
<td>0 - 3</td>
</tr>
<tr>
<td>Intensity</td>
<td>2.33</td>
<td>1.84</td>
<td>1.91</td>
</tr>
<tr>
<td>Total Warbles</td>
<td>7</td>
<td>35</td>
<td>42</td>
</tr>
</tbody>
</table>

(Tiemeier & Plenert 1964), and examined for cuterebrids. Due to the low numbers of juveniles collected, only adult jackrabbits were analyzed. The locations of larval development sites were recorded. The number of fetuses were determined in gravid jackrabbits. Representative specimens of *Cuterebra* sp. from black-tailed jackrabbits that were examined during this study are deposited in the parasite collection of the Caesar Kleberg Wildlife Research Institute at Kingsville, Texas (Accession No. 4629).

Chi-square analyses with the Yates Correction factor was used to test the effect of cuterebrid prevalence on host sex and female host gravidity. A general linear analyses of variance (PROC GLM; SAS 1989) was used to test the effect of cuterebrid abundance on host sex and female host gravidity. Statistical significance was inferred at P < 0.05. Data are reported as the mean ± standard error. The terms prevalence, abundance, and intensity follow the definitions of Margolis et al. (1982).

**Results and Discussion**

Twenty-two of 80 (27.5%) adult black-tailed jackrabbits were infected with 42 specimens of *Cuterebra* sp. larvae (Table 1). Number of larvae per hare ranged from 0 to 3 with an average relative abundance of 0.52 ± 0.1 larvae per jackrabbit. The most common infection site for larval development on black-tailed jackrabbits was the genital region (n = 16), followed by the rear flank (n = 5) and shoulder (n = 1) regions.

Prevalence of infection was greater ($\chi^2 = 24.0$, df = 1, $P < 0.001$) in female than male jackrabbits. The mean abundance of larval infection also was greater ($F = 10.32; df = 1, 78; P < 0.002$) in female (0.83 ± 0.16) than male (0.18 ± 0.11) hares (Table 1). Prevalence of cuterebrid infection was greater ($\chi^2 = 14.5$, df = 1, $P < 0.001$) in gravid than non-gravid females (Table 2). Number of fetuses in gravid females ranged from 1 to 3. There did not appear to be a difference in the number of developing fetuses between females infected with *Cuterebra* sp. larvae (1.8 ± 0.3, n = 15) and the female not infected ($\bar{x} = 2.0$, n = 1); however, sample sizes were inadequate for analysis. The mean relative abundance of larval infection was greater ($F = 4.98; df = 1, 40; P < 0.032$) in
Table 2. *Cuterebra* sp. infection of 25 gravid and 17 non-gravid female black-tailed jackrabbits collected in southern Texas during March through July, 1996. The terms prevalence, abundance, and intensity follow the definition of Margolis et al. (1982).

<table>
<thead>
<tr>
<th><em>Cuterebra</em> infection</th>
<th>Gravid</th>
<th>Non-gravid</th>
</tr>
</thead>
<tbody>
<tr>
<td>Prevalence</td>
<td>15/25 (60.0%)</td>
<td>4/17 (23.5%)</td>
</tr>
<tr>
<td>Relative Abundance</td>
<td>1.08</td>
<td>0.47</td>
</tr>
<tr>
<td>Range</td>
<td>0 - 3</td>
<td>0 - 3</td>
</tr>
<tr>
<td>Intensity</td>
<td>1.8</td>
<td>2.0</td>
</tr>
<tr>
<td>Total warbles</td>
<td>27</td>
<td>8</td>
</tr>
</tbody>
</table>

Gravid females (1.1 ± 0.2) than non-gravid females (0.5 ± 0.2) (Table 2).

The prevalence of infection with *Cuterebra* sp. larvae in this study is consistent with other reports. Baird (1983) in Idaho and Philip et al. (1955) in Nevada reported 9% and 68%, respectively, of black-tailed jackrabbits parasitized with *Cuterebra* sp. larvae. However, neither study found differences between the prevalence of infection in male and female jackrabbits as was found in this current study. Brigada et al. (1992) noted a greater prevalence of cuterebrid infection in female shrubland mice, *Akodon molinae*. They hypothesized that bot flies deposited their eggs near host nests resulting in a greater exposure to adult females. The same reasoning possibly could explain why a greater prevalence of infection in gravid than non-gravid female jackrabbits was noted in this study. Perhaps gravid females are less mobile and routinely use the same bedding sites, which in turn, increase their exposure to warble infection.

Jackrabbits in this study appeared normal (i.e., alert and mobile) prior to collection. Although *Cuterebra* sp. larvae usually are not considered a health risk to their hosts (Davidson & Nettles 1988), Philip et al. (1955) noted that 77% of jackrabbits in Nevada infected with larvae appeared disoriented. They proposed that this aberrant behavior was due to blindness caused by myiasis around the eyes of jackrabbits, which had an average intensity of 2.5 larvae. In this current study, myiasis occurred mainly near the genital region of the animals; average intensity was 1.9 larvae. Larvae were not collected from the head region of jackrabbits during this study, nor did they appear to cause debilitating effects. It has been suggested that *Cuterebra* sp. infection of the genital region can reduce the prevalence of gravid females in a population by making copulation difficult (Sealander 1961). However, this did not appear to be the case during this study because 60% of the females were gravid, of which the majority were infected with *Cuterebra* sp. larvae, and the prevalence of infection in males was low. Although litter sizes of jackrabbits in this study were smaller on average than expected, there is no reason to believe that *Cuterebra* sp. infection was the cause for a reduced litter size. Litter size for black-tailed jackrabbits range from one to six leverets (Davis & Schmidly 1994:94);
The data collected during this study is consistent with this range.

ACKNOWLEDGMENTS

The authors thank F. B. Steubing for assistance with jackrabbit collection, S. W. Stedman for access to his property, and the Caesar Kleberg Wildlife Research Institute for financial support. The project was approved by the Texas A&M University-Kingsville Animal Care and Use Committee. This is MS #98-105 of the Caesar Kleberg Wildlife Research Institute, Texas A&M University-Kingsville.

LITERATURE CITED


SEH at: kfseh00@tamuk.edu
DISTRIBUTION OF MULTIPLE OIL TOLERANT AND OIL DEGRADING BACTERIA AROUND A SITE OF NATURAL CRUDE OIL SEEPAGE

Robert S. Stewart, Jr., Christopher Emmons, Dana Porfirio and Robert J. Wiggers
Department of Biology, Stephen F. Austin State University
Nacogdoches, Texas 75962

Abstract.—Hydrocarbon degrading bacteria were isolated from the soil surrounding a natural seepage site of petroleum into freshwater. Thirty-six soil samples were collected at twelve locations and three depths over an area of about 36 m² centered around the freshwater basin. Twelve distinct isolates were identified to at least the genus level which were initially selected based on their petroleum tolerance, with seven of these found to be capable of utilizing crude oil or oil components as a sole carbon and energy source. There were statistically significant variations in the distribution of some organisms although this was not affected by the depth of sampling. The ability of each species to utilize specific fractions of hydrocarbons was also determined. The results indicate that the presence of a diverse petroleum utilizing bacterial community that exhibits considerable composition variation over relatively small geographic distances.

Petroleum utilizing bacteria are not uncommon in natural environments (ZoBell 1946; Atlas 1981; Leahy & Colwell 1990). Indeed, in areas exhibiting petroleum contamination, such utilizers may account for the entire bacterial community (Atlas 1981). Such petroleum utilizing bacterial communities arise by selection pressures exerted on the pre-existing population upon first exposure to petroleum (Atlas 1981; Cooney 1984) and the existence of such utilizers may become a permanent fixture in the community in areas exhibiting chronic exposure to petroleum.

Oil Springs, Texas represents a long-standing area of natural petroleum seepage into both freshwater and the surrounding soil (Pate 1987). Recent studies (Benoit & Wiggers 1995; Ferguson et al. 1997) partially characterized the bacterial communities found in two geographically isolated sites of petroleum contaminated freshwater at Oil Springs. The communities were found to be taxonomically diverse yet physiologically similar in that members isolated in both studies were able to utilize both crude oil and diesel fuel (representing straight and branched chain hydrocarbons). Most of the bacteria isolated from the water at both sites were able to utilize aromatic compounds. In addition to contaminated water, Oil Springs also offers the opportunity to study bacterial communities that have developed in soil environments chronically con-
taminated with petroleum. This report details the results of an expanded study conducted on the contaminated soil surrounding a freshwater basin receiving petroleum seepage previously described (Benoit & Wiggers 1995).

**Materials and Methods**

*Site description and sampling.*—The oil seepage is located in a wooded area approximately 25 miles southeast of the town of Nacogdoches, located in east Texas. Historical records indicate that petroleum has been present since at least 1790 (Pate 1977). Petroleum contaminated freshwater can be found in a stream and a catch basin and contaminated soil surrounds the catch basin. Samples were taken with a stainless steel sterilized 2.5 cm diameter core sampler. When the terrain allowed, samples were taken at two distances (2.1 m, 4.2 m) from the rough center of the catch basin and at three depths (surface, 45 cm, 90 cm). Prior to each use the core sampler was sterilized by being washed free of all debris and then flamed with 95% ethanol. Core samples of about 10 cm length were placed in sterile 50 ml centrifuge tubes for transport.

*Isolation and identification of bacterial species.*—Collected samples were transported at ambient temperature to the laboratory. Each core sample was removed from the transport tube in a sterile field, split in half lengthwise, and 1 gram from the center of each sample was placed into nutrient broth (Difco) with 1% sterile crude oil and grown on a shaker at 200 rpm for six days at room temperature. Nutrient agar plates were streaked with 1.0 ml of the broth from the liquid cultures and grown at 30°C to recover bacteria which were crude oil tolerant. Isolated colonies were identified by either the BIOLOG identification system or through standard microbiological techniques using *Berger’y’s Manual of Systematic Bacteriology* (Kreig & Sneath 1984).

*Hydrocarbon utilization.*—Isolates were tested for their ability to utilize petroleum as a sole energy source by inoculating 100 ml of a crude oil containing salts solution (Benoit & Wiggers 1995) with 1.0 ml of a 24 hour culture growing on nutrient broth and incubating for five days. Growth was considered positive if marked turbidity greater than a McFarland 2 standard was noted coupled with microscopic observation of cellular aggregates. Additionally, the ability of the representative isolates to utilize specific hydrocarbons which included mineral oil (representing the n-aliphatic compounds), diesel fuel (representing the straight and branched chain hydrocarbons), benzene and toluene (both
Table 1. Species identification and substrate utilization.

<table>
<thead>
<tr>
<th>Species</th>
<th>Crude Oil</th>
<th>Diesel</th>
<th>Mineral Oil</th>
<th>Toluene</th>
<th>Benzene</th>
</tr>
</thead>
<tbody>
<tr>
<td>Alcaligenes xylooxidans</td>
<td>+</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Bacillus cereus**</td>
<td>+</td>
<td>+</td>
<td>-</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Bacillus sp.**</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Chromobacterium violaceum</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Flavobacterium indologenes**</td>
<td>+</td>
<td>-</td>
<td>+</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Flavobacterium indologenes**</td>
<td>+</td>
<td>+</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Pseudomonas aeruginosa</td>
<td>T</td>
<td>+</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Serratia marcescens</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Kingella sp.***</td>
<td>T</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Bacillus sp.**</td>
<td>T</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Bacillus cereus**</td>
<td>T</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Bacillus mycoides</td>
<td>T</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
</tbody>
</table>

* (+) = growth, (-) = no growth; T = tolerant but non-crude oil utilizer
** Distinct biotypes
*** Presumptive; BIOLOG SIM < 0.5

representing aromatic hydrocarbons) was determined by inoculation of 1.0 ml of a 24 hour culture growing in nutrient broth into salts media containing these hydrocarbons individually (Benoit & Wiggers 1995) and incubation for four days.

Statistical analysis.—The mean numbers of strains isolated from each sample were compared using the paired t-test. Correlations between the recovery of individual strains at specific sites and depths were analyzed using linear regression analysis.

RESULTS

A total of 183 crude oil tolerant isolates were initially recovered from which 12 strains representing seven genera were identified (Table 1). Seven of these strains from five genera ultimately were found to be capable of utilizing crude oil or oil components as sole energy and carbon sources. Distinct biotypes of the same species were found for Bacillus cereus and Flavobacterium indologenes, as well as for Bacillus sp. Only one isolate (B. cereus) was able to utilize toluene and benzene.

Variations in geographic distribution was marked, ranging from the least isolated Chromobacterium violaceum (found in two of the 12 locations and only five of the 36 core samples) to the most common Pseudomonas aeruginosa (found in all 12 locations and 33 of the 36 core samples).
DISCUSSION

The petroleum contaminated soil surrounding the freshwater catch basin yielded 12 bacterial strains capable of tolerating crude oil. These 12 strains represented seven different genera (Table 1). While two of the isolates were identified as *Flavobacterium indologenes*, and two as *Bacillus cereus*, and two as *Bacillus* sp., they were all found to be distinct biotypes. Seven of these isolates proved capable of utilizing crude oil or another hydrocarbon fraction as a sole carbon source. Surprisingly *Pseudomonas aeruginosa* was unable to utilize crude oil but could use diesel as a sole carbon source. The crude oil from Oil Springs is rich in C-20 and greater hydrocarbon compounds and poor in the cyclic aromatic compounds (Pike 1977). In light of this, it is not surprising that most degradative ability was restricted to the mineral oil or diesel since these compounds most resemble hydrocarbons found at the site.

The distribution of organisms around the basin was not always random. One site in particular had a significantly different composition than two other locations (p < 0.04) which were 2.1 m and 5.7 m in distance, but not from all other locations ranging from 3.2 m to 8.4 m in distance (all p > 0.05).

Not all strains isolated were found in all the samples collected. Two isolates, *Alcaligenes xylosoxidans* and *Pseudomonas aeruginosa*, were found at all twelve locations and in a very high percentage of the samples collected (72% and 92% of the 36 samples respectively). On the other hand, *C. violaceum* was found at only two locations 2.1 m apart and isolated from only five of the 36 samples (14%). Three genera, *Chromobacterium*, *Bacillus*, and *Flavobacterium*, showed a statistically significant inverse relationship in distribution around the basin (p < 0.01). What this means is that whenever any of these three organisms were present, the other two tended not to be.

The remainder of the isolates were recovered from eight of the 12 sites (*F. indologenes*), nine of the 12 sites (*Kingella* sp. and *Serratia marcescens*), and 11 of the 12 (*Bacillus* spp.). Very recent work at the same site (Ferguson et al. 1997) reported the isolation of oil degrading bacteria of some of these same species as well as at least two more genera. This suggests that when contaminated areas are surveyed for oil degrading bacteria it may be necessary to sample over several locations.
surrounding the site to accurately reflect the bacterial community. Depth of sampling was not found to statistically affect the rates of isolation. Further comparisons with bacteria isolated from the water in the catch basin indicate community composition differences between water and soil. Only two species previously identified in the water of the catch basin, *P. aeruginosa* and *B. cereus* (cf. Benoit & Wiggers 1995) were also found in the soil. Whereas the *P. aeruginosa* isolates from both the water and soil were capable of hydrocarbon utilization, the *B. cereus* from the water was a non-utilizer (Benoit & Wiggers 1995) while the *B. cereus* from the soil here was capable of degrading all but mineral oil. This suggests that it is distinct from the *B. cereus* found in the water. This is further supported by the biotype variations within the *B. cereus*, *Bacillus* sp. and *F. indologenes* isolated here, as well as the *B. cereus* strain variations (MCM1 and MCM3) found by Ferguson et al. No other bacterial species were common to both the soil and water.

In summary, it would appear that similar selection pressures, namely the presence of hydrocarbons, are capable of producing markedly different bacterial communities when applied across geographic locations within the same environment. This suggests that when sampling hydrocarbon contaminated sites, researchers must not only sample across different environments but also at various geographic locations within the same environment in order to representatively describe the bacterial communities found at these sites.

**ACKNOWLEDGMENTS**

This work was supported in part by a Stephen F. Austin State University faculty research grant to R. Wiggers.

**LITERATURE CITED**


RSS at: rstewart@sfasu.edu
Collection efforts directed towards mammals of Stonewall County, Texas, over the past few decades have been sporadic, although specimens have accumulated through time in the collections of Midwestern State University (MWSU). Combined with more intensive systematic collecting during the past few years, it has been possible to verify the presence of 13 species not previously reported from the county. None is extralimital, although several species are reported from at or near the margins of their known ranges. These records aid in a more precise mapping of the distribution of these species in Texas.

Stonewall County is typical of the southwestern expanses of the Rolling Plains in Texas. Rugged, juniper-covered terrain dominates the western part, while mesquite grasslands occupy the rest of the county. Little specific information on mammals from this and adjacent counties is available. The area lies outside the geographic scope-of-coverage of north-central Texas mammals (Dalquest & Horner 1984), although the treatment of Texas mammals by Davis & Schmidly (1994) is useful in the more general sense.

*Cryptotis parva.*—Ten skulls (all cataloged under MWSU 19975) of the least shrew were salvaged from owl pellets recovered from under the U.S. Highway 83 bridge over the Salt Fork of the Brazos River, 12.6 mi NNW of Aspermont. This shrew ranges as far west as New Mexico (Hoditschek et al. 1985; Owen & Hamilton 1986), but is less common in west Texas than the more mesic eastern half of the state. This record is near the southwestern margin of the species' range in the Rolling Plains.

*Lasiurus cinereus.*—The hoary bat is a seasonal migrant throughout Texas, and is generally regarded as an uncommon species in the state. One female specimen was collected in March as it foraged over a stock-tank (MWSU 8027) 10.5 mi W of Rochester.

*Dasypus novemcinctus.*—The armadillo is less common in the western parts of its range in Texas, where it is mostly found along the creeks
and river terraces. One specimen (MWSU 19976) was collected 2 mi W of Peacock. This single specimen was a young male found dead on a bridge crossing the Salt Fork of the Brazos River.

Spermophilus tridecimlineatus.—This marginal record of the thirteen-lined ground squirrel is significant in that it demonstrates range overlap with the Mexican ground squirrel. The distributional relationship between the two sciurid species can best be described as parapatric, although a narrow band of sympatry occurs over the Llano Estacado where the two taxa are said to hybridize (Cothran 1983; Zimmerman & Cothran 1976). One specimen (MWSU 19917) was collected 6 mi S of Aspermont. This single specimen was a lactating female that was trapped after it was observed crossing the roadway.

Chaetodipus hispidus.—Two specimens of the hispid pocket mouse were taken in loose drift soils along fencerows, usually where traps were placed at the entrance to vertically inclined burrows characteristic of this species: one specimen (MWSU 19367) 12.4 mi NNW of Aspermont; and one specimen (MWSU 18882) 6 mi E of Aspermont.

Reithrodontomys montanus.—The plains harvest mouse is an expected resident of the region, especially in sparsely vegetated situations. One specimen was collected (MWSU 8493) 12.6 mi NNW of Aspermont. It was taken on a sandy river terrace in association with Ord’s kangaroo rat.

Reithrodontomys fulvescens.—The fulvous harvest mouse prefers denser vegetation that its smaller congener, R. montanus. Two specimens were collected: one specimen (MWSU 19026) 6 mi SW of Aspermont; one specimen (MWSU 18830) 6 mi E of Aspermont. These specimens represent marginal records along the northwestern range of the species in Texas.

Peromyscus attwateri.—The Texas mouse prefers broken terrain in association with juniper. Fourteen specimens were collected: one specimen (MWSU 18943) 12.6 mi NNW of Aspermont; eight specimens (MWSU 19092-19095, 19316, 19317, 19320 & 19321) 12.4 mi NNW of Aspermont; one specimen (MWSU 18944) 13 mi E of Aspermont; and four specimens (MWSU 18945 & 19342-19344) 6 mi SW of Aspermont. This mouse is often the most common mammal where ideal habitat is present.

Peromyscus maniculatus.—The deer mouse prefers short-grassed or sparsely vegetated situations, and can be expected in abundance where suitable conditions prevail. Eight specimens (MWSU 19028-19035) were
collected 6 mi SW of Aspermont.

*Peromyscus leucopus.*—The white-footed mouse occurs in a variety of habitats, although some woody vegetation seems a prerequisite. However, the presence of *P. atwatteri* precludes its local occurrence from much of the cedar-covered roughlands. Eleven specimens were collected: six specimens (MWSU 19027, 19040-19042, 19090 & 19091) 12.4 mi NNW of Aspermont; one specimen (MWSU 19872) 6 mi SSW of Aspermont; and four specimens (MWSU 19106, 19017, 19314 & 19315) 2 mi W of Aspermont.

*Sigmodon hispidus.*—The hispid cotton rat is abundant and widespread in the county, but only three representative examples were saved: one specimen (MWSU 21127) 6 mi E of Aspermont; and two specimens (MWSU 18883 & 18884) 2 mi W of Aspermont.

*Neotoma micropus.*—The conspicuous stick nests of the southern plains woodrat were commonly found in association with mesquite and in open rocky situations. Two specimens were collected: one specimen (MWSU 19096) 2 mi W of Aspermont; one specimen (MWSU 19995) 3 mi W of Peacock.

*Neotoma albigula.*—The white-throated woodrat occupies the western parts of the state, most commonly where rugged terrain occurs in association with juniper. The western parts of Stonewall County occur along the eastern limits of the species range in Texas. Four specimens were collected: one specimen (MWSU 19345) 12.4 mi NNW of Aspermont; two specimens (MWSU 9756 & 9757) 13 mi E of Aspermont; one specimen (MWSU 19966) 3 mi W of Peacock.

Acknowledgements

Thanks are due to Stonewall County residents Jeff and Bill Flowers for granting permission to collect on their property, and for their comments on mammals of the region. Collections were made under permits granted by the Texas Parks and Wildlife Department. Clyde Jones and an anonymous reviewer provided helpful comments on an earlier draft of this manuscript.

Literature Cited


Observations of Winter Interactions Between a Red-Headed Woodpecker (Melanerpes erythrocephalus) and Golden-Fronted Woodpeckers (M. aurifrons)

Michael S. Husak
Department of Biology, Angelo State University
San Angelo, Texas 76909

Present Address:
Department of Biological Sciences, Mississippi State University
Mississippi State, Mississippi 39762

Red-headed Woodpeckers (Melanerpes erythrocephalus) are resident over much of the eastern United States where they are sympatric with Red-bellied Woodpeckers, M. carolinus (A.O.U. 1983). Numerous authors have addressed ecological relationships and interactions between these congeners during both the breeding and winter seasons (e.g., Kilham 1958; Reller 1972; Jackson 1976; Moskovits 1978; Nichols & Jackson 1987). Migratory populations of Red-headed Woodpeckers often winter in portions of west-central Texas where they are found sympatriically with Golden-fronted Woodpeckers, M. aurifrons (cf. Texas Ornithological Society 1995). In Tom Green County, Texas, Red-headed Woodpeckers are a rare to uncommon winter resident (Maxwell 1979; Texas Ornithological Society 1995). Despite this seasonal sympatry, there are no published accounts of interactions between these species. This report describes observations of winter territorial behavior by a single Red-headed Woodpecker towards Golden-fronted Woodpeckers.

Observations were made of interactions between a single adult Red-headed Woodpecker and Golden-fronted Woodpeckers from 8 January - 25 February 1995 along the North Concho River at San Angelo State Park, Tom Green County, Texas. Woody vegetation was dominated by pecan (Carya illinoinensis) and mesquite (Prosopis glandulosa) with scattered stands of hackberry (Celtis sp.), western
soapberry (*Sapindus saponaria*), and black willow (*Salix nigra*). Underbrush was controlled by periodic mowing. Movements of the Red-headed Woodpecker were recorded on maps of the area produced from aerial photographs. Territory size was determined using 100% minimum polygon and Lind's (1979) cut and weigh technique. Behavior of both the Red-headed Woodpecker and Golden-fronted Woodpeckers in the area was recorded.

The Red-headed Woodpecker consistently defended a territory of 1.13 ha against numerous Golden-fronted Woodpeckers which frequently traveled into the area to forage on pecans. The Red-headed Woodpecker regularly supplanted and chased male and female Golden-fronted Woodpeckers from the area, never chasing beyond territory boundaries. The primary means of territory maintenance appeared to be by vocalizations. Displays by the Red-headed Woodpecker were not readily noted, but on 8 January a "head swinging" display was directed at a female Golden-fronted Woodpecker which had landed in a mesquite tree where numerous pecans were stored.

Golden-fronted Woodpeckers were always observed to retreat from confrontations; the only observable defensive behavior was "kek" and "chewump" calls which were given when supplanted and chased. Despite the apparent dominance of the Red-headed Woodpecker, Golden-fronted Woodpeckers regularly returned in attempt to collect pecan nuts. It is interesting to note that until the second week in February, Golden-fronted Woodpeckers were observed to forage communally in neighboring pecan stands. Also, while the Red-headed Woodpecker remained within the confines of its territory, Golden-fronted Woodpeckers were observed traveling in excess of 1 km to the pecan trees in the area, often crossing areas occupied by other Golden-fronted Woodpeckers.

Golden-fronted Woodpeckers began establishing breeding territories during the second week of February; however, none of the initial boundaries came into contact with those of the Red-headed Woodpecker. The Red-headed Woodpecker was last observed in the area on 25 February and within one week, a pair of neighboring Golden-fronted Woodpeckers extended their boundaries to include that area.

The 1.13 ha territory size is considerably larger than what has been reported for this species wintering in Maryland (Kilham 1958), Florida (Moskovits 1978), and Ohio (Doherty et al. 1996), but within the 0.8 - 1.2 ha range reported in Louisiana (MacRoberts 1975). Increased size may be a reflection of resource availability (MacRoberts 1975) or the
lack of conspecific competition (Kilham 1958).

In the eastern United States, wintering Red-headed and Red-bellied Woodpeckers will defend territories interspecifically (Reller 1972). Morphologically and behaviorally, Red-bellied and Golden-fronted Woodpeckers are very similar, so it was not surprising that the Red-headed Woodpecker was consistently aggressive towards Golden-fronted Woodpeckers. For this same reason though, the lack of agonistic behavior towards the Red-headed Woodpecker was unexpected. Perhaps the difference is a result of a seasonal reduction in aggression by Golden-fronted Woodpeckers, as was demonstrated by local intraspecific tolerance.

ACKNOWLEDGMENTS

Financial support was provided by the Rob and Bessie Welder Wildlife Foundation. I thank Terry Maxwell, Richard Conner, and an anonymous reviewer for comments on earlier versions of this manuscript. This is Rob and Bessie Welder Wildlife Foundation contribution 503.

LITERATURE CITED


MSH at: msh2@Ra.MsState.Edu
INDEX TO VOLUME 49 (1997)
THE TEXAS JOURNAL OF SCIENCE

John Beatty
Department of Biology, Angelo State University
San Angelo, Texas 76909

This index has separate subject and author sections. Words, phrases, locations, proper names and the scientific names of organisms are followed by the initial page number of the article in which they appeared. The author index includes the names of all authors followed by the initial page number of their respective article(s). References followed by "sup" refer to the supplement to 49(3).

SUBJECT INDEX

A
Aeromonas sp. 331
Aggressive behavior of lizards 49
Aimophila aestivalis: (Bachman’s sparrow) sup 123
Algorithms 223
American Fisheries Society sup 21
Ammodramus henslowii: (Henslow’s sparrow) sup 123
Annual fruit production 65
Aphyllophorales: Polyporaceae 169
Aquatic insects sup 35
Argentina, Eastern Chaco 41
Arizona 219
Ascaris suum: (parasitic worm) 319

B
Bacillus sp. 73
Baiomys taylori: (pygmy mouse) 57
Barstovian age 23
Bentsen-Rio Grande State Park 49
Big Thicket Region, Texas: sup 21, sup 35, sup 51
Bioindicator sup 51
Bison 78
Bivalve: Unionidae: Status in Eastern Texas sup 21
Lampsilis 255
Pyganodon 255
Utterbackia 255

Anodonta 255
Arcidens 255
Tritogonia 255
Quadrula 255
Cyrtonaias 255
Blarina brevicuadata: (shrew) 159
Blarina carolinensis: (shrew) 159
Blarina hylophaga: (shrew) 159
Brazos River 109
Book reviews:
The Garter Snakes: Evolution and Ecology 83
Freshwater Mussels of Texas 173
Bubo virginianus: (Gread-horned Owl) 215

C
Canonical correlation analysis sup 85
Cardinalis cardinalis: (Northern Cardinal) sup 123
Cell wall degrading enzymes 235
Cetacea 97
Chaetodipus hispidus: (pocket mouse) 57
Change ringing (computers) 295
Channel planform change 109
Chiroptera: Vespertilionidae 166
Cnemidophorus sexlineatus stephensi: (Yellow-faced racerunner) 143
Cnemidophorus laredonsis:  
(parthenogenic lizard) 49

Coleoptera: Cicindelide: 
*Cicindela pilatei*: (tiger beetle) sup 51
*Cicindela severa*:  
(tiger beetle) sup 51

Colorado sup 51

Computer networks 33

*Corynorhinus rafinesquii*:  
(Rafinesque’s big-eared bat) sup 181

Crotalus horridus:  
(Texas rattlesnake) sup 111

*Crotophaga sulcirostris*:  
(groove-billed ani) 247

Cuterebra sp. 335

*Cyanocorax yncas*: (Green jay) 247

*Cygnymys mexicanus*:  
(mexican prairie dog) 207

Cyprinella venusta sup 85

D

Dasyus novemcinctus:  
(Nine-banded armadillo) 57

*Dendroctonus frontalis*:  
(pine beetle) sup 139

*Dendroica cerulea*:  
(Cerulean Warbler) sup 123

*Dendroica discolor*:  
(Prairie Warbler) sup 123

Detrended Correspondence Analysis sup 67

Diptera: Cuterebridae 335

Distributional notes:  
Small mammals 57

Edwards plateau 267

Electron transfer complex 243

*Eptesicus fuscus*: (bat) sup 181

F

Fort Polk 23

Fruit productivity index 65

G

Geographic Information System:  
sup 13, sup 155

Geomys bursarius:  
(pocket gopher) 57, sup 111

Glen Rose Formation 199

*Globiformes graveolens*:  
(bracket fungus) 169

*Gulalupe river* 279

*Guiraca caerulea*:  
(Blue Grosbeak) sup 123

Gulf of Mexico 97

H

 Helmintheros vermivorus:  
(Worm-eating warbler) sup 123

Hibernation 41

Holdings of Texas Cooperative Wildlife Collection (Texas A&M) 97

I

*Icteria virens*:  
(Yellow-breasted chats) sup 123

Insectivora: Soricidae 159

Iron Bridge 3

J

*Juniper ashei*: (Juniper) 267

K

Kansas sup 51

L

Lake Tawakoni 3

*Lampropeltis pyromelana*:  
(moutain kingsnake) 219

*Lasiurus sp.:* (bat) sup 181

*Lepus californicus*:  
(black-tailed jackrabbit) 75, 335

*Limnuthlypis swainsonii*:  
(Swainson’s warblers) sup 123

Louisiana 5, 23, 169

M

Marine mammals 97

Matrices: parallel summable 91

*Melanerpes aurifrons*:  
(Golden-fronted woodpecker) 168, 348

*Melanerpes erythrocephalus*:  
(Reheaded woodpecker) 348
INDEX

Mexican States:
  Coahuila 207
  Nuevo Leon 207
  San Luis Potosi 207
  Sonora 219

Mimbres-Mogollon mortuary practices 163

Miocene terrestrial microvertebrate fauna 23

Myotis austroriparius: (bat) sup 181

N

Nebraska sup 51
Neches river sup 85
New Mexico 219, sup 51
NMR techniques 315

Nycticeius humeralis: (bat) sup 181

O

Oil Springs, Texas 73
Oklahoma 159

Onchopristis sp.:
  (sclerorhynchid sawfish) 199
Onychomys leucogaster:
  (grasshopper mouse) 57
Opuntia engelmannii: (pricklypear) 65
Ortalis vetula: (plain chachalaca) 247

P

Panhandle of Texas 57
Parthenogenic lizards 49

Parula americana:
  (Norther Parula) sup 123
Passerina ciris:
  (Painted Bunting) sup 123
Passerina cyanea:
  (Indigo Bunting) sup 123
Permutations 295

Perognathus flavus:
  (pocket mouse) 57
Peromyscus maniculatus:
  (deer mouse) 57

Phrynophyas venulosa:
  (veined tree frog) 41
Phyllocentropus harrissi:
  (caddisfly) sup 35

Piangra rubra: (summer tanagers) sup 123

Picoides borealis:
  (Red-cockaded woodpecker)
  sup 123, sup 139
Pierre Shale 179

Pinus echinata:
  (shortleaf pine) sup 123
Pinus palustris:
  (longleaf pine) sup 123
Pinus taeda: (loblolly pine) sup 123
Pipistrellus subflavus: (bat) sup 181
Pituophis melanoleucus ruthveni:
  (Louisiana Pine snake) sup 111

Plecostus rafinesquii:
  (big-eared bat) 166
Plecostus townsendii:
  (big-eared bat) 57

Pleistocene Tonk Creek Fauna 151
Pleistocene vertebrate fauna 3

Post Oak Savannah sup 51

Potamilus purpuratus:
  (freshwater mussel) 79

Principal component analysis sup 85

Protopnis glandulosa: (mesquite) 65
Protonotaria citrea:
  (Prothonotary warblers) sup 123

Pseudomonas sp. 331

Radicarbon dating 78
Rains County 3

Rajiformes: Sclerorhynchidae 199

Reithrodontomys montanus:
  (harvest mouse) 57
Rodents:
  geomyoid, cricetid, heteromyid 23

Salientia: Hylidae 41

Salmonella sp. 331

San Marcos river water quality 279

Sangamonian age 3

Sauria: Teiidae 49, 143

Sclerotium bataticola:
  (phytopathogenic fungus) 235

Sea turtles:
  Caretta caretta: (Loggerhead) 331
  Lepidochelys kempii:
    (Kemp’s ridley) 331
Seiurus motacilla:  
(Louisiana Waterthrush) sup 123
Serpentes: Colubridae 219
Setophaga ruticilla:  
(American Redstart) sup 123
Sigmodon hispidus: (cotton rat) 57
Sirenia 97
Sitta pusilla:  
(Brown-headed Nuthatches) sup 123
Somatochlora margarita:  
(dragonfly) sup 35
Spatial analysis sup 13
Spizella pusilla:  
(field sparrow) sup 123
Stress protein activation 319
Sylvilagus floridanus:  
(eastern cottontail) 75

T
Tadarida brasiliensis:  
(free-tailed bat) 57
Tadarida brasiliensis:  
(Brazilian free-tailed bat) 215
Taos County, New Mexico 78
Taphonomic analysis 3, 23

Tetrameryx shuleri:  
(Shuler’s prongorn antelope) 3
Texas Counties:  
Brooks 143
Cameron 143
Fannin 259
Hardin sup 85
Kenedy 143
Shelby 166
Stonewall 151 Webb 65
Time from sunrise to sunset 303
Token ring network 33
Triacromerum bonneri: (pliosaur) 179
Trinity river sup 67

U
USDA Forest Service sup 5

V
Vireo grieus:  
(White-eyed Vireos) sup 123
Vireo olivaceus:  
(Red-eyed Vireos) sup 123

W
Western Interior Seaway 179
AUTHOR INDEX

Abbott, J. C., sup 35
Adams, D. A., 179
Anderson, A. A., sup 67
Baumgardner, G. D., 97
Beekman, S. L., 73
Benoit, T. G., 73
Bhansali, K. G., 315
Boullion, T. L., 91
Branch, J. R., 199
Brooks, D. M., 247
Brown, P. F., 279
Burgdorf, S. J., sup 111
Cameron, G. N., sup 155
Cannon, A. C., 331
Cardona-Estrada, A., 207
Carr, C. B., 159
Cecil, D. R., 295
Cervantes, F. A., 75
Chao, S., 319
Clark, H. W., 163
Conner, R. N., sup 123, sup 139
Cordes, J. E., 143
Coulson, R. N., sup 139
Crenshaw, D. K., 335
Dickson, J. G., sup 123
Dixon, J. R., 41
Donahue, M. J., 319
Echols, J., 3
Emmons, C., 339
Engstrom, M. D., 75
Evans, R., sup 13
Ferguson, J. D., 73
Garrett, R. W., sup 181
Giardino, J. R., 109
Gillespie, B. M., 109
Goldberg, S. R., 219
Grant, W. E., 207
Groeger, A. W., 279
Hardy, L. M., 169
Harris, M. R., 243
Henke, S. E., 335
Howells, R. G., 79, 255, sup 21
Hubbs, C., sup 67
Husak, M. S., 168, 348
Jackson, J. T., 267
Jefferson, T. A., 97
Jones, C., 57, 166, 215
Kazmeirczak, A., 33, 223
Kelley, K. C., sup 51
Kelsey, T. C., 279
Lance, R. F., sup 181
Leach, J. D., 163
Leipnik, M. R., sup 13
Lorenzo, C., 75
Lucas, S. G., 78
Marsh-Matthews, E., sup 67
Masarachia, R. A., 319
Matloubimoghadam, F., 315
Matthews, W. J., sup 67
McDonough, T. J., 259
McKay, K. A., 243
Mercolli, C., 41
Metcalfe, A. L., 173
Milton, S. G., 315
Morgan, G. S., 78
Moriarty, L. J., sup 85
Mosley, J. L., 199
Moulton, S. R., sup 35
Odell, P. L., 91
Ortega, J., 235
Outcalt, K. W., sup 5
O’Neill, M., 78
Parmley, D., 151
Paulissen, M. A., 49, 143
Perry, I., sup 13
Peterson, J. A., 163
Pfau, R. S., 151
Pinsof, J. D., 3
Porfirio, D., 339
Raymond, L. R., 169
Roberts, K. J., 57, 215
Robertson, B. A., 331
Rudolph, D. C., sup 111, sup 139
Ruhl, M. W., 345
Saenz, D., sup 139
Scheel, D., sup 155
Schiebout, J. A., 23
Seamon, J. O., sup 155
Shrestha, P. S., sup 13
Spears, R. K., 169
Stangl, F. B., 159, 259, 345
Stewart, R. S., 339
Stewart, K. W., sup 35
Tietjen, T. E., 279
Treviño-Villarreal, J., 207
Van Auken, O. W., 267
Vaughan, R. K., 83
Walker, J. M., 143
Welsh, S. C., 295
Wiggers, R. J., 339
Windberg, L. A., 65
Winemiller, K. O., sup 85
Yancey, F. D., 57, 166, 215
Yanosky, A. A., 41
The Editorial staff wishes to acknowledge the following individuals for serving as reviewers for those manuscripts considered for publication in Volume 49. Without your assistance it would not be possible to maintain the quality of research results published in this volume of the *Texas Journal of Science*.

<table>
<thead>
<tr>
<th>Arnold, K.</th>
<th>Lundelius, E.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Baca, E.</td>
<td>Maxey, R.</td>
</tr>
<tr>
<td>Baumgardner, G.</td>
<td>Maxwell, T</td>
</tr>
<tr>
<td>Blackwell, M.</td>
<td>MacCune, D.</td>
</tr>
<tr>
<td>Blair, K.</td>
<td>Merchant, M.</td>
</tr>
<tr>
<td>Bradley, R.</td>
<td>Minckley, W.</td>
</tr>
<tr>
<td>Bryant, V.</td>
<td>Murray, P.</td>
</tr>
<tr>
<td>Burt, B.</td>
<td>Neck, R.</td>
</tr>
<tr>
<td>Campbell, D.</td>
<td>Neely, J.</td>
</tr>
<tr>
<td>Conner, R.</td>
<td>Nelson, R.</td>
</tr>
<tr>
<td>Davis, J.</td>
<td>Roberts, W.</td>
</tr>
<tr>
<td>Dickson, J.</td>
<td>Saenz, D.</td>
</tr>
<tr>
<td>Dixon, J.</td>
<td>Schiebout, J.</td>
</tr>
<tr>
<td>Dowler, R.</td>
<td>Schreur, B.</td>
</tr>
<tr>
<td>Drawe, L.</td>
<td>Scifres, C.</td>
</tr>
<tr>
<td>Edwards, R.</td>
<td>Shackleford, C.</td>
</tr>
<tr>
<td>Fisher, D.</td>
<td>Smith, S.</td>
</tr>
<tr>
<td>Ford, N.</td>
<td>Stangl, F.</td>
</tr>
<tr>
<td>Fountain, M.</td>
<td>Stevens, M.</td>
</tr>
<tr>
<td>Garono, R.</td>
<td>Stewart, R.</td>
</tr>
<tr>
<td>Grace, S.</td>
<td>Strader, R.</td>
</tr>
<tr>
<td>Hafner, D.</td>
<td>Strahan, R.</td>
</tr>
<tr>
<td>Harcombe, P.</td>
<td>Taylor, J.</td>
</tr>
<tr>
<td>Hard, R.</td>
<td>Thompson, B.</td>
</tr>
<tr>
<td>Harrel, R.</td>
<td>Thompson, F.</td>
</tr>
<tr>
<td>Harris, A.</td>
<td>Thurmond, J.</td>
</tr>
<tr>
<td>Haywood, D.</td>
<td>Trauth, S.</td>
</tr>
<tr>
<td>Hubbs, C.</td>
<td>Villarreal, J.</td>
</tr>
<tr>
<td>Jones, C.</td>
<td>Waggerman, G.</td>
</tr>
<tr>
<td>Judd, F.</td>
<td>Wiggers, R.</td>
</tr>
<tr>
<td>Leach, J.</td>
<td>Wilkins, K.</td>
</tr>
<tr>
<td>Ledbetter, W.</td>
<td>Wilson, J.</td>
</tr>
<tr>
<td>Lehman, T.</td>
<td>Winkler, D.</td>
</tr>
</tbody>
</table>
IN RECOGNITION OF THEIR ADDITIONAL SUPPORT OF
THE TEXAS ACADEMY OF SCIENCE DURING 1997

Patron Members
Don W. Killebrew
Ned E. Strenth

Sustaining Members
Dovalee Dorsett
Deborah D. Hettinger

Supporting Members
Frances Bryan Edens
Donald E. Harper, Jr.
Donivan Porterfield
William F. Reynolds
Margaret S. Stevens
Plan Now for the
101st Annual Meeting of the
Texas Academy of Science

March 5 - 7, 1998
University of Texas at Tyler

Program Chair
Dovalee Dorsett
Department of Information Systems
Baylor University
P. O. Box 98005
Waco, Texas 76798-8005
Ph. 254/710-2258
FAX 254/710-1091
E-mail: dovallee_dorsett@baylor.edu

Local Host
Don Killebrew
Department of Biology
University of Texas at Tyler
3900 University Boulevard
Tyler, Texas 75799
Ph. 903/566-7252
FAX 903/566-7189
E-mail: don_killebrew@mail.uttyl.edu

For additional information relative to the 101st Annual Meeting,
please access the meeting homepage at:
http://www.uttyl.edu/~cosc/tas/

Future Academy Meetings
1999-Texas Lutheran University
2000-Texas A&M University-Corpus Christi
2001-Stephen F. Austin State University
**Statement of Ownership, Management, and Circulation**

(Required by 39 U.S.C. 3685)

<table>
<thead>
<tr>
<th>Publication Title</th>
<th>Publication No.</th>
<th>Filing Date</th>
</tr>
</thead>
<tbody>
<tr>
<td>The Texas Journal of Science</td>
<td>04040403</td>
<td>October 1997</td>
</tr>
</tbody>
</table>

**Issue Frequency**
Quarterly

**No. of Issues Published Annually**
4

**Annual Subscription Price**

- $50 Membership
- $50 Subscription

**Complete Mailing Address of Known Office of Publication (Street, City, County, State, and ZIP-4) (Not Printer)**

Biology Department, Angelo State University
2601 West Avenue N, Tom Green County, San Angelo, TX 76909

**Full Names and Complete Mailing Addresses of Publisher, Editor, and Managing Editor (Do Not Leave Blank)**

- **Publisher (Name and Complete Mailing Address)**
  
  Dr. Ned E. Strenth, Biology Department
  
  Angelo State University
  
  San Angelo, TX 76909

- **Editor (Name and Complete Mailing Address)**
  
  Dr. Jack D. McCullough, Department of Biology
  
  Box 13003, Stephen F. Austin State University
  
  Nacogdoches, TX 75962

- **Managing Editor (Name and Complete Mailing Address)**
  
  Dr. Ned E. Strenth, Biology Department
  
  Angelo State University
  
  San Angelo, TX 76909

**Owner**

- If owned by a corporation, its name and address must be stated and also immediately thereafter the names and addresses of stockholders owning or holding 1 percent or more of the total amount of stock. If not owned by a corporation, the names and addresses of the individual owners must be given. If owned by a partnership or other unincorporated firm, its name and address as well as that of each individual must be given. If the publication is published by a nonprofit organization, its name and address must be stated (Do Not Leave Blank).

<table>
<thead>
<tr>
<th>Full Name</th>
<th>Complete Mailing Address</th>
</tr>
</thead>
<tbody>
<tr>
<td>N/A</td>
<td></td>
</tr>
</tbody>
</table>

1. **Known Bondholders, Mortgages, and Other Security Holders Owning or Holding 1 Percent or More of Total Amount of Bonds, Mortgages, or Other Securities.** If none, check here.

<table>
<thead>
<tr>
<th>Full Name</th>
<th>Complete Mailing Address</th>
</tr>
</thead>
<tbody>
<tr>
<td>N/A</td>
<td></td>
</tr>
</tbody>
</table>

2. For completion by nonprofit organizations authorized to mail at special rates. The purpose, function, and nonprofit status of this organization and the exempt status for federal income tax purposes: (Check one)

- [ ] Has Not Changed During Preceding 12 Months
- [ ] Has Changed During Preceding 12 Months

If changed, publisher must submit explanation of change with this statement.

Form 3526, October 1994

(See Instructions on Reverse)
The Texas Journal of Science

<table>
<thead>
<tr>
<th>Extent and Nature of Circulation</th>
<th>Average No. Copies Each Issue During Preceding 12 Months</th>
<th>Actual No. Copies of Single Issue Published Nearest to Filing Date</th>
</tr>
</thead>
<tbody>
<tr>
<td>a. Total No. Copies (Net Press Run)</td>
<td>1100</td>
<td>1100</td>
</tr>
<tr>
<td>b. Paid and/or Requested Circulation</td>
<td></td>
<td></td>
</tr>
<tr>
<td>(1) Sales Through Dealers and Carriers, Street Vendors, and Counter Sales (Not Mailed)</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>(2) Paid or Requested Mail Subscriptions (Include Advertisers' Proof Copies/Exchange Copies)</td>
<td>1000</td>
<td>1000</td>
</tr>
<tr>
<td>c. Total Paid and/or Requested Circulation (Sum of 15b(1) and 15b(2))</td>
<td>1000</td>
<td>1000</td>
</tr>
<tr>
<td>d. Free Distribution by Mail (Samples, Complimentary, and Other Free)</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>e. Free Distribution Outside the Mail (Carriers or Other Means)</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>f. Total Free Distribution (Sum of 15d and 15e)</td>
<td>1000</td>
<td>1000</td>
</tr>
<tr>
<td>g. Total Distribution (Sum of 15c and 15g)</td>
<td>1000</td>
<td>1000</td>
</tr>
<tr>
<td>h. Copies Not Distributed</td>
<td></td>
<td></td>
</tr>
<tr>
<td>(1) Office Use, Leftovers, Spoiled</td>
<td>100</td>
<td>100</td>
</tr>
<tr>
<td>(2) Return from News Agents</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>i. Total (Sum of 15g, 15h(1), and 15h(2))</td>
<td>1100</td>
<td>1100</td>
</tr>
<tr>
<td>Percent Paid and/or Requested Circulation (15c / 15g x 100)</td>
<td>1000</td>
<td>1000</td>
</tr>
</tbody>
</table>

Percent Paid and/or Requested Circulation

16 The Statement of Ownership will be printed in the vol. 49, #4 issue of this publication. □ Check box if not required to publish.

17 Signature and Title of Editor, Publisher, Business Manager, or Owner

I certify that all information furnished on this form is true and complete. I understand that anyone who furnishes false or misleading information on this form or who omits material or information requested on the form may be subject to criminal sanctions (including fines and imprisonment) and/or civil sanctions (including multiple damages and civil penalties).

Instructions to Publishers

1. Complete and file one copy of this form with your postmaster on or before October 1, annually. Keep a copy of the completed form for your records.

2. Include in items 10 and 11, in cases where the stockholder or security holder is a trustee, the name of the person or corporation for whom the trustee is acting. Also include the names and addresses of individuals who are stockholders who own or hold 1 percent or more of the total amount of bonds, mortgages, or other securities of the publishing corporation. In item 11, if none, check box. Use blank sheets if more space is required.

3. Be sure to furnish all information called for in item 15, regarding circulation. Free circulation must be shown in items 15d, e, and f.

4. If the publication had second-class authorization as a general or requester publication, this Statement of Ownership, Management, and Circulation must be published; it must be printed in any issue in October or the first printed issue after October, if the publication is not published during October.

5. In item 16, indicate date of the issue in which this Statement of Ownership will be printed.

6. Item 17 must be signed.

Failure to file or publish a statement of ownership may lead to suspension of second-class authorization.

PS Form 3526, October 1994 (Reverse)
THE TEXAS ACADEMY OF SCIENCE, 1997-98

OFFICERS

President: Ronald S. King, University of Texas at Tyler
President Elect: Dovalee Dorsett, Baylor University
Vice-President: James W. Westgate, Lamar University
Immediate Past President: Kenneth L. Dickson, University of North Texas
Executive Secretary: Brad C. Henry, University of Texas-Pan American
Corresponding Secretary: Deborah D. Hettinger, Texas Lutheran University
Manuscript Editor: Jack D. McCullough, Stephen F. Austin State University
Managing Editor: Ned E. Strenth, Angelo State University
Treasurer: Michael J. Carlo, Angelo State University
AAAS Council Representative: Sandra S. West, Southwest Texas State University

DIRECTORS

1995 Thomas Atchison, Stephen F. Austin State University
Charles H. Swift, Hutchinson Junior High School in Lubbock
1996 Robert D. Owen, Texas Tech University
Andrew J. Tirpak, Jr., Texas A&M University at Galveston
1997 Olufisayo Jejelowo, Texas Southern University
Orlan L. Ihms, TU Electric of Dallas

SECTIONAL CHAIRPERSONS

Anthropology: Jeff D. Leach, Centro de Investigaciones Arqueologicas
Biological Science: David Marsh, Angelo State University
Botany: Allan Nelson, Texas A&M University-Kingsville
Chemistry: Delphia F. Harris, University of St. Thomas
Computer Science: John A. Ward, Brooke Army Medical Center
Conservation and Management: Michael F. Small, Texas A&M University-Kingsville
Environmental Science: Irene Perry, Sam Houston State University
Freshwater and Marine Science: Cynthia Gorham-Test, Environmental Protection Agency
Geography: David R. Hoffpauir, Sam Houston State University
Geology: Betsy Torrez, Sam Houston State University
Mathematics: Ben Sultenfuss, Stephen F. Austin State University
Physics: Cyrus D. Cantrell, University of Texas at Dallas
Science Education: Ann S. Turney, Caldwell ISD
Systematics and Evolutionary Biology: Jim Collins, Kilgore College
Terrestrial Ecology: Monte Thies, Sam Houston State University

COUNSELORS

Collegiate Academy: Jim Mills, St. Edward's University
Junior Academy: Kathy Mittag, University of Texas at San Antonio
Vince Schielack, Texas A&M University