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RELATIONSHIPS OF THE *MARMORATUS*  
SPECIES GROUP (AMPHIBIA, LEPTODACTYLIDAE)  
WITHIN THE SUBFAMILY LEPTODACTYLINAE

By W. RONALD HEYER

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RELATIONSHIPS OF THE *MARMORATUS*  
SPECIES GROUP (AMPHIBIA, LEPTODACTYLIDAE) WITHIN  
THE SUBFAMILY LEPTODACTYLINAE<sup>1</sup>

By W. RONALD HEYER<sup>2</sup>

**ABSTRACT:** The relationships of the *marmoratus* group (subfamily Leptodactylinae) are analyzed. Primitive and derived states for 50 morphological characters are categorized and directions of change of character states are hypothesized for each character. The study sample of 29 taxa includes the five currently recognized species of the *marmoratus* group of the genus *Leptodactylus* and representatives of the other genera comprising the subfamily Leptodactylinae as defined by Lynch (1971). Relationships among the 29 taxa are analyzed by computer on the basis of clusterings of shared advanced character states. The results indicate that the relationships of the *marmoratus* group are best expressed by placing the group in a distinct genus, for which the name *Adenomera* is available. An additional systematic change resulting from the study is the placement of *Leptodactylus discodactylus* Boulenger in the genus *Lithodytes*. The genera *Adenomera*, *Leptodactylus*, and *Lithodytes* are redefined.

INTRODUCTION

The composition of the *marmoratus* species group of the genus *Leptodactylus* has recently been reviewed (Heyer, 1973). The purpose of this paper is to examine the relationships of the *marmoratus* species group to the other species groups within the genus and to other genera within the subfamily Leptodactylinae.

METHODS AND MATERIALS

One aim of this analysis is to utilize suites of different types of characters to infer relationships. My working hypothesis is that the total information gathered from the external morphology of adults and larvae, musculature and osteology of adults, egg morphology, and life history patterns, will more closely approximate relationships than could be inferred by using any one character suite by itself. Two overlapping levels of difference of kinds of information are involved in the hypothesis. Both assume that closeness of relationships are re-

<sup>1</sup>REVIEW COMMITTEE FOR THIS CONTRIBUTION

Robert L. Bezy  
Hymen Marx  
David B. Wake  
John W. Wright

<sup>2</sup>Research Associate in Herpetology, Natural History Museum of Los Angeles County; and Division of Amphibians and Reptiles, Smithsonian Institution, Washington, D.C. 20560

flected by similarities of genotypes. The first level of difference can be explained by comparing possible information content from characters of external morphology and life history patterns. Both are samplings, albeit indirect, of the genotype. If one of the taxa being compared is a forest floor frog and the other is a burrowing frog, but they have identical reproductive patterns of aquatic eggs and larvae, then different inferences regarding relationships may be deduced depending on the character suite examined. Based upon external morphology, the taxa would be considered quite different, due to differences in body proportions, metatarsal tubercle development, etc. Based on reproductive patterns, the taxa would be considered quite similar. Only by using both subset samples of the genotype would the relationships be best approximated. The second level of difference can be explained by comparing information content of external morphology and skeletal morphology. Here, the respective samples of the genotype may well be overlapping to a greater degree than in the previous example. The information content of the two character suites may thus be more similar and, indeed, one would expect parallel changes in both systems corresponding with a given functional shift. I assume that the two character sets do sample different parts of the genotype, at least in part, and for the same reasons as stated above, the relationships would best be approximated by using the information from both morphological systems. The two aspects of the hypothesis as described here are examined further in a separate paper.

The study organisms were chosen to represent as fully as possible the range of variation within the subfamily. Lynch's (1971) classification is used. Briefly, Lynch recognized four Neotropical subfamilies; the Ceratophryinae, Elosiinae, Leptodactylinae, and Telmatobiinae. Within the subfamily Leptodactylinae, he recognized the following genera: *Barycholos*, *Edalorhina*, *Hydrolaetare*, *Leptodactylus*, *Limnomedusa*, *Lithodytes*, *Paratelmatobius*, *Physalaemus*, *Pleurodema*, *Pseudopaludicola*. In this study, data were gathered from examination of specimens (Table 1), from the data presented in Lynch (1971), and a few life history character states were provided by the individuals mentioned in the acknowledgments. Information from all five species of the *marmoratus* group is compared with 10 other species of *Leptodactylus*, one species of *Edalorhina*, one *Limnomedusa*, one *Paratelmatobius*, five *Physalaemus*, two *Pleurodema*, one *Pseudopaludicola*, and the monotypic genera *Barycholos*, *Lithodytes* and *Hydrolaetare*. The ten species of *Leptodactylus* and five *Physalaemus* were chosen to represent the range of variation within the genera. The study specimens were considered to be representative of their respective species; for this analysis, the species is used as the unit of study.

Analysis of the data to infer relationships is done in two stages. The first stage is to analyze the characters, determining primitive and derived states. When more than two states are recognized, direction of change of state is inferred. The second stage of analysis is to use the combinatorial method to produce alternative phylogenies from information based on the direction of ad-

vanced character states. The combinatorial method is described in the relationships section. The determination of primitive and derived character states requires further discussion at this point.

The reasoning of Marx and Rabb (1970) is followed. They recognized ten criteria to determine directional change of character states. Certain of their criteria are not applicable in this study. Those that are, are combined in part and rephrased in terms of the present study sample.

I. Outgroup comparisons—Character state uniform in the outgroup. In order to use this criterion, information is needed from a group of organisms outside the study sample. Ideally, the outgroup would be the ancestral stock to the Subfamily Leptodactylinae. As the ancestral group is not known, generalized leptodactylids which would be expected to contain many of the ancestral states are used. Lynch (1971) has been the only recent author to review the leptodactylids at the family level. He indicated that evolution of the leptodactylids occurred independently through much of their total evolutionary history on the three continents where they are presently distributed. For this reason, the outgroup is limited to the Neotropics for the present paper. On the basis of osteology, life history, and some myology, Lynch (1971) postulated that the following taxa are relatively unspecialized with respect to the Leptodactylinae and are therefore used as the main outgroup for the present analysis: subfamily Ceratophryinae; *Ceratophrys* and *Lepidobatrachus*, and the following tribes of the subfamily Telmatobiinae; Telmatobiini; *Batrachophrynus*, *Caudiverbera*, *Telmatobufo*, Odontophrynini; *Odontophrynus*, *Proceratophrys*, and Alsodini; *Batrachyla*, *Eupsophus*, *Hylorina*, *Thoropa*. When the character states are not known for this outgroup, or when the evidence is unclear, other outgroups are or could be used. When the unmodified term outgroup appears in this paper from here on, it refers to the above assemblage of genera, however.

A character state is presumed to be primitive if it is found throughout the outgroup and derived if unique or nearly so in the leptodactylines. Marx and Rabb provide the reasoning for this, but one exception is possible. The outgroup may collectively share a character state that represents a specialization with respect to the actual ancestral stock of the Leptodactylines. As the evolutionary process is not always logical, this exception is expected to be a rare, but real, possibility. The sample size of the characters examined must be large enough so the exceptions do not distort the results significantly.

II. Outgroup comparisons—Character state polymorphism in the outgroup. This criterion differs in degree from the first. A character state is presumed to be primitive if it is widespread in the outgroup and derived if unique or nearly so in the Leptodactylines. Marx and Rabb (1970) effectively argue the reasoning for this, but further comment is required here. In criterion I, if the methodology as outlined is followed, there is only one logical determination of whether a given state is primitive or derived. This is not true of criterion II. I nevertheless think that this criterion is useful as long as two conditions are

met. First, most of the outgroup must share a state for it to be considered primitive. Second, a large sample size of characters must be used so that the infrequent misinterpretation of states does not invalidate the results.

III. Morphological and/or ecological specialization. A character state is assumed to be derived if it is predominant in some adaptive specialization. The function of the morphological specialization does not necessarily need to be fully understood. One such adaptive specialization in the subfamily Leptodactylinae involves a shift towards terrestriality.

IV. Correlation of derived states. A concordance of derived states is assumed to be the result of a common genetic history of the taxa.

TABLE 1  
List of Specimens Examined

(M indicates muscles examined, C indicates cleared and stained specimen examined, D indicates dry skeleton examined)

- Adenomera andreae*—Personal collection of W. R. Heyer (WRH) 16, C; University of Kansas, Museum of Natural History (KU) 119331, M.
- A. bokermanni*—Personal collection of W. C. A. Bokermann (WCAB) 34470, C, M; WCAB 14650, M.
- A. hylaedactyla*—Natural History Museum, Los Angeles County (LACM) 44338, C; LACM 44373, M.
- A. marmorata*—WCAB 30563, C; WCAB 30567, M.
- A. martinezi*—Museum of Zoology, University of São Paulo (DZ) 25321, C, M.
- Barycholos pulcher*—United States National Museum (USNM-GOV) 6475, M; USNM-GOV 8015, C.
- Edalorhina perezi*—University of Southern California (USC-PERU) 250, M.
- Hydrolaetare schmidtii*—DZ 1455, M; KU 110613, D.
- Leptodactylus bolivianus*—USC-CRE 178, M; USC-CRE 8256, C.
- L. bufonius*—WRH 17, C; WRH 35, C; WRH 41, D; WRH 1589, M.
- L. chaquensis*—Field Museum of Natural History (FM) 69196, M; WRH 36, D; WRH 1587, M.
- L. fuscus*—WRH 20, C, M; WRH 1387, M.
- L. latinasus*—WRH 22, C, M; WRH 1434, M.
- L. melanonotus*—WRH muscle #1, M; WRH 1-12, C; USC-JMS 766, D.
- L. mystaceus*—WCAB 30850, M; WRH 19, M, C; WRH 34, C; WRH 159, M.
- L. ocellatus*—FM 80393, M; FM 80396, M; FM 80398, M; FM 80400, M; FM 80402, M; FM 80404, M; FM 80412, M; FM 80415, M; FM 80422, M; FM 80427, M.
- L. pentadactylus*—USC-CRE 505, M; USC-JMS 277, D; USC-JMS 435, D.
- L. wagneri*—USC-JMS 881, D; USC-PERU 701, M; WRH 33, C; WRH 42, D; WRH 924, M.
- Limnomedusa macroglossa*—FM 10252, M; KU 92960, C; KU 92961, D.
- Lithodytes discodactylus*—USNM-JAP 6156, C; WRH 1138, M.
- L. lineatus*—KU 104340, C; KU 125941, D; USNM-JAP 2183, C; WRH 1199, M.
- Paratelmatobius lutzii*—KU 92981, C; 107089, C; Museu Nacional, Rio de Janeiro, no number, M.
- Physalaemus albonotatus*—LACM 73443, M; KU 92987, C.
- P. biligonigerus*—LACM 74018, M; KU 84768-775, D.
- P. fuscumaculatus*—LACM 37697, M; KU 80811, C; KU 84776, D; KU 93010, C.

- P. nattereri*—KU 92845, D; WCAB 39209, M.  
*P. signiferus*—FM 134305, M; KU 93033, C.  
*Pleurodema brachyops*—KU 96159, D; 104318, C.  
*P. thaul*—FM 44205, M.  
*P. tucumana*—LACM 73426, M.  
*Pseudopaludicola falcipes*—FM 9748, M; KU 93056, C.

#### ACKNOWLEDGMENTS

The following persons and institutions loaned material for myological and osteological examination: Antenor Leitao de Carvalho, Museu Nacional, Rio de Janeiro; William E. Duellman and J. T. Collins, Museum of Natural History, University of Kansas; Hymen Marx, Field Museum of Natural History; Paulo E. Vanzolini, Museo de Zoologia da Universidade de São Paulo; John W. Wright, Natural History Museum of Los Angeles County.

Avelino Barrio, Centro Nacional de Investigaciones Iologicas, Buenos Aires; Werner C. A. Bokermann, Fundação Parque Zoológica, São Paulo; and Holly Starrett, University of Southern California provided information on certain character states.

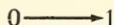
Joseph Felsenstein, University of Washington, patiently ran the computer program on the computer facilities at the University of Washington.

Without the kind assistance of all these people or without the support of a grant from the National Science Foundation, GB 27280, administered by Pacific Lutheran University, this report would not have been possible.

#### ANALYSIS OF CHARACTERS Adult External Morphology

Character 1—Pupil shape. Two states are recognized: 0) pupil horizontal, 1) pupil vertical.

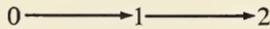
Lynch (1971) recorded state 1 as being rare among leptodactylids. He records 4 out of 11 living genera of the outgroup as having vertical pupils. State I is polymorphic within the tribes and subfamilies of the outgroup and therefore does not allow criterion II to be used. If the neotropical portion of the family Leptodactylidae is taken as the outgroup, then criterion II can be invoked in assuming that State I is the derived state. The direction of change of character states is:



Character 2—Tympanum visibility. Three states are recognized: 0) tympanum distinct externally, 1) tympanum somewhat covered by skin, but still barely visible externally, 2) tympanum completely hidden and not visible externally.

All three states are relatively common in the outgroup (Lynch, 1971). The covering of the tympanum is part of the trend leading to earlessness, a

well documented morphological specialization among frogs. State 2 is assumed to be derived on the basis of criterion III. The direction of change of character states is:



Character 3—External vocal sacs. The states are determined from preserved males. Four states are recognized: 0) a large, expanded, single vocal sac, 1) no vocal sac visible externally, although present internally, 2) indications of lateral vocal folds, 3) paired lateral vocal sacs well developed.

Within the genus *Leptodactylus*, there has been a trend towards terrestriality. One character correlating with the trend is the vocal sac. In the more aquatic members, state 1 is the rule. In the more terrestrial members, states 2 and 3 are common. Based on criterion III, state 3 is assumed to be advanced over state 1 with state 2 being intermediate. The outgroup does not provide any clear cut clue as both states 0 and 1 are represented. Morphologically it is simplest to assume that state 0 is an independent advancement over state 1. The directions of change of character states are:



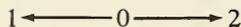
Character 4—Male thumb. Three states are recognized: 0) male thumb lacking any modifications, 1) thumb with brown or black nuptial adspersities, resembling sandpaper, 2) thumb with one or two horny spines.

State 1 is the commonest state in the outgroup, uniform in the Ceratophryinae and Alsodini (Lynch, 1971) and assumed to be the primitive state based on criterion II. State 2 is a rare state in leptodactylid frogs and is assumed to be derived on the basis of criterion II. State 0 has seemingly been derived via two routes. In the case of members of the *fuscus* species group of *Leptodactylus*, state 0 is derived from state 2 (Heyer, 1969b). This route is indicated as state 3. There is no evidence that state 0, as found in other leptodactylines, has gone through state 1. Morphologically the simplest assumption is that these other cases of state 0, here indicated 0, have been derived directly from state 1. The directions of change of character states are:



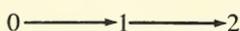
Character 5—Glands. The extent, type, and shape of body glands varies considerably in the Leptodactylinae. Only three extreme states are recognized: 0) no well defined glands of states 1 and 2, 1) glandular dorsolateral folds, 2) distinct inguinal gland.

State 0 is the commonest state in the outgroup with only *Hylorina* having state 1 (Lynch, 1971) and is assumed to be the primitive state on the basis of criterion II. Morphologically it is easiest to assume that states 1 and 2 are independent derivations of state 0. The directions of change of character states are:



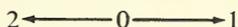
Character 6—Toe disks. Three states are recognized: 0) tips of the toes not expanded into disks, 1) tips of the toes expanded into distinct disks but the dorsal surfaces of the disks not divided, 2) dorsal surfaces of the disked toes divided longitudinally. Only *Leptodactylus bokermanni* and *hylaedactylus* show intraspecific variation in some specimens having state 0, others state 1. For the present purposes, both species are coded as having state 1.

State 0 is common in the outgroup, only some Alsodini have state 1 (Lynch, 1971) and is assumed to be the primitive state on the basis of criterion II. In the present analysis, state 2 is rarer than state 1, and as state 2 is the rarest state in leptodactylids as a group (Lynch, 1971), it is assumed to be the most derived state. The direction of change of character states is:



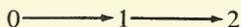
Character 7—Tarsus. Three states are recognized: 0) tarsus with at least some indication of a fold extending from the inner metatarsal tubercle to from one half to the full length of the tarsus, 1) tarsal fold short, ending in a tubercle about mid-tarsus, 2) tarsus smooth, lacking tubercles or folds. In some species categorized as exhibiting state 1, the fold is extremely weakly developed and in *Barycholos pulcher* the fold is absent, leaving only the tubercle.

State 0 is the common state for all frogs, including the outgroup, and is assumed to be the primitive state on the basis of criterion I. The directions of change of character states are:



Character 8—Metatarsal tubercles. Three states are recognized: 0) metatarsal tubercles not pronounced or cornified, 1) tubercles pronounced and pointed, 2) tubercles enlarged and heavily cornified.

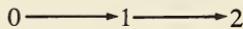
State 0 is the commonest state in the outgroup, although state 2 is reasonably represented (Lynch, 1971). The spadelike tubercles of state 2 are adaptations for burrowing. The members of the outgroup are either fossorial or aquatic frogs. It is impossible to tell *a priori* whether the leptodactylines had a more fossorial or aquatic ancestor. Therefore, it is difficult to determine which state is primitive. The spade of the outgroup is a single spade, the modified inner tubercle, while state 2 of the leptodactylines is composed of double spades, both tubercles being enlarged. The evidence suggests that state 0 is primitive. The direction of change of character states is:



Character 9—Toe webbing. Three states are recognized: 0) toes webbed, at least basally, 1) toes with lateral fringes but not distinctly webbed, 2) toes without webs or fringes. I interpret state 2 narrowly, state 1 broadly.

State 0 is the most common in the outgroup; state 1 found only in some Odontophrynini and Alsodini, state 2 found only in some Alsodini (Lynch, 1971). There is a general trend in leptodactylids from aquatic to terrestrial

life histories which correlates with webbing for aquatic members, free toes in terrestrial species. State 0 is assumed to be primitive on the basis of criteria II and III. The direction of change of character states is:



#### Egg and Larval External Morphology

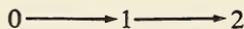
Character 10—Larval vent. Two states are recognized: 0) vent median, 1) vent dextral.

State 0 is most common in the outgroup, state 1 is confined to the *Telmatobiini* (Lynch, 1971) and is assumed to be the primitive state on the basis of criterion II. The direction of change of character states is:



Character 11—Larval denticle rows. Three states are recognized: 0) larval denticle rows  $\frac{2}{3}$ , well developed, 1) denticle rows  $\frac{2}{3}$ , weakly developed, 2) denticle rows absent.

State 0 is most common in the outgroup, the exceptions being the *Ceratophryinae* and *Caudiverbera* (Lynch, 1971) and assumed to be the primitive state based on criterion II. State 2 appears to be a morphological derivative of state 1. The direction of change of character states is:



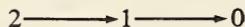
Character 12—Egg pigment. Two states are recognized: 0) eggs with melanin, 1) eggs lacking melanin.

State 0 eggs are typically aquatic pond eggs, state 1 eggs are usually hidden in some fashion. State 1 is assumed the derived state on the basis of criterion III. The direction of change of character states is:



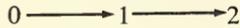
Character 13—Clutch size. Three states are recognized: 0) small clutch size (<50 eggs/clutch), 1) moderate clutch size (50-1000 eggs/clutch), 2) large clutch size (>1000 eggs/clutch). There is an inverse relationship of clutch size and size of individual egg.

Large clutches are associated with more aquatic breeding habits, small clutches are associated with more terrestrial life histories. Large clutches are assumed to be primitive on the basis of criterion III. The direction of change of character states is:



Character 14—Egg deposition. Three states are recognized: 0) eggs deposited in a gelatinous mass on top of the water, 1) eggs deposited in a foam nest on top of the water, 2) eggs deposited in a foam nest in burrows away from the water.

State 0 is found in the outgroup (Lynch, 1971) and assumed to be the primitive state on the basis of criterion I. State 2 is an ecological specialization leading towards terrestriality and assumed to be the most derived state on the basis of criterion III. The direction of change of character states is:



#### Adult Musculature

Three muscle complexes were examined to attempt to sample different functional units: 1) jaw musculature. The depressor mandibulae and adductor mandibulae open and close the jaws. 2) hyoid musculature. Although both the jaw muscles and hyoid muscles are involved in feeding, there may be different strategies involved. For example, the jaws may act as the sole means of food capture or the hyoid and tongue may act as the means of capturing food. 3) hindlimb musculature associated with the femur. These muscles control locomotion in part.

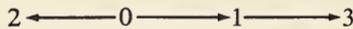
#### *Jaw Muscles*

Starrett's (1968) terminology is followed. No variation was found in the adductor muscles studied: all specimens lacked the adductor mandibulae externus superficialis, all specimens had the adductor mandibulae posterior subexternus.

Character 15—Depressor mandibulae. Four states are recognized. State 0 consists of three sites of origin: on the dorsal fascia, on the squamosal bone or the crista parotica, and on the annulus tympanicus. There may be distinct slips (DFSQAT in Starrett's (1968) terminology) or fibers to the annulus tympanicus may not be clearly demarcated from the fibers to the squamosal or the crista parotica. In all cases, the extent of origin from the three areas is roughly equivalent. State 1 consists of two equal sites of origin, the dorsal fascia and the squamosal bone or the crista parotica. There is intraspecific variation in whether or not a few fibers originate from the annulus tympanicus. State 2 is similar to state 1, except the two slips are not in the same plane. The slip from the squamosal region originates deeper than the slip originating from the dorsal fascia (DFSQd in Starrett's (1968) terminology). State 3 is characterized by the mass of the muscle originating from the dorsal fascia with a smaller slip originating from the squamosal region (DFsq in Starrett's (1968) terminology). There is intraspecific variation in whether or not a few fibers originate from the annulus tympanicus.

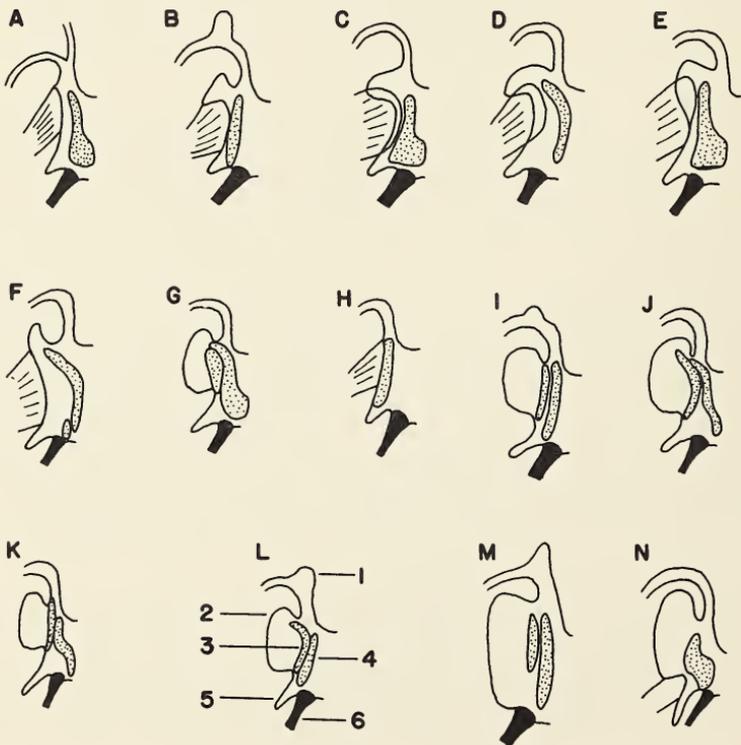
Starrett (1968) thought that a double origin of the depressor mandibulae from the dorsal fascia and squamosal region was primitive to a single origin from the squamosal region. Her reasoning was that the double origin is widespread in frogs, reptiles, and other amphibians. In the frogs Starrett examined representative of the Ceratophryinae and Odontophrynini, all had character

state 0. This state is assumed to be primitive using criterion I. A shift to more or less equal origin from the dorsal fascia and squamosal region is assumed to be derived; there are two patterns, states 1 and 2 which are assumed to be independently derived. A major origin from the dorsal fascia with a small slip originating from the squamosal region, state 3, is assumed to be secondarily derived from state 1. The directions of change of states are summarized as:



### *Hyoid Musculature*

Trewavas (1933) examined the hyolaryngeal apparatus in a broad spectrum of frogs. Her terminology is followed here. Lynch (1971) used certain characteristics from the hyoid complex in his classification. The following muscles were examined in this study: geniohyoideus medialis, geniohyoideus lateralis, anterior petrohyoideus, sternohyoideus, omohyoideus, and hyoglossus. There is considerable variation in the hyoid apparatus and associated musculature (Fig. 1). The only muscle examined which did not vary was the hyoglossus.



Before describing the variation found, a comment on the function of the apparatus is warranted. DeJongh and Gans (1969) and Martin and Gans (1972) have shown that with the exception of the hyoglossus, all the muscles examined function in both respiration and calling. It is reasonable to assume that the hyoglossus is involved in tongue movement associated with feeding. There appear to be two ends of a continuum involving hyoid shape and insertion of the anterior petrohyoideus and sternohyoideus muscles in particular. Based on the little comparative work that has been done, one can not determine *a priori* which pattern might lead to a more efficient adaptive type when any one of the three functions in which the apparatus is involved is being most strongly selected for.

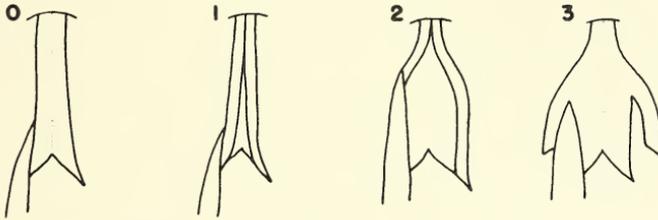


FIGURE 2. Character states of geniohyoideus medialis muscle. Sternohyoideus muscle present on left of diagrams, removed on right of diagrams. See text.

Character 16—Geniohyoideus medialis. Four states are recognized (Fig. 2). In state 0, the muscle is continuous medially, dividing posteriorly where the posteromedial processes of the hyoid articulate with the body of the hyoid. The hyoglossus muscle is completely covered ventrally by the geniohyoideus medialis. In state 1, the muscle is divided medially, exposing part of the hyoglossus. The sternohyoideus covers little of the geniohyoideus medialis. In state 2, the muscle is divided ventrally. The posterior half of the geniohyoideus muscle is covered by the sternohyoideus. An external slip is present in state 3

FIGURE 1. Diagrammatic representations of hyoid apparatus and attachments of anterior petrohyoideus and sternohyoideus muscles from ventral view for selected leptodactylines. Insertion of anterior petrohyoideus on edge of hyoid plate only indicated by muscle outline (A), insertion on edge and ventral body of hyoid indicated by muscle outline extending onto hyoid (C), insertion on ventral body of hyoid only indicated by outline of insertion area (L, 3). 1—Anterior process of hyale, 2—alary process, 3—area of insertion of anterior petrohyoideus muscle, 4—area of insertion of sternohyoideus muscle, 5—posterolateral process, 6—posteromedial process. A—*Barycholos pulcher*, B—*Edalorhina perezii*, C—*Leptodactylus bokermanni*, D—*Leptodactylus hylaedactylus*, E—*Leptodactylus andreae*, F—*Leptodactylus marmoratus*, G—*Leptodactylus martinezi*, H—*Limnomedusa macroglossa*, I—*Physalaemus biligonigerus*, J—*Physalaemus fuscomaculatus*, K—*Physalaemus signiferus*, L—*Physalaemus albonotatus*, M—*Pseudopaludicola falcipes*, N—*Hydrolaetare schmidti*.

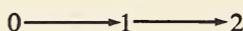
which is lacking in the other three states. The additional slip attaches to the posteromedial process of the hyoid apparatus. The internal slip is the same as the entire muscle of state 0. Character state 2 is confined to those species having broad winglike alary processes of the hyoid.

As Lynch (1971) points out, winglike processes of the alary are rare in leptodactylids and represent a derived condition. As only taxa with winglike alary processes have state 2, I used criterion IV in determining state 2 as a derived state. State 1 is intermediate between states 0 and 2. State 3 is unique as far as I know to *Limnomedusa macroglossa* and is assumed to be derived on the basis of criterion I. The directions of change in character states are:



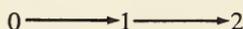
Character 17—Geniohyoideus lateralis. Three states are recognized. In state 0, the geniohyoideus lateralis originates on the anterior lower jaw and separates into two slips posteriorly. The internal slip inserts on the posteromedial process of the hyoid, the external slip inserts on the posterolateral process of the hyoid or on the body of the hyoid in the region where the posterolateral process would be, were it present. In some specimens, there appeared to be an attachment of the muscle to the hyale, but may have been due to method of preservation. State 1 is similar to state 0 except that there is a definite attachment of the muscle to the hyale, which is indicated by a lateral flaring of the muscle to attach to the hyale anterolaterally. State 2 is similar to state 1 and differs in that a distinct muscle slip attaches to the hyale anterolaterally.

State 2 occurs rarely among frogs in general (Trewavas, 1933) and in the study sample and is assumed to be derived on the basis of criterion II. State 1 appears to be an intermediate condition. The direction of change in character states is:



Character 18—Anterior petrohyoideus. The patterns of insertion of this muscle are quite variable (Fig. 1). Three states appear to encompass the variation noted. In state 0, the anterior petrohyoideus inserts entirely on the edge of the hyoid apparatus (Fig. 1, A, B, F, H, N). In state 1, the muscle inserts in part on the edge of the hyoid and on the ventral body of the hyoid in part (Fig. 1, C, D, E). In state 2, the muscle inserts entirely on the ventral surface of the hyoid body (Fig. 1, G, I, J, K, L, M).

Lynch (1971) indicated that the outgroup has state 0 and that state 2 is a rare state in leptodactylid frogs. State 2 is assumed to be advanced on the basis of criterion I. State 1 appears to be intermediate between states 0 and 2. The direction of change in character states is:



Character 19—Sternohyoideus origin. All specimens have a lateral or external slip that is continuous with the rectus abdominis muscle. The varia-

tion occurs where the sternohyoideus originates from the posterior sternal apparatus. Three states are recognized. In state 0, a single medial slip originates from the meso- and xiphisterna. The actual attachment may vary from the condition figured (Fig. 3, 0) to attachment on the anterior portion of the mesosternum (only) and the xiphisternum, but in all cases a single muscle slip is involved. In state 1, a distinct slip originates from the anterior portion of the mesosternum, another slip originates from the posterior meso- and/or the xiphisternum (Fig. 3, 1). In state 2, a single medial slip originates from the anterior mesosternum only (Fig. 3, 2).

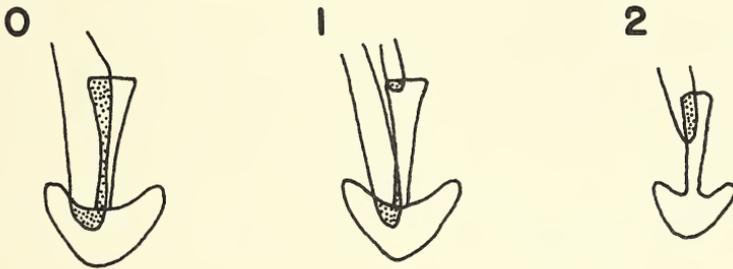
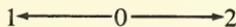


FIGURE 3. Character states of sternohyoideus origin. Stippling indicates area of attachment. See text.

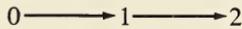
State 2 is unique in the sample and is assumed to be derived on the basis of criterion I. The situation for the outgroup is not known. All members of the outgroup have a cartilaginous plate for the meso- and xiphisternum and probably have a single medial slip originating from the sternal plate. As Lynch (1971) suggests, the sternal conditions of the Leptodactylinae are derived for the family; state 1 of the sternohyoid origin is only found with the derived sternal apparatus, hence state 1 is assumed derived on the basis of criterion IV. The simplest explanation for direction of character states is that the two derived states are independent derivations of state 0:



Character 20—Sternohyoideus insertion. The variation in patterns of insertion on the hyoid body is great (Fig. 1). Three states appear to encompass the variation. In state 0, the sternohyoideus inserts in a narrow band near the lateral edges of the hyoid (Fig. 1, B, H, I, L, M). In state 1, the muscle has some fibers inserting near the lateral edges of the hyoid and some fibers also attaching near the midline of the hyoid posteriorly (Fig. 1, C, E, G). In state 2, the sternohyoideus inserts in a narrow band with the fibers attached near the midline posteriorly (Fig. 1, D, F, J, K).

Lynch (1971) indicates the pattern in the outgroup corresponds to state

0 and that state 2 is rare in leptodactylid frogs. State 2 is assumed to be derived over state 0 based on criterion I. State 1 appears to be an intermediate condition between states 0 and 2. The direction of change in character states is:



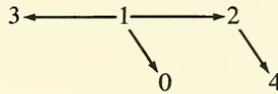
Character 21—Omohyoideus. Four states are recognized. In state 0 the muscle is lacking. In state 1, the muscle inserts partly on the hyoid plate and partly on the fascia between the posterolateral and posteromedial processes of the hyoid (Fig. 4, 1). In state 2, the muscle inserts entirely on the body of the hyoid plate ventrally (Fig. 4, 2). In state 3, the muscle inserts on the edge of the hyoid plate anterolaterad to the posteromedial process of the hyoid (Fig. 4, 3). A certain amount of intraspecific variation was noted. In the individual of *Edalorhina perezii* I examined, the omohyoideus was absent (state 0), while Trewavas (1933) indicated the specimen she examined had state 1 of the omohyoideus. In two individual *L. bokermanni* I examined, one had state 0, the other state 2, but the muscle was composed of few fibers.



FIGURE 4. Character states of omohyoideus insertion. Insertion indicated by stippling (1, 2) or muscle outline (3). See text.

No information is available from the outgroup. State 2 is almost always associated with derived states of the anterior petrohyoideus and sternohyoideus muscles and is assumed to be derived over state 1 on the basis of criterion IV. The loss of the muscle has occurred from both states 1 and 2 and is assumed to be a derived state over the presence of the muscle. For directional purposes, where intraspecific variation occurs, the state 0 is treated as a derived state of the state the muscle shows when present. For *P. signiferus*, the only state noted was state 0, but as all other *Physalaemus* examined showed state 2, *P. signiferus* state 0 is assumed to be a derived state of state 2 and is indicated as state 4. State 3 is unique in this study to *Pleurodema thaul* and assumed to be a derived

state of state 1 on the basis of criterion I. The directions of change of character states are:



### *Thigh Muscles*

In general, the methods of Limeses (1964) were followed so that the present observations would be consistent with hers. Intraspecific variation was handled in the following three ways: 1) More than one individual of a species was examined during the present analysis, 2) A series of 10 *Leptodactylus ocellatus* were examined five years ago as a part of another study (Heyer, 1968b). This species is not one included in the study, but does serve as one source of character variability within a species, 3) Observations were made on different individual specimens of the same species five years ago and for the present study. In some cases, differences of judgment are involved rather than an actual difference in character state. These differences were included as intraspecific variation as the differences would probably occur if other workers categorized the variation. The following complexes and muscles were examined: Complex of distal tendons, iliacus externus, iliacus internus, tensor fasciae latae, gracilis minor, semitendinosus, sartorius, accessory head of the adductor magnus, adductor longus, gluteus. I was unable to categorize the minimal variation encountered in the development of the iliacus internus muscle. Limeses (1964) provides data on representatives of Lynch's subfamily Ceratophryinae and tribe Odontophrynini. This information is used for comparative purposes as the outgroup to the Leptodactylinae.

Character 22—Complex of distal thigh muscle tendons. Limeses (1964) recognized three states which are followed here. In state 3, the tendon of the semitendinosus attaches on the knee below the insertion of the sartorius and the tendons of the gracilis minor and major pass dorsad to the tendon of the semitendinosus (Limeses, 1964, case A, Fig. 1). In state 0, the tendon of the semitendinosus is confluent with the posterior portion of the sartorius insertion on the knee and the tendons of the gracilis minor and major pass dorsad to the tendon of the semitendinosus (Limeses, 1964, case B, Fig. 1). In state 1, the tendon of the semitendinosus pierces the tendon of the gracilis minor and major (Limeses, 1964, case C, Fig. 1). Recent careful examination indicates that my previous interpretation of the distal tendon complex in *L. marmoratus* is wrong (Heyer, 1968b, 1969a). Previously I stated the tendons involved were fused into a single plane. Examination of muscle stained specimens indicates that all members of the *marmoratus* group have state 0. Intraspecific variation exists with states 0 and 1 occurring in a single species. These cases are recognized as state 2.

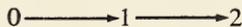
Limeses (1964) states that case 3 is primitive as it is found in bufonids,

the presumed ancestral stock of the Ceratophrynids. She also demonstrated that state 3 is by far the commonest state among the Ceratophryinae and Odontophrynini she examined. State 3 is assumed to be primitive on the basis of criterion II. State 0 is the commonest state in this study sample; state 1 is the rarest, with state 2 intermediate between states 0 and 1. State 1 is assumed to be the most derived on the basis of criterion II. The direction of change of character states is:



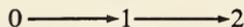
Character 23—Iliacus externus. Three states are recognized. In state 0, the iliacus externus muscle extends no more than half the distance anteriorly on the iliac bone from where the leg muscles join the iliac to the anterior extremity of the iliac (medium and short states of Limeses, 1964, Fig. 2). In state 1, the iliacus externus extends from over one half to not more than three quarters the distance of the iliac (Long A state of Limeses, 1964, Fig. 2). In state 2, the iliacus externus extends from three quarters to the full length of the iliac (Long B state of Limeses, 1964, Fig. 2). The states are categorized so that all intraspecific variation observed occurs within a single state.

State 0 is by far the commonest state of Ceratophryinae and Odontophrynini, the exception occurring in some *Ceratophrys* (Limeses, 1964) and thus assumed to be primitive on the basis of criterion II. The direction of change of character states is as follows:



Character 24—Tensor Fasciae Latae. Three states are recognized. In state 0, the tensor fasciae latae inserts posterior to the iliacus externus muscle on the iliac bone (States C-1 and C-2 of Limeses, 1964, Fig. 4). There is intraspecific variation on the relative sizes of the origin and insertion portions of the muscle. In state 1, the tensor fasciae latae inserts at the same level on the iliac bone as the iliacus externus muscle (State D of Limeses, 1964, Fig. 4). In state 2, the tensor fasciae latae inserts anterior to the iliacus externus muscle on the iliac bone.

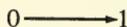
State 0 is the commonest state found in the ceratophryines and odontophrynins, the exception occurring in some *Lepidobatrachus* and is assumed to be primitive on the basis of criterion II. State 1 is morphologically intermediate between states 0 and 2. The direction of change of character states is:



Character 25—Gracilis Minor. The variation observed was very difficult to categorize. The muscle varies in its breadth and thickness. It is particularly difficult to determine the state of a very broad but thin muscle. Only two extreme states are recognized. In state 0, the muscle is broad, covering the gracilis major entirely. The muscle may also cover part of the adductor magnus and may be either relatively thick or thin (voluminous and well-developed states of Limeses, 1964). In state 1, the muscle covers only part of the gracilis

major and is composed of a few weak fibers (rudimentary state of Limeses, 1964).

State 1 is rare in the present sample as well as the outgroup, being found only in some *Ceratophrys* (Limeses, 1964) and is assumed to be derived on the basis of criterion II. The direction of change of character states is:



Character 26—Semitendinosus. Four states are recognized. In state 0, the interior (with respect to the femur) and exterior portions of the semitendinosus unite in a common tendon distally. There is no distinct tendon of the exterior portion. The two portions may be equal in development, or the exterior portion is larger than the interior (Fig. 5, 0, also Limeses, 1964, Fig. 5, A, B-1, B-2. The reason for combining all of Limeses' states is that six species demonstrate intraspecific variation between her states A, B-1, one species has states B-1 and B-2, and one species has states A, B-1, and B-2). In state 1, the exterior portion has a distinct distal tendon which attaches to the bulk of the interior portion. The exterior portion is well developed, but smaller than the interior portion (Fig. 5, 1). State 2 is similar to state 1 except the exterior portion is much reduced (Fig. 5, 2). In state 3, the exterior portion has a distinct tendon which attaches to the bulk of the interior portion. The two portions are about equally developed, but they are displaced so the bulk of the exterior portion is proximal, the bulk of the interior portion is distal (Fig. 5, 3).

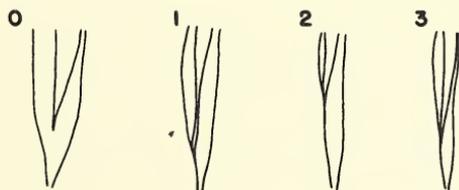
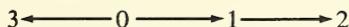


FIGURE 5. Character states of semitendinosus muscle. See text.

The outgroup uniformly has state 0 (Limeses, 1964) and is assumed to be the primitive state on the basis of criterion I. There appear to be two morphological specializations of state 0; one leading to state 3, the other leading to state 2 with state 1 as an intermediate. The directions of change of character states are:



Character 27—Sartorius. Three states are recognized. In state 0, the sartorius is moderately developed (Narrow type of Limeses, 1964). In state 1, the sartorius is a broad muscle, completely covering the adductor longus and

almost all of the adductor magnus (wide type of Limeses, 1964, Fig. 6 B). In state 2, the sartorius is a very narrow muscle, exposing much of the adductor longus and adductor magnus muscles (very narrow type of Limeses, Fig. 6 A).

As Limeses (1964) points out, state 0 is the commonest condition found in any grouping of frogs and is assumed to be primitive on the basis of criterion II. The directions of change of character states are:

$$2 \longleftarrow 0 \longrightarrow 1$$

Character 28—Accessory head of the adductor magnus. Three states are recognized. In state 0, there is no distinct tendon of the accessory head of the adductor magnus. Either the fibers of the accessory head join the tendon of the interior portion of the semitendinosus or the fibers of the accessory head of the adductor magnus and interior portion of the semitendinosus join together to form a common tendon (Fig. 7, A-1, A-2, B of Limeses, 1964). The reason for combining all her types into a single state is that one species has types A-1 and A-2, three species have states A-1 and B, and two species have states A-2 and B). In state 1, the accessory head of the adductor magnus ends proximally in a tendon which attaches to the muscle fibers of the interior portion of the semitendinosus. In state 2, the accessory head of the adductor magnus is absent.

The commonest condition of the outgroup is state 0, state 2 is found in *Lepidobatrachus* and one *Ceratophrys* (Limeses, 1964) and is assumed to be the primitive state on the basis of criterion II. The directions of change of character states are:

$$2 \longleftarrow 0 \longrightarrow 1$$

Character 29—Adductor longus. Three states are recognized. In state 0 the adductor longus is well developed and inserts either entirely on the knee, on the knee and on the adductor magnus muscle, or on the adductor magnus muscle only but near the knee. Except in specimens which have state 1 of the sartorius muscle, the adductor longus is visible without dissection. In state 1, the adductor longus is reduced, the insertion is entirely on the adductor magnus muscle, not next to the knee region and always covered by the sartorius muscle completely. In state 2, the adductor longus is absent.

Based on Limeses' Figures (1964, Plates I, II, III), the state of the outgroup is 1 and is thus assumed to be the primitive state based on criterion I. The directions of change of character states are:

$$0 \longleftarrow 1 \longrightarrow 2$$

Character 30—Gluteus. Two states are recognized. In state 0, the gluteus is well developed, but smaller than the cruralis. The muscle inserts both on the cruralis muscle and on the knee. In state 1, the gluteus is smaller than in state 0 and inserts entirely on the cruralis muscle.

Based on Limeses' figures (1964, Plates I, II, III) the state of the out-

group is for the gluteus to be equal to or greater in bulk than the cruralis and the insertion is entirely on the knee. Assuming this state is primitive on the basis of criterion I, state 1 is morphologically the most advanced with state 0 being intermediate. The direction of change of character states is:

0 → 1

#### Adult Skeleton

Character 31—Quadratojugal. Two states are recognized: 0) quadratojugal well developed, contacting maxilla, 1) quadratojugal reduced or absent, not contacting maxilla.

State 0 is the common state of the outgroup, state 1 occurring in two genera of the *Alsodini* (Lynch, 1971) and is assumed to be the primitive state based on criterion II. The direction of change of character states is:

0 → 1

Character 32—Maxillary teeth. Two states are recognized: 0) maxillary teeth present, 1) maxillary teeth absent. Rudimentary maxillary teeth are categorized as state 0.

The commonest state in the outgroup is state 0, state 1 occurring in two genera of *Telmatobiini* (Lynch, 1971) and is assumed to be the primitive state based on criterion II. The direction of change of character states is:

0 → 1

Character 33—Nasals. Two states are recognized: 0) nasals fused or just separated from each other, 1) nasals widely separated.

State 0 is the commonest state in the outgroup, state 1 being found in the *Alsodini* (Lynch, 1971) and is assumed to be the primitive state based on criterion II. The direction of change of character states is:

0 → 1

Character 34—Frontoparietal fontanelle. Three states are recognized: 0) no frontoparietal fontanelle, 1) frontoparietal fontanelle present, small, 2) frontoparietal fontanelle present, extensive. State one includes species showing intraspecific variation with either a small fontanelle present or absent.

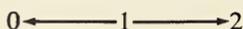
All three states are about equally represented in the outgroup (Lynch, 1971). States 1 and 2 are probably paedomorphic states of state 0 and thus are derived. The direction of change of character states is:

0 → 1 → 2

Character 35—Squamosal. Three states are recognized: 0) the zygomatic ramus is much longer than the otic ramus, the otic ramus is rudimentary, 1) the zygomatic ramus is just longer than, just shorter than, or equal to the otic

ramus, 2) the zygomatic ramus is much shorter than the otic ramus, the zygomatic ramus is rudimentary.

State 2 is rare in the outgroup, being found only in *Thoropa* (Lynch, 1971) and is assumed to be derived based on criterion II. States 0 and 1 are both well represented in the outgroup (Lynch, 1971). If state 2 is derived, then morphologically it is simplest to assume that state 0 is independently derived from state 1. The directions of change of character states are:



Character 36—Vomerine teeth. Two states are recognized: 0) vomerine teeth present, 1) vomerine teeth absent. Rudimentary vomerine teeth are included in state 0.

State 0 is the commonest in the outgroup, state 1 found only in *Batrachophrynus* (Lynch, 1971) and is assumed to be the primitive state based on criterion II. The direction of change of character states is:



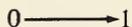
Character 37—Median contact of vomers. Two states are recognized: 0) vomers not in contact medially, 1) vomers in broad median contact.

State 0 is the commonest state in the outgroup (Lynch, 1971) and is assumed to be primitive on the basis of criterion II. The direction of change of character states is:



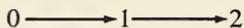
Character 38—Anterior articulation of vomer. Two states are recognized: 0) the vomer does not articulate with either the premaxilla or maxilla, 1) the vomer articulates with either the premaxilla or maxilla.

Both states are reasonably represented in the outgroup (Lynch, 1971). State 1 strengthens the snout region and correlates with a fossorial habitat. State 1 is assumed derived on the basis of criterion III. The direction of change of character states is:



Character 39—Relationship of sphenethmoid with the optic foramen. Three states are recognized: 0) the posterior extent of the sphenethmoid is widely separated from the optic foramen, 1) the posterior extent of the sphenethmoid closely approximates the optic foramen, 2) the posterior extent of the sphenethmoid borders the optic foramen.

State 2 gives greater strength to the central skull region and correlates with a fossorial habitat within *Leptodactylus* (Heyer, 1969b). State 2 is assumed derived on the basis of criterion III. The direction of change of character states is:



Character 40—Anterior extent of sphenethmoid. Two states are recog-

nized: 0) sphenethmoid extending anteriorly no more than the middle of the vomerine bones, 1) sphenethmoid extending anteriorly beyond the middle of the vomerine bones. State 1 includes calcification of the ethmoid region which is fused with the sphenethmoid bone.

The state 1 condition gives a stronger snout. This is correlated with a fossorial habitat within the genus *Leptodactylus* (Heyer, 1969b) and is assumed to be the derived state based on criterion III. The direction of change of character states is:

0 → 1

Character 41—Pterygoid-parasphenoid overlap. Three states are recognized: 0) no pterygoid-parasphenoid overlap in an anterior-posterior plane, 1) the pterygoid overlaps the parasphenoid in an anterior-posterior plane, but the elements are not in contact, 2) the pterygoid and parasphenoid overlap and are in contact. I find the condition in *Pleurodema* and *Pseudopaludicola* to be state 0, which agrees with Lynch on pages 173 and 185 but disagrees with Lynch on page 51.

State 2 is the common condition in the outgroup, state 0 found in some Telmatobiini and one genus of Alsodini (Lynch, 1971) and is considered the primitive condition based on criterion II. Morphologically, state 1 is intermediate between states 0 and 2. The direction of change of character is:

2 → 1 → 0

Character 42—Occipital condyles. Two states are recognized: 0) occipital condyles closely juxtaposed, 1) occipital condyles moderately or widely separated.

State 0 is the common state within the outgroup, state 1 found only in two genera of Alsodini (Lynch, 1971) and is assumed to be the primitive state based on criterion II. The direction of change of character states is:

0 → 1

Character 43—Anterior processes of the hyale. Two states are recognized: 0) anterior processes of the hyale are present, 1) there are no anterior processes of the hyale. Figure 2F in Heyer (1969a) is incorrect as the process of the hyale indicated is actually a nerve. I disagree with Lynch (1971:35) who stated that anterior processes of the hyale are present in *Lithodytes*.

Anterior processes of the hyale represent parts of the hyoid skeletal arches that are lost in frogs lacking the processes. State 0 is thus assumed to be the primitive state. The direction of change of character states is:

0 → 1

Character 44—Alary process of hyoid. The variation in configuration of the alary process is considerable (Fig. 1). Three states are arbitrarily defined. In state 0 the process is extremely reduced or absent (Fig. 1, A, H). In state 1, the alary process is somewhat narrow and often stalked (Fig. 1, B, C, D, E,

## Character states of 29 species

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
<i>Barycholos pulcher</i>	0	0	0	0	0	1	1	0	2	9	9	1	0	9	0	2	0	0	1	
<i>Edalorhina perezi</i>	0	0	1	1	2	0	1	0	1	0	0	9	9	9	0	1	1	0	1	
<i>Hydrolaetare schmidtii</i>	1	0	1	0	0	0	0	0	0	9	9	9	9	9	3	0	0	0	1	
<i>Leptodactylus bokermanni</i>	0	0	2	0	0	1	0	0	2	0	1	1	0	2	3	0	0	1	0	
<i>L. bolivianus</i>	0	0	1	2	1	0	0	0	1	0	0	0	2	1	3	0	0	0	1	
<i>L. bufonius</i>	0	0	3	3	0	0	0	0	2	0	0	1	1	2	3	0	2	0	0	
<i>L. chaquensis</i>	0	0	2	2	1	0	0	0	1	0	0	0	2	1	3	0	0	0	0	
<i>L. discodactylus</i>	0	0	1	3	0	2	0	0	1	9	9	1	2	9	3	0	0	0	1	
<i>L. fuscus</i>	0	0	3	3	1	0	0	0	2	0	0	1	1	2	3	0	1	0	1	
<i>L. hylaedactylus</i>	0	0	2	0	0	1	0	0	2	0	2	1	0	2	3	2	1	1	0	
<i>L. latinasus</i>	0	0	2	3	0	0	0	0	2	0	0	1	1	2	3	0	2	0	0	
<i>L. andreae</i>	0	0	2	0	0	1	0	0	2	9	9	1	0	9	3	0	0	1	1	
<i>L. marmoratus</i>	0	0	2	0	0	1	0	0	2	9	9	1	0	2	3	2	2	0	0	
<i>L. martinezi</i>	0	0	1	0	0	0	0	0	2	9	9	1	0	9	3	2	0	2	0	
<i>L. melanonotus</i>	0	0	1	2	0	0	0	0	1	0	0	0	2	1	3	0	0	0	0	
<i>L. mystaceus</i>	0	0	2	3	1	0	0	0	2	0	0	1	1	2	3	0	1	0	0	
<i>L. pentadactylus</i>	0	0	1	2	1	0	0	0	2	0	0	9	9	1	3	0	0	0	0	
<i>L. wagneri</i>	0	0	1	2	0	0	0	0	1	0	0	0	2	1	3	0	0	0	0	
<i>Limnomedusa macroglossa</i>	1	0	1	1	0	0	0	0	1	9	9	9	9	9	3	3	0	0	1	
<i>Lithodytes lineatus</i>	0	0	9	0	0	2	0	0	2	9	9	1	9	9	3	0	0	0	1	
<i>Physalaemus albonotatus</i>	0	1	0	1	0	0	1	1	1	1	0	1	9	1	1	1	0	2	1	
<i>P. biligonigerus</i>	0	2	0	1	0	0	1	2	1	1	0	1	9	1	3	0	0	2	1	
<i>P. fuscomaculatus</i>	0	2	0	1	2	0	1	2	1	1	0	1	2	1	1	0	0	2	0	
<i>P. nattereri</i>	0	2	0	1	2	0	1	2	2	1	0	1	9	1	1	2	0	2	0	
<i>P. signiferus</i>	0	1	0	1	2	0	0	1	2	1	0	1	9	1	1	2	0	2	0	
<i>Pleurodema thaul</i>	0	1	0	1	2	0	0	1	1	0	0	0	9	0	1	1	0	0	0	
<i>P. tucumana</i>	0	0	0	1	0	0	0	2	1	0	0	9	9	1	0	0	0	0	0	
<i>Pseudopaludicola falcipes</i>	0	2	0	0	0	0	1	1	1	1	0	0	9	0	2	1	0	2	2	
<i>Paratelmatobius lutzi</i>	0	2	1	1	0	0	2	0	0	9	9	0	9	9	0	2	0	0	1	

Information is indicated by a 9

TES

	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50
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2	2	0	0	0	0	0	1	0	0	1	0	0	0	1	1	1	1	2	1	1	2	0	9	0	0	0	0
2	0	0	0	0	0	0	1	0	0	1	0	1	0	0	1	2	0	1	1	1	1	0	1	1	0	2	0
2	0	0	0	0	0	0	1	0	0	1	0	1	0	0	0	0	0	1	1	1	1	0	1	0	0	2	0
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2	0	0	0	0	0	0	0	0	0	1	0	1	0	0	1	2	1	1	1	1	1	0	1	2	0	2	0
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2	0	0	0	0	0	0	1	0	0	1	1	1	0	0	0	0	0	1	1	1	1	0	1	0	0	2	0
2	0	0	0	0	0	0	1	0	0	1	0	1	0	0	1	2	1	1	1	1	1	0	1	0	0	2	0
2	0	0	0	1	0	0	1	0	0	1	0	1	0	0	0	1	1	1	1	1	1	0	1	0	0	2	0
2	0	0	0	0	0	0	1	0	0	1	0	1	0	0	1	0	0	1	1	1	1	0	1	0	0	2	0
2	0	0	0	0	0	0	1	0	0	1	0	1	0	0	1	0	0	1	1	1	1	0	1	0	0	2	0
2	0	2	0	0	1	1	0	0	1	2	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0	1	2
2	0	0	1	0	0	0	1	0	0	1	0	1	0	0	1	0	0	0	1	1	1	0	1	2	0	2	0
2	0	1	3	0	1	0	1	0	0	1	0	2	1	0	0	0	0	0	1	0	2	0	0	0	0	1	2
2	0	1	0	0	0	0	0	0	0	1	0	2	0	0	0	0	0	0	1	0	2	0	0	0	0	1	2
2	1	0	0	0	0	0	0	0	0	1	0	2	1	0	1	0	0	0	1	1	2	0	0	0	0	1	2
2	0	0	1	0	1	0	1	0	1	1	0	2	1	0	0	0	0	0	1	1	2	0	0	0	1	1	2
2	0	0	3	0	1	2	1	0	1	1	0	1	1	0	0	0	0	0	1	1	2	0	0	0	0	1	0
2	0	0	3	0	1	0	0	1	0	1	2	2	0	0	0	0	0	0	1	1	1	0	0	0	0	2	1
2	0	0	3	2	1	0	0	1	0	1	2	2	0	0	0	0	0	0	1	0	1	0	0	0	0	2	1
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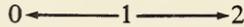


## Character states of 29 species. No information is indicated by a 9

	CHARACTER STATES																		CHARACTER STATES																																		
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50			
<i>Barycholos pulcher</i>	0	0	0	0	0	1	1	0	2	9	9	1	0	9	0	2	0	0	1	1	0	2	0	0	2	0	0	1	1	0	0	1	0	0	1	0	2	0	0	0	0	0	0	1	0	0	0	1	2	0	0	1	2
<i>Edalorhina perezii</i>	0	0	1	1	2	0	1	0	1	0	0	9	9	9	0	1	1	0	1	1	0	1	0	0	2	2	1	1	1	0	0	1	0	1	0	0	0	0	0	0	0	1	1	0	1	0	0	0	0	0	1		
<i>Hydrolaetare schmidti</i>	1	0	1	0	0	0	0	0	0	9	9	9	9	9	3	0	0	0	1	1	0	2	2	0	0	0	0	0	0	1	0	0	1	0	0	1	0	0	0	1	1	1	2	1	1	2	0	9	0	0	0	0	
<i>Leptodactylus bokermanni</i>	0	0	2	0	0	1	0	0	2	0	1	1	0	2	3	0	0	1	0	1	0	2	0	0	0	0	0	0	0	1	0	0	1	0	1	0	1	0	0	1	2	0	1	1	1	1	0	1	1	0	2	0	
<i>L. bolivianus</i>	0	0	1	2	1	0	0	0	1	0	0	0	2	1	3	0	0	0	1	1	2	2	0	0	0	0	0	0	1	0	0	1	0	0	1	0	0	0	0	1	1	1	1	1	0	1	0	0	2	0			
<i>L. bufonius</i>	0	0	3	3	0	0	0	0	2	0	0	1	1	2	3	0	2	0	0	1	0	2	0	0	0	1	0	0	1	0	0	1	0	1	0	1	0	1	1	2	1	1	1	1	1	0	1	0	0	2	0		
<i>L. chaquensis</i>	0	0	2	2	1	0	0	0	1	0	0	0	2	1	3	0	0	0	0	1	0	2	2	0	0	0	0	0	1	0	0	1	0	1	0	1	0	0	0	0	0	2	1	1	1	0	1	0	0	2	0		
<i>L. discodactylus</i>	0	0	1	3	0	2	0	0	1	9	9	1	2	9	3	0	0	0	1	1	0	2	0	1	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	0	1	1	1	1	0	1	2	0	2	0			
<i>L. fuscus</i>	0	0	3	3	1	0	0	0	2	0	0	1	1	2	3	0	1	0	1	1	0	2	0	0	0	0	0	0	1	0	0	1	0	1	0	1	0	0	2	1	2	1	1	1	0	1	0	0	2	0			
<i>L. hylaedactylus</i>	0	0	2	0	0	1	0	0	2	0	2	1	0	2	3	2	1	1	0	1	0	2	0	0	0	0	0	0	1	0	0	1	0	1	0	1	0	0	1	0	0	1	1	1	0	1	0	1	0	2	0		
<i>L. latinasus</i>	0	0	2	3	0	0	0	0	2	0	0	1	1	2	3	0	2	0	0	1	0	2	0	0	0	0	0	0	1	0	0	1	0	1	0	1	0	1	0	2	1	1	1	1	1	0	1	0	0	2	0		
<i>L. andreae</i>	0	0	2	0	0	1	0	0	2	9	9	1	0	9	3	0	0	1	1	1	0	2	0	1	0	0	0	0	1	0	0	1	0	1	0	1	0	0	0	0	0	0	1	1	1	0	1	1	0	2	0		
<i>L. marmoratus</i>	0	0	2	0	0	1	0	0	2	9	9	1	0	2	3	2	2	0	0	1	0	2	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	2	1	1	1	1	1	0	1	2	0	2	0			
<i>L. martínezii</i>	0	0	1	0	0	0	0	0	2	9	9	1	0	9	3	2	0	2	0	1	0	2	0	0	0	0	0	0	1	0	0	1	1	1	0	0	0	0	0	1	1	2	0	1	1	0	1	0	2	0			
<i>L. melanotus</i>	0	0	1	2	0	0	0	0	1	0	0	0	2	1	3	0	0	0	0	1	0	2	0	0	0	0	0	0	1	0	0	1	1	1	0	0	0	0	0	1	1	1	1	0	1	0	0	2	0				
<i>L. mystaceus</i>	0	0	2	3	1	0	0	0	2	0	0	1	1	2	3	0	1	0	0	1	0	2	0	0	0	0	0	0	1	0	0	1	0	1	0	1	0	0	1	2	1	1	1	1	1	0	1	0	0	2	0		
<i>L. pentadactylus</i>	0	0	1	2	1	0	0	0	2	0	0	9	9	1	3	0	0	0	0	1	0	1	0	0	0	1	0	0	1	0	0	1	0	1	0	0	1	0	0	0	1	1	1	1	1	0	1	0	0	2	0		
<i>L. wagneri</i>	0	0	1	2	0	0	0	0	1	0	0	0	2	1	3	0	0	0	0	1	0	2	0	0	0	0	0	1	0	0	1	0	1	0	1	0	0	1	0	0	1	1	1	1	0	1	0	0	0	2	0		
<i>Limnomedusa macroglossa</i>	1	0	1	1	0	0	0	0	1	9	9	9	9	3	3	0	0	1	0	1	0	0	2	0	2	0	0	1	1	0	0	1	1	0	2	1	0	0	0	0	0	1	0	1	0	0	0	0	1	2			
<i>Lithodytes lineatus</i>	0	0	9	0	0	2	0	0	2	9	9	1	9	9	3	0	0	0	1	1	0	2	0	0	1	0	0	0	1	0	0	1	0	1	0	1	0	0	1	0	0	0	1	1	1	0	1	2	0	2	0		
<i>Physalaemus albonotatus</i>	0	1	0	1	0	0	1	1	1	1	0	1	9	1	1	1	0	2	1	1	0	1	0	1	3	0	1	0	1	0	0	1	0	2	1	0	0	0	0	0	0	1	0	2	0	0	0	0	1	2			
<i>P. billgoigerus</i>	0	2	0	1	0	0	1	2	1	1	0	1	9	1	3	0	0	2	1	1	0	1	2	0	1	0	0	0	0	0	0	0	1	0	2	0	0	0	0	0	0	0	1	0	2	0	0	0	0	1	2		
<i>P. fuscomaculatus</i>	0	2	0	1	2	0	1	2	1	1	0	1	2	1	1	0	0	2	0	1	0	1	1	0	0	0	0	0	0	0	0	0	1	0	2	1	0	0	0	0	1	1	2	0	0	0	0	1	2				
<i>P. nattereri</i>	0	2	0	1	2	0	1	2	2	1	0	1	9	1	1	2	0	2	0	1	0	1	0	0	1	0	1	0	1	0	1	0	1	0	2	1	0	0	0	0	0	1	2	0	0	0	0	1	2				
<i>P. signiferus</i>	0	1	0	1	2	0	0	1	2	1	0	1	9	1	1	2	0	2	0	1	0	1	0	0	3	0	1	2	1	0	1	1	0	1	1	0	0	0	0	0	0	1	1	2	0	0	0	0	1	0			
<i>Pleurodema thaul</i>	0	1	0	1	2	0	0	1	1	0	0	0	9	0	1	1	0	0	0	1	0	1	0	0	3	0	1	0	0	1	0	1	2	2	0	0	0	0	0	0	1	1	1	0	0	0	0	2	1				
<i>P. tucumana</i>	0	0	0	1	0	0	2	1	0	0	9	9	1	0	0	0	0	0	0	1	0	1	0	0	3	2	1	0	0	1	0	1	2	2	0	0	0	0	0	0	0	1	0	1	0	0	0	0	2	1			
<i>Pseudopaludicola falcipes</i>	0	2	0	0	0	0	1	1	1	1	0	0	9	0	0	1	0	2	2	0	0	2	0	0	2	0	0	1	0	0	1	1	0	2	1	0	0	0	0	0	0	1	0	1	0	0	0	0	2	1			
<i>Paratelmatoobius lutzi</i>	0	2	1	1	0	0	2	0	0	9	9	0	9	9	0	2	0	0	1	1	0	1	0	1	3	0	1	0	0	0	0	0	2	1	0	0	0	0	0	0	0	1	0	1	0	0	0	0	3	0			

F). In state 2, the alary process is broad and winglike (Fig. 1, G, I, J, K, L, M).

Two conditions are found in the outgroup, state 0 and state 1 (Lynch, 1971). In the evolutionary process, it is easier to lose a structure than gain it. State 1 is thus assumed to be primitive. States 0 and 2 are both rare in leptodactylid frogs (Lynch, 1971), and are assumed to be independently derived from state 1. The directions of change of character states are:



Character 45—Posterolateral process of hyoid. Two states are recognized: 0) the process is present, 1) it is absent.

State 1 is unique to *Pseudopaludicola falcipes* in this study and is very rare among leptodactylids (Lynch, 1971). State 1 is thus assumed to be derived on the basis of criterion I. The direction of change of character state is:



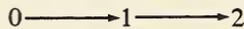
Character 46—Dorsal crest of ilium. Two states are recognized: 0) ilium without dorsal crest, or a dorsal crest weakly developed, 1) ilium with a well-developed dorsal crest.

State 0 is the common condition in the outgroup, the exception being *Caudiverbera* (Lynch, 1971) and is assumed to be primitive on the basis of criterion II. The direction of change of character states is:



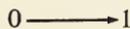
Character 47—Terminal phalanges. Three states are recognized: 0) terminal phalanges knobbed, either single or slightly bifurcate, 1) terminal phalanges definitely T-shaped, but not expanded, 2) terminal phalanges T-shaped, expanded.

State 0 is the commonest condition in the outgroup, the exceptions are two genera of Alsodini (Lynch, 1971) and is assumed to be the primitive state based on criterion II. The direction of change of character states is:



Character 48—Omosternum. Two states are recognized: 0) omosternum present, expanded, 1) omosternum absent, the entire anterior sternum a slender rod.

State 0 is the common condition in frogs and is assumed to be primitive on the basis of criterion I. The direction of change of character states is:



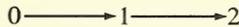
Character 49—Mesosternum. Four states are recognized: 0) mesosternum a broad bony element, single posteriorly (Lynch, 1971, Fig. 35A), 1) mesosternum a broad bony element, bifurcate posteriorly (Lynch, 1971, Fig. 35C), 2) mesosternum a bony style (Lynch, 1971, Fig. 35B), 3) mesosternum an amorphous broad bony element (Lynch, 1971, Fig. 35D).

The outgroup members all have large cartilagenous plates (Lynch, 1971), designated here as state 4. Lynch argued that state 0 is a morphological advancement over the cartilage plate and that states 1 and 2 are derived from state 0. State 3 appears to be an independent specialization of a cartilagenous plate, with deposition of bone salts to strengthen the mesosternal region. Apparently this same phenomenon has occurred in the genus *Eleutherodactylus* (Lynch, 1971, Fig. 34C). The directions of change of character states are:



Character 50—Xiphisternum. Three states are recognized: 0) xiphisternum entire, single, 1) xiphisternum single, bifurcate posteriorly, 2) xiphisternum double.

State 2 is rare in leptodactylid frogs and is assumed to be derived on the basis of criterion I. The direction of change of character states is:



The listing of character states by species is presented in Table 2.

#### RELATIONSHIPS

The combinatorial method of Sharrock and Felsenstein (personal communication) was used to organize the preceding data into clusters of species sharing derived character states. Phylogenies were then constructed with the clustering information. The combinatorial method utilizes the computer to scan the data, producing all subsets of the data which share character states. The method assumes that the direction of change of character states within a character is not reversible. Several options are available with the combinatorial method. I chose to ignore the primitive states and form the clusters of shared character states on the basis of derived character states only. The reasoning is that primitive states indicate that the organism has not changed from the ancestral condition and tell nothing of the evolutionary history of the organism. This is basically the Hennig approach which is currently the focus of much discussion; any recent copy of Systematic Zoology will introduce the interested reader to this literature.

A large number of phylogenies can be constructed from the combinatorial information. To build the phylogeny of Figure 6, two guidelines were followed. First, the data were examined for presence of sister-groups consisting of two taxa. The top branches of the tree were chosen as the pairs of species that share the most characters in a derived state. In this study, the two species sharing the most derived character states are *Physalaemus fuscomaculatus* and *P. nattereri*. The next largest assemblage of species containing both *P. fuscomaculatus* and *P. nattereri* is a group of three, adding *P. biligonigerus*,



etc. A second sister group is *Leptodactylus hylaedactylus* and *L. marmoratus*, etc. In other words, the phylogeny was constructed so that the number of shared character states was maximized. Second, where certain alternative routes were possible, I chose the alternative consistent with one of the following three clusterings. The compositions of these clusterings were chosen to reduce the total number of alternative phylogenies. The three clusterings are: 1) *Pleurodema thaul* and *P. tucumana*; 2) the *marmoratus* group—*L. andreae*, *bokermanni*, *hylaedactylus*, *marmoratus*, *martinezi*; 3) the following *Leptodactylus*—*L. bufonius*, *fuscus*, *latinasus*, *mystaceus*.

The reasoning behind using this operational guideline is as follows. Suppose *Pleurodema thaul* shares 5 advanced character states with *P. tucumana* and species A. According to the first operational guideline, alternative phylogenies could be constructed, the first uniting *P. thaul* and *P. tucumana*, the second uniting *P. thaul* and sp. A. By using the second guideline, the choice is made for *P. thaul* and *P. tucumana*. This implies that the several characters shared by *P. thaul* and sp. A represent convergent adaptations. In essence, by recognizing the three clusters a known element is being added to the phylogeny construction process, but only where the first operational guideline allows it. The danger in using this guideline is, of course, that if the clusterings recognized in this guideline are not natural, then the resultant phylogeny will not be the best phylogeny possible. Extreme care must be used in recognizing the clusterings used in the second operational guideline. I feel that the available evidence is strong that these groupings are natural (i.e. that the included species are more closely related to one another than to species of other groups) and that they can be considered as operational knowns. Although it would be more satisfying intellectually to utilize only the first guideline and then discuss the relative merits of all possible phylogenies so constructed, the maintenance of these groupings would be the major criterion by which the phylogenies would be judged. By having these few known elements to aid in making choices when choices are possible by the first guideline, the number of phylogenies is reduced from a rather high number to a much more reasonable number. The time saved in actual phylogeny construction and in manuscript space explaining the relative merits of the phylogenies constructed using only guideline one are considerable.

The combinatorial method of data organization does not produce a phylogeny, but organizes the data so that phylogenies can be constructed from large amounts of data. The value of the method is that all combinations are available, so that the phylogeny builder knows exactly where each choice was made, what taxa are involved in the choices, and what character states are involved in the choices.

As indicated, the phylogeny of Figure 6 is not the only phylogeny possible; the possible changes are now examined.

First, using the guidelines as described above, there are minor branching sequence possibilities within four lines. In each case, all variations in branch-

ing sequence have a common ancestral condition. The five species of *Physalae-mus* can be reordered, but the five species, regardless of the branching sequence among them, always have a common ancestral condition which separates them from any other taxa. Similarly, *Leptodactylus bolivianus*, *chaquensis*, *melanonotus*, and *wagneri* could be reordered among themselves; *Leptodactylus bufonius*, *fuscus*, *latinasus*, and *mystaceus* could be reordered among themselves; and *L. andreae*, *bokermanni*, *hylaedactylus*, *marmoratus*, and *martinezi* could be reordered among themselves. All these changes are minor; what stands out is that the groupings are distinctive.

The alternative locations of *Barycholos* in the phylogeny presents a different kind of problem. The most characters it shares with any given taxon is 21 and the taxon is *Physalae-mus nattereri*. But *P. nattereri* shares 31 advanced character states with *P. fuscomaculatus*, so that relationship is chosen. *Barycholos* shares 20 advanced character states (not all the same) with each of the following taxa individually: *L. andreae*, *hylaedactylus*, *marmoratus*, and *martinezi*. *Leptodactylus hylaedactylus* and *marmoratus* share 30 advanced character states between them, however, so that arrangement is preferred. The highest number of shared advanced character states that *Barycholos* shares with any group of taxa is 16 with members of the *marmoratus* group. The character states shared are 7, 18, 19, 23, 24, 25, 40, 43, 48, 49, 65, 77, 78, 83, 84, 87. Four of these are shared by all taxa under consideration: 18, 48, 78, 87. The remaining are states of the following characters: male thumb, toe webbing, egg pigmentation, clutch size, sternohyoideus insertion, omohyoideus, iliacus externus muscle, nasal bone, pterygoid-parasphenoid relationship, ilium, and terminal phalanges. (See Table 3 for correlation of the character state numbers used in the phylogeny with the character and state numbers used in the analysis of characters section.) The phylogeny of Figure 6 represents this position. *Barycholos* shares 11 advanced states with the five species of *Physalae-mus* including the four states shared by all taxa under consideration. The remaining 7 are 4, 23, 43, 65, 76, 77, 88, and are states of the following characters: vocal sac, egg pigmentation, omohyoideus, nasal bones, pterygoid-parasphenoid relationship, and mesosternum. At the same level, however, *Pseudopaludicola* shares 14 advanced states with the five *Physalae-mus* species. To fit *Barycholos* at a lower branching sequence would put it sharing 7 advanced character states with a combination of *Physalae-mus*, *Pleurodema*, and *Pseudopaludicola*. A better alternative is 13 character states shared with *Edalorhina*. The 9 character states (excluding the same 4 as above) are 14, 31, 38, 53, 54, 62, 65, 77, 91 and are states of the following characters: tarsal element structures, geniohyoideus medialis, sternohyoideus origin, semitendinosus, gluteus, nasal bones. What is involved, then, is an attempt to determine the best fit among the following taxa: *marmoratus* group, *Barycholos*, *Physalae-mus*, *Pseudopaludicola*, and *Edalorhina*. The 10 advanced states shared by *Physalae-mus* and *Pseudopaludicola* (excluding the same 4 as above) are 2, 4, 16, 20, 36, 37, 43, 76, 77, 81, which are states of the follow-

TABLE 3  
Character State Directory

A. Character state number as used in Phylogenies, B. Character number used in Character Analysis, C. Character state number used in Character Analysis.

A.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
B.	1	2	2	3	3	3	4	4	4	5	5	6	6	7	7	8	8	9	9
C.	1	1	2	0	2	3	0	2	3	1	2	1	2	1	2	1	2	1	2
A.	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38
B.	10	11	11	12	13	13	14	14	15	15	15	16	16	16	17	17	18	18	19
C.	1	1	2	1	0	1	1	2	1	2	3	1	2	3	1	2	1	2	1
A.	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57
B.	19	20	20	21	21	21	21	22	22	23	23	24	24	25	26	26	26	27	27
C.	2	1	2	0	2	3	4	1	2	1	2	1	2	1	1	2	3	1	2
A.	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76
B.	28	28	29	29	30	31	32	33	34	34	35	35	36	37	38	39	39	40	41
C.	1	2	0	2	1	1	1	1	1	2	0	2	1	1	1	1	2	1	0
A.	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92			
B.	41	42	43	44	44	45	46	47	47	48	49	49	49	49	50	50			
C.	1	1	1	0	2	1	1	1	2	1	0	1	2	3	1	2			

ing characters: tympanum visibility, vocal sac, metatarsal tubercles, tadpole vent, anterior petrohyoideus, omohyoideus, ptergoid-parasphenoid relationships, and alary process of the hyale. I subjectively evaluate the shared character state combinations of the *Barycholos-Edalorhina* combination being the weakest because it is the only combination which lacks a distinctive skeletal feature (the nasal bone state is involved several times in this clustering). There does not appear to be any clear cut reason for choosing any pair among the other possibilities as better, based on the character states involved. This includes choosing between *Barycholos-Physalaemus* and *Pseudopaludicola-Physalaemus*. Thus, on the basis of number of shared states, it seems best to choose the *Pseudopaludicola-Physalaemus* pair. The next best choice (aside from with the *marmoratus* group) of alternate placement of *Barycholos* would be to pair it with *Edalorhina*, even though the character state combinations appear weakest among all possible groupings. The resultant phylogeny (Fig. 7) has certain advantages to compensate the apparent worse fit of *Barycholos*. The new phylogeny has nine fewer character state convergences than the old phylogeny and the relationships among *Lithodytes*, the *marmoratus* group, and the remaining *Leptodactylus* are tightened up. This is consistent with all three groups being recognized as part of the same genus from time to time. For these reasons, I prefer the phylogeny represented in Figure 7 as best representing the probable phylogeny of the taxa under consideration.



The placement of two taxa, *Pseudopaludicola* and *Leptodactylus discodactylus* requires further comment. The position of *Pseudopaludicola* is further substantiated by the fact that it shares the most advanced states (21) with *Physalaemus nattereri* and the cluster that it shares the most number of advanced states with is *Physalaemus*, as represented in the phylogeny. The close relationship of *Lithodytes lineatus* and *Leptodactylus discodactylus* was not anticipated but apparently is warranted. The species with which *Lithodytes lineatus* shares the most characters (22) is *L. andreae*. *Leptodactylus andreae* shares 23 states with the cluster of *L. bokermanni*, *L. hylaedactylus*, and *L. marmoratus*. Further, this breaks up members of the *marmoratus* group which is not warranted on the basis of current systematic consensus. *Lithodytes* shares 20 or 21 characters with several combinations of species from the *marmoratus* group. *Lithodytes* also shares 20 characters with *L. discodactylus*. The highest number of shared states that *L. discodactylus* shares with any taxon is 20 with *Lithodytes*.

#### TAXONOMIC CONCLUSIONS

The study set out to analyze the relationships of the *marmoratus* group within the subfamily and the study sample was chosen to accomplish this purpose. The way in which the study sample was chosen places limitations on speculations beyond how the *marmoratus* group relates to the other taxa.

Within the limits of this study, I think the following conclusions are justifiable:

1) Within the subfamily, two major clusters of taxa are evident, what had been termed *Lithodytes* and *Leptodactylus* on the one hand, and *Physalaemus*, *Pleurodema*, and *Pseudopaludicola* on the other.

2) Within the *Lithodytes*-*Leptodactylus* cluster, three groups are evident corresponding to A) *Lithodytes lineatus* and *L. discodactylus*, B) The *marmoratus* group, and C) Remaining *Leptodactylus*.

My concept of the genus is that it: 1) is a taxon of convenience, 2) should represent a single line of ancestry, and 3) should represent a unique adaptational complex if at all possible. With respect to point one, the size of the genus should be manageable. In my opinion, the genus *Eleutherodactylus* should be divided on this basis. In the present instance, convenience does not apply as the maximum number of species involved in the genus *Leptodactylus* (broad sense) is under 50. With respect to point two, three alternatives are possible to reflect lines of ancestry depending on the level preferred:

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FIGURE 7. Preferred phylogenetic relationships among the 29 taxa of this study with *Barycholos* nearest *Edalorhina*. Generic names are used as recognized in this study and are placed at character state cluster points so that all taxa above that point will be included within the genus. Also see text.

A) a single genus, which would be indicated at the state cluster (28, 30, 60, 65, 79, 83, 89) of Fig. 7; B) two genera, the genus *Leptodactylus* represented as it is in Fig. 7, the second genus would be indicated at state cluster (23, 49, 77, 84) of Fig. 7; C) three genera, as indicated in Fig. 7. I use the third point in choosing among these alternatives. As developed elsewhere, members of the *marmoratus* group are forest frogs and their adaptations are in response to the forest environment (Heyer, 1973) while members of the genus *Leptodactylus* (narrow sense, as in Fig. 7) are savanna frogs and their adaptations are in response to the savanna environment (Heyer, 1969b, 1973). Thus, the relationships between these two assemblages are best represented at the generic level. The two species included in *Lithodytes* in Fig. 7 are not as well understood as some members of the other two groups. The two species do share a number of advanced states in common, one of which, dorsally divided toe disks, is unique in the study sample. As a genus name is already available for this unit, I prefer to recognize these two species as a genus distinct from *Leptodactylus* and *Adenomera*.

*Leptodactylus* is thus restricted to include members of the *melanonotus*, *ocellatus*, *pentadactylus*, and *fuscus* species groups with the exception of *L. discodactylus*. *Adenomera* includes members of the *marmoratus* group. *Lithodytes* consists of *L. lineatus* and *L. discodactylus*. This arrangement of *Lithodytes* may be subject to further evaluation as almost nothing is known of the life histories of the two included species and the karyotypes have not been compared. The only further change would be recognition of *L. discodactylus* as a distinct genus as it is clearly not closely related to either *Adenomera* or *Leptodactylus*.

3) The relationships of *Barycholos*, *Edalorhina*, *Hydrolaetare*, *Limnomedusa*, (which does not appear on Figs. 6 or 7) and *Paratelmatobius* are removed from the two major clusters within the subfamily. This can be explained in two different ways; 1) either these taxa represent early, specialized divergences from a common ancestor or, 2) closer relatives may be found in the subfamily Telmatobiinae as defined by Lynch (1971). The comparison of these taxa with members of the subfamily Telmatobiinae (fide Lynch) is not only recommended but necessary if formal names are to be applied to suprageneric taxonomic groupings.

#### COMPARISON WITH PREVIOUSLY PROPOSED PHYLOGENIES

Lynch (1971) provides a summary of previous phylogenetic schemes for the taxa under consideration, so that comparison with his conclusions will suffice. The similarities and differences between his analysis and this one should be pointed out. We both use many of the same characters and character states, with some exceptions. The major difference is in the treatment of the character states. Lynch apparently used a combination of primitive and

derived states in determining the relationships and he gave some characters greater weight than others. In this study, only derived character states were used in determining relationships and the only weighting of the characters was in choosing which characters and states would be included in the study.

Lynch (1971) was more concerned with relationships among the subfamilies he recognized than relationships with the subfamilies. He did comment on certain intergeneric relationships, however, which can be compared with the relationships proposed herein. He synonymized a group of previously recognized genera into the genus *Physalaemus*. The results of this study are consistent with his action, but it should be pointed out that in the present study, representatives of *Physalaemus* were not chosen to elucidate relationships among themselves. Lynch did not recognize the subgeneric category in his work, but did recognize it informally within the genus *Leptodactylus* to separate the *marmoratus* group from the other species. Here the distinction is raised to the generic level.

Lynch (1971:182) considered *Physalaemus* and *Pseudopaludicola* to be closely related; this is supported in the present study. The interpretation of the placement of *Barycholos*, *Pleurodema*, *Paratelmatoobius*, *Edalorhina*, and *Hydrolaetare* differ. Lynch (1971:192) indicates that *Barycholos* is most closely related to the subgenus *Adenomera* and *Lithodytes*; that *Pleurodema* is the most primitive genus (p. 207); that *Paratelmatoobius* has its nearest relation to *Physalaemus* although the relationship is not close (p. 184); that *Edalorhina* is an intermediate between *Lithodytes* and *Physalaemus* (p. 178); and infers that the closest relationship of *Hydrolaetare* within the subfamily is with *Leptodactylus*. The results of this study indicate that if the genera *Barycholos*, *Edalorhina*, *Hydrolaetare*, and *Paratelmatoobius* do in fact have their closest relationship with the other members of the subfamily, then they are earlier offshoots of the leptodactyline stock and hence more primitive than *Pleurodema*.

#### CHARACTER STATE EVALUATIONS

The character states can be evaluated in two different ways. Blocks of character states representing different functional systems can be compared to see if the components yield the same results as the total data set. This aspect is examined elsewhere. The aspect examined here is the evaluation of how the individual character states relate within the preferred phylogenetic diagram. In the following subjective classification, all character states are assumed to be adaptive. The only criterion that is used to determine whether the character state is of value in determining the proposed phylogenetic relationships is where the particular state appears in the tree. For example, if a state appears once in the phylogeny in a cluster leading to *Adenomera* and *Lithodytes*, that character state is considered very useful in determining relationships. Alternatively, a character state that appears 11 times, each time at a different end

point of the phylogeny is not considered useful in elucidating relationships.

The following character states are considered the best states in determining relationships: 8, 13, 16, 18, 20, 23, 37, 48, 78, 83, 87. States 13, 16, 18, 20, 48, 78, 87 are represented by a single appearance in the phylogeny. States 8, 37, and 83 are represented twice, state 23 is represented three times.

The following character states are useful in determining relationships but not to the degree as the previous states: 2, 4, 7, 9, 19, 24, 25, 26, 30, 36, 54, 67, 73, 74, 75, 81, 84, 88, 89. These states are represented on the diagram (Fig. 7) from 2 to 6 times and do not define clusters as neatly as the previous character states. In the character analysis, *Lithodytes discodactylus* was coded as state 9, meaning that the lack of thumb spines had gone through an ancestral state to thumb spines present. This was based on the false assumption that the species was related to members of the *melanonotus* species group of the genus *Leptodactylus*. The results of this study indicate that the state in question should have been coded as a 7, which would then place state 7 as an ancestral condition to both *Adenomera* and *Lithodytes*.

The following states are neutral in their usefulness in determining relationships: 1, 5, 6, 10, 12, 15, 17, 21, 22, 27, 28, 29, 34, 39, 41, 43, 44, 46, 59, 61, 65, 79. Of these, 1, 15, 22, 29, 39, 44, 46, 59, 61, are unique to individual end-point taxa and are of no use in determining relationships. The remainder are represented from two to five times in the phylogeny (Fig. 7) and do not appear to either add or detract in determining relationships.

The following states, if used to cluster groups of species, would yield a very different phylogeny, and are thus of negative value in determining relationships within the context of the preferred phylogeny (Fig. 7): 3, 11, 14, 31, 32, 33, 35, 38, 40, 42, 45, 46, 47, 49, 50, 51, 52, 53, 55, 56, 57, 58, 60, 62, 66, 69, 70, 71, 72, 76, 77, 80, 85, 86, 91. The states are represented from 2 to 11 times in the phylogeny. Three alternatives are possible to account for this category: 1) the character states did in fact arise independently in limited clusters of taxa several times; 2) the character states within characters need to be redefined; or 3) the assumed direction of change of character states within characters is incorrect. These possibilities are explored further after the following section which accounts for alternative one in part.

*Character State Clusters*—Two types of character state clusters are examined: 1) those clusters of character states shared by related taxa; and 2) certain clusters of character states shared by taxa not closely related.

The clusters of shared character states leading to and including the generic clusters are characterized by having at least one state from the first two categories listed above, that is, at least one of the states in each cluster is relatively diagnostic of only that cluster. Examination of the states involved in the clusters indicates a scattering of states from all sorts of systems which do not appear to represent a single functional adaptation with two exceptions. The combination of a male thumb lacking nuptial adspersities, toes lacking fringe or web, and less than 50 eggs/clutch defining *Adenomera* in part sug-

gests a basic adaptation towards terrestriality. Advanced states of the semi-tendinosus, accessory head of the adductor magnus, and adductor longus muscles of the thigh in the two *Pleurodema* examined suggest a functional change in the leg musculature. Further species within the genus would need to be examined to see if this in fact represents a basic functional generic adaptation.

*Adenomera* and members of the *fuscus* species group share several states, listed in order of degree of sharing, beginning with the states shared by all species of both groups: (19) toes free, (23) eggs lacking melanophores, (25) 50-1000 eggs/clutch, (49) iliacus externus muscle extends from  $\frac{3}{4}$  to full length of the iliac bone anteriorly, (5) indications of paired lateral vocal sacs, (77) pterygoid and parasphenoid bones overlap but are not in contact, (26, 27) the foam nest is placed away from water, (72) vomer bones articulate with the premaxilla and/or maxilla, (34) geniohyoideus lateralis muscle has a lateral flare, (73, 74) the sphenethmoid bone borders the optic foramen, (75) the sphenethmoid bone extends anteriorly beyond the vomers. Character states 19, 23, 25, 5, 27, 72, 73, 74, and 75 appear to be related to the same general functional complex. Both groups are more terrestrial than other closely related groups and a key feature to achieving a greater degree of terrestriality is placement of the foam nest out of the water into an incubating chamber which is constructed by the frogs. The anterior portion of the skull is strengthened in these forms as they apparently use the snout and the hind limbs in forming the incubating chamber. With males calling from isolated locations away from the water, a different type of call is more appropriate (Heyer and Bellin, 1973, Heyer and Straughan, Ms.), which is reflected morphologically by the indications of paired lateral vocal sacs to radiate the call. Since the eggs are out of direct sunlight, the melanophores have been lost.

*Adenomera* and *Physalaemus* share several states, listed in order of degree of sharing, beginning with the states shared by all the species of both groups: (28) depressor mandibulae with two sites of equal origin on the dorsal fascia and the squamosal bone or the crista parotica, (65) the nasal bones are separated, (23) eggs lack melanophores, (77) the pterygoid and parasphenoid bones overlap without contact, (43) the omohyoideus is on the ventral surface of the body of the hyoid plate, (60) the adductor longus muscle is well developed, (26) the foam nest is placed on the water, (40) the sternohyoideus inserts near the edge and the midline of the hyoid body, (79) the anterior process of the hyale is absent, (36) the anterior petrohyoideus inserts on the edge and body of the hyoid plate, (62) gluteus small, (38) the sternohyoideus originates as two slips, (76) the pterygoid and parasphenoid elements do not overlap, (31, 32) the geniohyoideus medialis is divided ventrally, (37) the anterior petrohyoideus inserts on the hyoid body only, (81) the alary process of the hyoid is broad and winglike. Character states 43, 40, 79, 36, 38, 31, 32, 37, 81 are all involved with the hyoid apparatus and asso-

ciated musculature. Basically, the difference is broad and winglike or narrow and stalked alary processes with associated muscle attachment patterns.

*Limnomedusa* shares the most character states with the following four taxa: *Physalaemus biliginogerus*, 18, 28, 30, 38, 50, 51, 53, 65, 77, 87, 88, 91, 92; *Barycholos pulcher*, 18, 38, 53, 54, 62, 65, 77, 80, 87, 88, 91, 92; *Physalaemus nattereri*, 18, 28, 53, 62, 65, 77, 79, 87, 88, 91, 92; *Hydrolaetare schmidti*, 1, 28, 30, 38, 50, 51, 62, 65, 79, 87. Derived states of the mesosternum are shared by all combinations, and *Limnomedusa* also shares derived states of the xiphisternum with all but *Hydrolaetare*. *Limnomedusa* and *Barycholos* are unique in sharing reduced or absent alary processes of the hyoid, *Limnomedusa* and *Hydrolaetare* are unique in having vertical pupils. Beyond these observations, examination of the states does not indicate any possible groupings of significance.

*Possible Errors in Character State Evaluations*—The direction of character state changes were evaluated using a certain set of guidelines. As the guidelines were logical, some character state determinations may be incorrect as organisms do not always follow logical evolutionary pathways. The purpose of this section is not to improve the phylogeny or the data on which it is based but rather to point out those characters which appear to have been incorrectly evaluated. Once pointed out, applications of more data or different analytic procedures can determine the best arrangement of the characters. One of the advantages of the combinational method of analysis is that possible errors can be located.

The approach is 1) to identify the character states that correlate poorly with the phylogeny, 2) to try different character state interpretations, and if the 3) new interpretations are much more consistent with the phylogeny, then 4) one may conclude that the original interpretations might be incorrect and should be examined further. One of the main criteria used to determine whether a change in states is an improvement is whether the total number of convergences in the phylogeny is reduced by the change. This method thus allows for a somewhat independent evaluation of character states. Again, to make the point clear, the purpose of this section is to point out possible errors, not to reevaluate them.

As documented above, *Lithodytes discodactylus* has character state 7 rather than 9.

Certain character states that were assigned a negative value in predicting relationships have been accounted for. States 31, 32, 38, 40, 72 have been shown to be linked to a hyoid unit change which has probable functional significance and has been derived independently several times. Character state 33 is unique to *Limnomedusa* and state 80 is shared with *Barycholos* only. Examination of the remaining states having negative value in determining relationships allows three groupings. The first is comprised of states which appear to have independently arisen more than once. In other words, there is no strong evidence to suspect otherwise. The states are 3, 11, 14, 35, 42, 45, 47,

50, 51, 52, 53, 55, 56, 57, 58, 66, 69, 70, 71, 85, 86, 91 which each appear from 2 to 6 times on the phylogenetic diagram (Fig. 7). The second category is comprised of states 76 and 77 in which an apparent redefinition of states is called for. Both 76 and 77 are states of the same character involving the relationship of pterygoid and the parasphenoid bones. The best adjustment that could be made with the information as coded would be to combine states 76 and 77 into one primitive state. That would make the previous primitive state the derived state which would then combine *Hydrolaetare*, *Leptodactylus chaquensis*, and *L. fuscus*. This arrangement is not predictive in determining relationships either. If there is useful information in the pterygoid-parasphenoid bone relationship, the variation might be categorized into different states than I recognized. The third grouping consists of character states in which the direction of change of states was probably incorrectly inferred. Three states are involved, 49, 60, 62. State 49 is the length of the iliacus externus muscle along the iliac bone and was assumed to be the most derived state of the three states recognized of the character. The previous ordering was character 23, state 0  $\longrightarrow$  state 1 (now state 48)  $\longrightarrow$  state 2 (now state 49). Reversing the direction of change to 2  $\longrightarrow$  1  $\longrightarrow$  0 would result in the following clusters: state 1, *Edalorhina*, *Leptodactylus pentadactylus*, all *Physalaemus*, *Pleurodema*, and *Paratelmatobius*; state 0, *Limnomedusa*. This would improve the phylogeny considerably by removing seven convergences that are accounted for by state 49 from the phylogeny. A reversal of direction involving state 60 would improve the phylogeny by removing six convergences and adding only two. The previous state change directions of character 29 (adductor longus muscle) were 0 (now state 60)  $\longleftarrow$  1  $\longrightarrow$  2 (now state 61). The new directions of change for character 29 would be 1  $\longleftarrow$  0  $\longrightarrow$  2. The taxa sharing state 1 are *Barycholos*, *Edalorhina*, and *Limnomedusa*. The result would add to the relationship of *Barycholos* and *Edalorhina* in the phylogeny. State 62 is a state of the gluteus muscle. Reversing the direction of change of states would improve the phylogeny slightly by substituting seven convergences for 11 represented by state 62. The previous direction of change was for character 30, state 0  $\longrightarrow$  state 1 (now 62). The new direction would be 1  $\longrightarrow$  0, which groups the following taxa: *Lithodytes discodactylus*, *Adenomera marmorata*, *Physalaemus biligonigerus* and *Juscomaculatus*, both *Pleurodema*, *Pseudopaludicola*, and *Paratelmatobius*. This clustering would be rather neutral in its usefulness in defining the relationships presented in Figure 7. The high number of convergences (7) still remaining after the change suggests that the variation present in the character might be profitably redescribed. The criteria used in determining the direction of change of states in all three cases were I and II, which would indicate that most or all of the outgroup might have advanced states for these three characters. It is interesting to note that if incorrect inferences were made in these three characters, they were not sufficient to drastically alter the relationships. In other words, the data sample is large enough to allow for a few errors.

*Character State Predictions*—The phylogenetic diagram (Fig. 7) allows character state predictions where information was not available in some cases. This was most true for life history data in the present case. According to the diagram (Fig. 7) a foam nest is not required for *Lithodytes*, *Barycholos*, *Edalorhina*, *Hydrolaetare*, or *Paratelmatoebius* for which no breeding behavior is known. With the known information, a foam nest has apparently been independently derived four times. As this is a key adaptation towards terrestriality at least in *Adenomera* and *Leptodactylus* (Heyer, 1969b, 1973), it is interesting to note that true independence of the pond for all of the life cycle has only been attained once among these genera, in the genus *Adenomera*.

#### GENERIC REDEFINITIONS

The results of this study require the redefinition of three genera. These follow. Full generic synonymies may be found in Lynch (1971).

##### *Adenomera* Fitzinger in Steindachner, 1867

Type species: *Adenomera marmorata* Fitzinger in Steindachner, 1867, by monotypy.

Diagnosis: The only leptodactylid genera in the New World having a bony style for the mesosternum are *Adenomera*, *Leptodactylus*, *Lithodytes*, and *Pleurodema*. *Adenomera* differs from *Pleurodema* in not having a well developed frontoparietal fontanelle (well developed in *Pleurodema*), the quadratojugal contacts the maxilla (incomplete maxillary arch), and smaller size, less than 31 mm snout-vent length (35-65 mm S-VL). *Adenomera* differs from *Leptodactylus* in having T-shaped terminal phalanges (knobbed in *Leptodactylus*). *Adenomera* differs from *Lithodytes* in not having the dorsal toe disk surfaces divided.

Definition: Pupil horizontal; tympanum distinct; male vocal sac internal, indications of lateral vocal folds present or absent; male thumb lacking nuptial adspersities; body lacking distinct glands; toe tips expanded into disks or not, if disked, dorsal surfaces not divided; tarsal fold present or weakly developed; metatarsal tubercles neither pronounced or cornified; toes without web or fringe, free; larval vent median; larval denticle rows  $\frac{2}{3}$ , weakly developed or absent; eggs lacking melanophores; few eggs per clutch (<50/clutch); eggs in foam nest deposited away from standing water; depressor mandibulae condition DFsq; geniohyoideus medialis continuous medially or divided ventrally; geniohyoideus lateralis with or without distinct slip to hyale; anterior petrohyoideus insertion on edge, edge and body, or body of hyoid; sternohyoideus origin from one or two slips on meso- and xiphisternum; sternohyoideus insertion near lateral edge and midline of hyoid or midline of hyoid only; omohyoideus insertion on body of hyoid or absent; tendon of semitendinosus confluent with posterior portion of sartorius insertion on knee and tendons of gracilis minor and major passing dorsad to tendon of semitendinosus; iliacus

externus extending from  $\frac{3}{4}$  to full length of iliac bone; tensor fasciae latae insertion posterior to iliacus externus on iliac bone; gracilis minor broad or narrow; interior and exterior portions of semitendinosus united in common distal tendon, two portions equal in bulk or exterior larger; sartorius moderately developed; accessory head of adductor magnus without distinct tendon; adductor longus well developed; gluteus insertion on cruralis and knee or cruralis only; quadratojugal well developed, contacting maxilla; maxillary teeth present; nasal bones widely separated; small frontoparietal fontanelle or absent; zygomatic ramus of squamosal just longer than, just shorter than, or equal to otic ramus; vomerine teeth present; vomers not contacting medially; vomer articulation with premaxilla and/or maxilla present or absent; posterior extent of sphenethmoid widely separated from or bordering optic foramen; sphenethmoid extending anteriorly to middle of vomers or beyond; occipital condyles moderately or widely separated; no anterior processes of hyale; alary process of hyoid somewhat narrow and often stalked or broad and winglike; posterolateral process of hyoid present; ilium with well-developed dorsal crest; terminal phalanges T-shaped, expanded or not; omosternum present, expanded; mesosternum a bony style; xiphisternum single, entire; diploid chromosome number 24 or 26 (Bogart, personal communication).

Content: Five species are recognized in the most recent revision (Heyer, 1973, and Table 4). One and possibly two more species are being described by other workers.

#### *Leptodactylus* Fitzinger, 1826

Type species: *Rana fusca* Schneider, 1799. Lynch (1971:187) stated, "*Rana typhonia* Daudin is *R. sibilatrix* Wied, 1824, which Heyer (1968[a]) considered identical with *Rana fusca* Schneider, 1799, for which he designated a neotype. However, at least some of the syntypes of *Rana fusca* are extant (W. C. A. Bokermann, personal communication), and study of these must be made before Heyer's action can be accepted." I have subsequently asked W. C. A. Bokermann if he knew Schneider's types are extant. He indicated that Lynch mistranslated his comments. What Bokermann expressed to Lynch was that he preferred to designate type species where the collecting locality was known with some precision. As this is truer for *Rana typhonia* than either *Rana fusca* or *Rana sibilatrix* his preference would be to designate *Rana typhonia* as the type species of the genus. Bokermann did not think Schneider's types were still extant and in subsequent inquiries to individuals and institutions not contacted previously I have been unable to locate anyone who thinks Schneider's types are extant. Based on the rules of priority and due to the confusion regarding use of the names *sibilatrix*, *sibilator*, and *typhoni*us for the same taxon, I still think the best solution consistent with the available evidence is to regard *Rana fusca* Schneider as the appropriate name for the taxon in question.

Diagnosis: The only leptodactylid genera in the New World having a

bony style for the mesosternum are *Adenomera*, *Leptodactylus*, *Lithodytes*, and *Pleurodema*. *Leptodactylus* differs from *Pleurodema* in not having a well developed frontoparietal fontanelle (well developed in *Pleurodema*), and the quadratojugal contacts the maxilla (incomplete maxillary arch). *Leptodactylus* differs from *Adenomera* and *Lithodytes* in having knobbed shaped terminal phalanges (T-shaped in *Adenomera* and *Lithodytes*).

Definition: Pupil horizontal; tympanum distinct; vocal sac internal, paired external vocal sacs present, weakly developed, or absent; male thumb with horny spines or not; glandular dorsolateral folds present or absent; toe tips usually not expanded into disks; tarsal fold present; metatarsal tubercles neither pronounced nor cornified; toes with lateral fringes or not; larval vent median; larval denticle rows  $\frac{2}{3}$ , well developed; eggs with or without melanophores; moderate (50-1000 eggs) or large (>1000 eggs) clutch size; eggs deposited in foam nest on top of water or in burrows away from water; depressor mandibulae condition DFsq; geniohyoideus medialis continuous medially; geniohyoideus lateralis not attaching to hyale or attaching with or without a definite slip; anterior petrohyoideus inserts on edge of hyoid body; sternohyoideus origin with single or double slips from meso- and xiphisternum; sternohyoideus insertion on narrow band near lateral edge of hyoid body; omohyoideus insertion on hyoid plate and fascia between posterolateral and posteromedial processes of the hyoid; tendon of semitendinosus confluent with posterior portion of sartorius insertion on knee and tendons of gracilis minor and major passing dorsad to tendon of semitendinosus or tendon of semitendinosus piercing tendon of gracilis minor and major; iliacus externus extending from  $\frac{1}{2}$  to full length of ilium; tensor fasciae latae inserting posterior to iliacus muscle on iliac bone; gracilis minor broad; interior and exterior portions of semitendinosus uniting in common tendon distally, two portions equal in development or exterior portion larger; sartorius moderate or broad; no distinct tendon of accessory head of adductor magnus; adductor longus well developed; gluteus inserting entirely on cruralis; quadratojugal well developed, contacting maxilla; maxillary teeth present; nasals widely separated; frontoparietal fontanelle small or absent; zygomatic ramus of squamosal just longer than, just shorter than, or equal to otic ramus; vomerine teeth present; vomers in broad median contact or not; vomer articulating with premaxilla and/or maxilla or not; posterior extent of sphenethmoid widely separated from optic foramen to bordering optic foramen; sphenethmoid extending anteriorly to middle of vomers or beyond; occipital condyles moderately or widely separated; no anterior process of hyale; alary process somewhat narrow and stalked; posterolateral process of hyoid present; ilium with well developed dorsal crest; terminal phalanges knobbed; omosternum present, expanded; mesosternum a bony style; xiphisternum entire, single; diploid chromosome number 22.

Content: Approximately 35 species tentatively arranged in four species groups (Table 4).

*Lithodytes* Fitzinger, 1843

Type species: *Rana lineata* Schneider, 1799, by original designation.

Diagnosis: The only leptodactylid genera in the New World having a bony style for the mesosternum are *Adenomera*, *Leptodactylus*, *Lithodytes*, and *Pleurodema*. Among these, *Lithodytes* is the only genus to have large toe disks with divided dorsal surfaces.

Definition: Pupil horizontal; tympanum distinct; vocal sac internal; male thumb without nuptial adspersities; body without well-defined glands; toes disked with dorsal surfaces divided longitudinally; tarsal fold present; metatarsal tubercles neither pronounced nor cornified; toes with lateral fringes or free; eggs lacking melanophores; large clutch size (>1000 eggs); depressor mandibulae condition DFsq; geniohyoideus medialis continuous medially; geniohyoideus lateralis without lateral flare or slip; anterior petrohyoideus insertion on edge of hyoid; sternohyoideus origin with distinct slips from anterior mesosternum and another from posterior meso- and/or xiphisternum; sternohyoideus insertion near lateral edge of hyoid; omohyoideus insertion on hyoid plate and fascia between posterolateral and posteromedial process of hyoid; tendon of semitendinosus confluent with posterior portion of sartorius insertion on knee and tendons of gracilis minor and major passing dorsad to tendon of semitendinosus or tendon of semitendinosus piercing tendon of gracilis minor and major; iliacus externus extending from  $\frac{3}{4}$  to full length of iliac bone; tensor fasciae latae insertion posterior to iliacus externus on iliac bone; gracilis minor narrow to broad; interior and exterior portions of the semitendinosus uniting in common tendon distally, exterior portion larger or equal to interior (smaller) portion with distinct distal tendon attaching to bulk of interior portion; sartorius moderately developed; accessory head of adductor magnus without distinct tendon; adductor longus well developed; gluteus insertion on cruralis only or cruralis and knee; quadratojugal well developed, contacting maxilla; maxillary teeth present; nasals widely separated; no frontoparietal fontanelle; zygomatic ramus of squamosal just longer than, just shorter than, or equal to otic ramus; vomerine teeth present; vomers not in medial contact; vomer articulation with premaxilla and/or maxilla; posterior extent of sphenethmoid widely separated from optic foramen; sphenethmoid extending anteriorly to middle of vomers; occipital condyles moderately or widely separated; no anterior processes of hyale; alary process of hyoid somewhat narrow and stalked; posterolateral process of hyoid present; ilium with well-developed dorsal crest; terminal phalanges T-shaped, expanded; mesosternum a bony style; xiphisternum entire, single; diploid chromosome number 18 (for *L. lineatus*).

Content: Two species are now recognized (Table 4). *Plectomantis rhodostima* Cope, 1874 may also be referable to this genus. E. Malnate (personal communication) has not been able to locate the type at this time, but the type may be identified at a later time in the Philadelphia collections.

TABLE 4

Species proposed or commonly associated with the genus *Leptodactylus*. For the genus *Leptodactylus*, provisional assignments into species groups are indicated by F (Fuscus group), M (Melanonotus group), O (Ocellatus group), and P (Pentadactylus group). Allocations immediately following a question mark are uncertain

Name Proposed	Present Allocation
<i>Cystignathus albilabris</i> Gunther, 1859	<i>Leptodactylus albilabris</i> F
<i>Leptodactylus anceps</i> Gallardo, 1964	<i>Leptodactylus latinasus</i> F
<i>Leptodactylus andicola</i> Boettger, 1891	<i>Leptodactylus</i> ? <i>andicola</i> F
<i>Leptodactylus andreae</i> Muller, 1923	<i>Adenomera andreae</i> , new combination
<i>Leptodactylus bokermanni</i> Heyer, 1973	<i>Adenomera bokermanni</i> , new combination
<i>Leptodactylus bolivianus</i> Boulenger, 1898	<i>Leptodactylus bolivianus</i> O
<i>Leptodactylus brevipes</i> Cope, 1887	<i>Leptodactylus wagneri</i> M
<i>Leptodactylus bufo</i> Andersson, 1911	<i>Leptodactylus pentadactylus</i> P
<i>Leptodactylus bufonius</i> Boulenger, 1894	<i>Leptodactylus bufonius</i> F
<i>Leptodactylus caliginosus</i> Girard, 1853	<i>Leptodactylus ocellatus</i> O
<i>Leptodactylus chaquensis</i> Cei, 1950	<i>Leptodactylus chaquensis</i> O
<i>Leptodactylus curtus</i> Barbour and Noble, 1920	<i>Leptodactylus labrosus</i> F
<i>Leptodactylus dantasi</i> Bokermann, 1959	<i>Leptodactylus dantasi</i> M
<i>Leptodactylus darlingtoni</i> Cochran, 1935	<i>Eleutherodactylus jugans</i>
<i>Leptodactylus diptychus</i> Boulenger, 1918	<i>Leptodactylus</i> ? <i>poecilochilus</i> F
<i>Leptodactylus diptyx</i> Boettger, 1885	<i>Adenomera hylaedactyla</i>
<i>Leptodactylus discodactylus</i> Boulenger, 1883	<i>Lithodytes discodactylus</i> , new combination
<i>Cystignathus discolor</i> Reinhardt and Lutken, 1861	<i>Eupsophus miliaris</i>
<i>Leptodactylus dominicensis</i> Cochran, 1923	<i>Leptodactylus</i> ? <i>albilabris</i> F
<i>Leptodactylus dominicensis</i> Muller, 1923	<i>Leptodactylus</i> ? <i>pentadactylus</i> P
<i>Cystignathus echinatus</i> Brocchi, 1877	<i>Leptodactylus melanonotus</i> M
<i>Leptodactylus fallax</i> Muller, 1926	<i>Leptodactylus</i> ? <i>pentadactylus</i> P
<i>Leptodactylus flavopictus</i> Lutz, 1926	<i>Leptodactylus pentadactylus</i> P
<i>Cystignathus fragilis</i> Brocchi, 1877	<i>Leptodactylus labialis</i> F
<i>Rana fusca</i> Schneider, 1799 <sup>a</sup>	<i>Leptodactylus fuscus</i> F
<i>Leptodactylus gaigae</i> Cochran, 1938	<i>Paratelmatobius gaigae</i>
<i>Rana giga</i> Spix, 1824	<i>Leptodactylus</i> ? <i>pentadactylus</i> P
<i>Leptodactylus glandulosus</i> Cope, 1887	<i>Adenomera hylaedactyla</i>
<i>Leptodactylus goliath</i> Jimenez de la Espada, 1875	<i>Leptodactylus pentadactylus</i> P
<i>Cystignathus gracilis</i> Dumeril and Bibron, 1841	<i>Leptodactylus gracilis</i> F
<i>Leptodactylus gualambensis</i> Gallardo, 1964	<i>Leptodactylus fuscus</i> F
<i>Hylodes hallowellii</i> Cope, 1862	? <i>Leptodactylus hallowellii</i>
<i>Leptodactylus hemidactyloides</i> Andersson, 1945	<i>Lithodytes lineatus</i>

TABLE 4 (continued)

Name Proposed	Present Allocation
<i>Leptodactylus hololius</i> Boulenger, 1918	<i>Adenomera hylaedactyla</i>
<i>Cystignathus hylaedactylus</i> Cope, 1868	<i>Adenomera hylaedactyla</i> , new combination
<i>Cystignathus hylodes</i> Reinhardt and Lutken, 1861	<i>Leptodactylus pentadactylus</i> P
<i>Leptodactylus inoptatus</i> Barbour, 1914	<i>Eleutherodactylus inoptatatus</i>
<i>Leptodactylus insularum</i> Barbour, 1906	<i>Leptodactylus</i> ? <i>bolivianus</i> O
<i>Leptodactylus intermedius</i> Lutz, 1930	<i>Leptodactylus wagneri</i> M
<i>Leptodactylus knudseni</i> Heyer, 1972	<i>Leptodactylus knudseni</i> P
<i>Leptodactylus krefftii</i> Werner, 1904	? <i>Eupsophus</i>
<i>Cystignathus labialis</i> Cope, 1877	<i>Leptodactylus labialis</i> F
<i>Leptodactylus labrosus</i> Jimenez de la Espada, 1875	<i>Leptodactylus labrosus</i> F
<i>Rana labyrinthica</i> Spix, 1824	<i>Leptodactylus pentadactylus</i> P
<i>Leptodactylus laticeps</i> Boulenger, 1918	<i>Leptodactylus laticeps</i> P
<i>Leptodactylus latinus</i> Jimenez de la Espada, 1875	<i>Leptodactylus latinus</i> F
<i>Rana latrans</i> Steffen, 1815	<i>Leptodactylus ocellatus</i> O
<i>Eleutherodactylus leptodactyloides</i> Andersson, 1945	<i>Leptodactylus wagneri</i> M
<i>Rana lineata</i> Schneider, 1799	<i>Lithodytes lineatus</i>
<i>Leptodactylus longirostris</i> Boulenger, 1882	<i>Leptodactylus</i> ? <i>longirostris</i> F
<i>Rana luctator</i> Hudson, 1892	<i>Leptodactylus ocellatus</i> O
<i>Leptodactylus macroblepharus</i> Miranda-Ribeiro, 1926	<i>Leptodactylus pentadactylus</i> P
<i>Leptodactylus maculilabris</i> Boulenger, 1896	<i>Leptodactylus poecilochilus</i> F
<i>Leptodactylus mantipus</i> Boulenger, 1908	? <i>Eleutherodactylus</i>
<i>Adenomera marmorata</i> Fitzinger in Steindachner, 1867	<i>Adenomera marmorata</i>
<i>Leptodactylus martinezi</i> Bokermann, 1956	<i>Adenomera martinezi</i> , new combination
<i>Cystignathus melanonotus</i> Hallowell, 1860	<i>Leptodactylus melanonotus</i> M
<i>Leptodactylus melini</i> Lutz and Kloss, 1952	<i>Adenomera hylaedactyla</i>
<i>Cystignathus microtis</i> Cope, 1879	<i>Leptodactylus melanonotus</i> M
<i>Leptodactylus minutus</i> Nobel, 1923	<i>Adenomera hylaedactyla</i>
<i>Rana mystacea</i> Spix, 1824	<i>Leptodactylus mystaceus</i> F
<i>Cystignathus mystacinus</i> Burmeister, 1861	<i>Leptodactylus mystacinus</i> F
<i>Leptodactylus nanus</i> Muller, 1922	<i>Adenomera marmorata</i>
<i>Leptodactylus natalensis</i> Lutz, 1930	<i>Leptodactylus wagneri</i> M
<i>Leptodactylus nattereri</i> Lutz, 1926	<i>Leptodactylus podicipinus</i> M
<i>Cystignathus nebulosus</i> Girard, 1853	? <i>Eupsophus</i>
<i>Leptodactylus nigrescens</i> Andersson, 1945	<i>Lithodytes discodactylus</i>
<i>Leptodactylus novaeutoniae</i> Ahl, 1936	<i>Limnomedusa macroglossa</i>
<i>Leptodactylus occidentalis</i> Taylor, 1937	<i>Leptodactylus melanonotus</i> M

TABLE 4 (continued)

Name Proposed	Present Allocation
<i>Rana ocellata</i> Linneaus, 1758	<i>Leptodactylus ocellatus</i> O
<i>Leptodactylus ocellatus macrosternum</i> Miranda-Ribeiro, 1926	<i>Leptodactylus</i> ? <i>macrosternum</i> O
<i>Leptodactylus ocellatus reticulata</i> Ceii, 1949	<i>Leptodactylus ocellatus</i> O
<i>Leptodactylus ochraceus</i> Lutz, 1930	? <i>Eleutherodactylus</i>
<i>Rana octoplicata</i> Werner, 1893	<i>Leptodactylus ocellatus</i> O
<i>Leptodactylus pachyderma</i> Miranda-Ribeiro, 1926	<i>Leptodactylus pentadactylus</i> P
<i>Rana pachypus</i> Spix, 1824	<i>Leptodactylus pentadactylus</i> P
<i>Leptodactylus pallidirostris</i> Lutz, 1930	<i>Leptodactylus wagneri</i> M
<i>Cystignathus parvulus</i> Girard, 1853	<i>Zachaenus parvulus</i>
<i>Rana pentadactyla</i> Laurenti, 1768	<i>Leptodactylus pentadactylus</i> P
<i>Leptodactylus pentadactylus dengleri</i> Melin, 1941	<i>Leptodactylus pentadactylus</i> P
<i>Leptodactylus pentadactylus mattogrossensis</i> Schmidt and Inger, 1951	<i>Leptodactylus pentadactylus</i> P
<i>Leptodactylus pentadactylus rubidooides</i> Andersson, 1945	<i>Leptodactylus pentadactylus</i> P
<i>Cystignathus perlaevis</i> Cope, 1879	<i>Leptodactylus melanonotus</i> M
<i>Platymantis petersii</i> Steindachner, 1864	<i>Leptodactylus wagneri</i> M
<i>Leptodactylus plaumanni</i> Ahl, 1936	<i>Leptodactylus fuscus</i> F
<i>Cystignathus podicipinus</i> Cope, 1862	<i>Leptodactylus podicipinus</i> M
<i>Cystignathus poecilochilus</i> Cope, 1862	<i>Leptodactylus poecilochilus</i> F
<i>Leptodactylus poeppigi</i> Melin, 1941	<i>Adenomera hylaedactyla</i>
<i>Leptodactylus prognathus</i> Boulenger, 1888	<i>Leptodactylus latinasus</i> F
<i>Leptodactylus pulcher</i> Boulenger, 1898	<i>Barycholos pulcher</i>
<i>Leptodactylus pumilio</i> Boulenger, 1920	<i>Eleutherodactylus parvus</i>
<i>Entomoglossus pustulatus</i> Peters, 1870	<i>Leptodactylus pustalatus</i> M
<i>Rana pygmaea</i> Spix, 1824	<i>Leptodactylus</i> ? <i>ocellatus</i> O
<i>Leptodactylus quadrivittatus</i> Cope, 1893	<i>Leptodactylus poecilochilus</i> F
<i>Leptodactylus raniformis</i> Werner, 1899	<i>Leptodactylus</i> ? <i>raniformis</i> F
<i>Leptodactylus rhodomystax</i> Boulenger, 1883	<i>Leptodactylus rhodomystax</i> P
<i>Leptodactylus rhodonotus</i> Gunther, 1868	<i>Leptodactylus rhodonotus</i> P
<i>Plectomantis rhodostima</i> Cope, 1874	? <i>Lithodytes rhodostima</i>
<i>Leptodactylus romani</i> Melin, 1941	<i>Leptodactylus bolivianus</i> O
<i>Gnathophysa rubido</i> Cope, 1874	<i>Leptodactylus rhodonotus</i> P
<i>Leptodactylus rugosus</i> Nobel, 1923	<i>Leptodactylus rugosus</i> P
<i>Leptodactylus rugosus</i> Melin, 1941	<i>Adenomera hylaedactyla</i>
<i>Cystignathus schomburgkii</i> Troschel, 1848	<i>Leptodactylus fuscus</i> F
<i>Leptodactylus serialis</i> Girard, 1853	<i>Leptodactylus ocellatus</i> O
<i>Rana sibilatrix</i> Wied-Neuwied, 1825	<i>Leptodactylus fuscus</i> F
<i>Leptodactylus stenodema</i> Jimenez de la Espada, 1875	<i>Leptodactylus stenodema</i> P
<i>Leptodactylus stictigularis</i> Noble, 1923	<i>Leptodactylus rhodomystax</i> P
<i>Leptodactylus syphax</i> Bokermann, 1969	<i>Leptodactylus syphax</i> P
<i>Leptodactylus trivittatus</i> Lutz, 1926	<i>Adenomera marmorata</i>

TABLE 4 (continued)

Name Proposed	Present Allocation
<i>Leptodactylus troglodytes</i> Lutz, 1926	<i>Leptodactylus bufonius</i> F
<i>Leptodactylus tuberculosus</i> Andersson, 1945	<i>Ischnocnema quixensis</i>
<i>Rana typhonia</i> Daudin, 1803	<i>Leptodactylus fuscus</i> F
<i>Cystignathus typhonius</i> Dumeril and Bibron, 1841	<i>Leptodactylus fuscus</i> F
<i>Leptodactylus validus</i> Garman, 1887	<i>Leptodactylus wagneri</i> M
<i>Leptodactylus vastus</i> Lutz, 1930	<i>Leptodactylus pentadactylus</i> P
<i>Leptodactylus ventrilineatus</i> Shreve, 1936	<i>Eleutherodactylus ventrilineatus</i>
<i>Leptodactylus ventrimaculatus</i> Boulenger, 1902	<i>Leptodactylus ventrimaculatus</i> F
<i>Leptodactylus vilarsi</i> Melin, 1941	<i>Leptodactylus ? rhodomystax</i> P
<i>Plectromantis wagneri</i> Peters, 1862	<i>Leptodactylus wagneri</i> M
<i>Leptodactylus wuchereri</i> Jimenez de la Espada, 1875	<i>Leptodactylus pentadactylus</i> P

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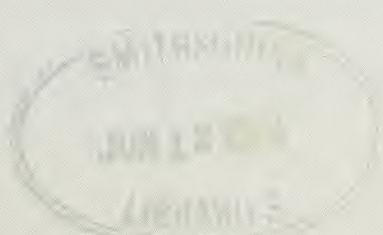
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A NEW RECORD AND A NEW SPECIES OF LANTERNFISH,  
GENUS *DIAPHUS* (FAMILY MYCTOPHIDAE),  
FROM THE NORTH ATLANTIC OCEAN

By BASIL G. NAFPAKTITIS

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A NEW RECORD AND A NEW SPECIES OF LANTERNFISH,  
GENUS *DIAPHUS* (FAMILY MYCTOPHIDAE),  
FROM THE NORTH ATLANTIC OCEAN<sup>1</sup>

By BASIL G. NAFAKTITIS<sup>2</sup>

ABSTRACT: *Diaphus adenomus* Gilbert, 1905, heretofore known only from off Hawaii and southern Japan, is recorded from the North Atlantic. A new species, *Diaphus roei*, is described on the basis of numerous specimens all caught in the vicinity of the Caribbean Islands. The new species is closely related to *D. effulgens*, from which it is distinguished by its lack of an Ant luminous organ, the higher position of its PLO and SAO<sub>3</sub>, and its higher gill raker counts (22-25 vs 19-22). The two forms reported herein raise the number of species of *Diaphus* in the North Atlantic to 23.

The purpose of this paper is to update the work of Nafpaktitis (1968) on the genus *Diaphus* in the North Atlantic. Two additional species belonging to this large and complex genus have been found in the course of a more recent investigation on the myctophids of the western North Atlantic. Of the two, one is a new and rather startling record of *D. adenomus* Gilbert, 1905, until now known only from the Hawaiian Islands and from off southern Japan. The other is a new species. The two additions bring the total number of species of *Diaphus* in the North Atlantic to 23, which constitutes approximately 26 per cent of the entire myctophid fauna in that ocean.

*Diaphus adenomus* Gilbert

Figure 1

*Diaphus adenomus* Gilbert, 1905: 592, Pl. 68, fig. 1; type locality, the Kaiwi Channel between Oahu and Molokai, Hawaii, 335 to 350 fms; holotype USNM 51588.

*Diaphus anteorbitalis* Gilbert, 1913: 92, Pl. 12, fig. 1; type locality, off Shiwo Misako, 33°24'50"N, 135°38'40"E, 253 fms; holotype, USNM 74471.

*Distinctive characters.* *D. adenomus* is easily distinguished from all other North Atlantic members of the genus by the large luminous organs around the eye, especially the long supraorbital organ that extends along most of the dorsal orbital margin.

*Description.* D. 15 (14); A. 15 (16); P. 12 (11); V. 8; gill rakers on first

<sup>1</sup>REVIEW COMMITTEE FOR THIS CONTRIBUTION

James Craddock

John E. Fitch

Robert J. Lavenberg

<sup>2</sup>Department of Biological Sciences, University of Southern California, Los Angeles, California 90007; and Research Associate In Ichthyology, Natural History Museum, Los Angeles, California 90007

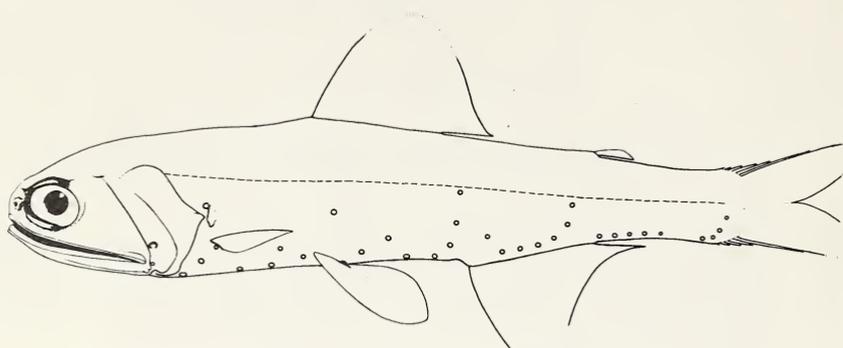


FIGURE 1. *Diaphus adenomus*. Young individual, 96.0 mm SL; R/V Oregon station 3616, off Nicaragua (Caribbean).

arch  $5 + 1 + 11$ ; AO 6 (7) + 5(4-6), total 11 (12); lateral line scales 37.

One of the largest members of the genus. Mouth large, terminal, its cleft oblique; length of upper jaw 1.3 to 1.4 in length of head and extending 1 to 1.3 times the diameter of eye behind vertical through posterior margin of orbit. Eye large, its diameter 2.4 to 3 in length of upper jaw and 3.2 to 4 in length of head. Operculum tapering posteriorly to a point at or slightly below PLO. Pterotic spine prominent, sharp.

Origin of dorsal fin over base of ventral fin. Origin of anal fin behind vertical through end of base of dorsal fin. Pectoral fin short, extending to, or somewhat beyond  $PO_4$ . Base of adipose fin somewhat in advance of vertical through end of base of anal fin.

A small, shallow Dn. Vn extending along ventral and anterior border of orbit, to level of Dn. A supraorbital organ, similar in form to Vn, between eye and supraorbital frontal ridge. Both Vn and supraorbital organs framed by black tissue, and extending posteriorly to about vertical through center of lens in specimens smaller than 95 mm SL, reaching vertical through posterior margin of lens in larger individuals.

PLO midway between base of pectoral fin and lateral line or somewhat higher. VLO midway between base of ventral fin and lateral line or slightly higher. SAO on a straight or very nearly straight, subvertical line;  $SAO_1$  well above and behind  $VO_5$ ;  $SAO_3$  in advance of vertical through origin of anal fin and about its own diameter below lateral line. First AOa highly elevated, the series forming a trough continuous posteriorly with  $PO_1$  which is 1.5 to 2 times its own diameter below lateral line. AOp evenly spaced, level, with  $AOP_1$  behind, seldom over, end of base of anal fin. Prc evenly spaced, forming a gentle curve;  $Prc_4$  3 to 4 times its own diameter below lateral line.

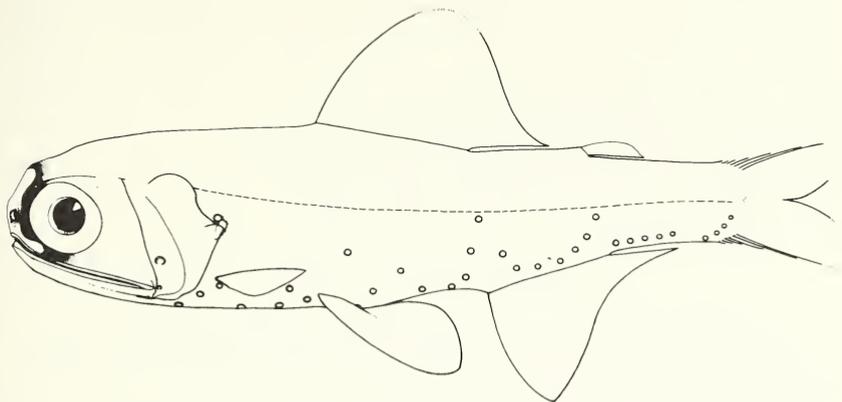


FIGURE 2. *Diaphus roei*. Holotype; 89.0 mm SL; USNM 210553.

A vertically elongate luminous scale at PLO.

*Size.* The 62 North Atlantic specimens examined measured 61.5–181 mm SL; no gravid female was found among them.

*Range.* *D. adenomus* has so far been taken close to the bottom, on or near continental and island shelves in the Caribbean Sea and the waters off the Bahamas. The only record from the eastern North Atlantic is that from off Casablanca, Morocco.

*Remarks.* Eight years after he described *D. adenomus* from Hawaiian waters, Gilbert (1913) described another myctophid from off southeastern Japan under the name *Diaphus anteorbitalis*. Gilbert himself admitted that *D. anteorbitalis* was "very closely allied to *D. adenomus* . . . differing only in the greater development of the circumocular luminous bodies, in the slightly higher position of the suprapectoral photophore (= PLO), and in the larger eye" (Gilbert, 1913:92). I have examined the type material of both species and I fully agree with Parr (1929:41) that there is no difference in the development of the circumorbital luminous organs between the two forms. The difference in the position of the PLO between the two forms is insignificant, and so is the difference in the size of the eye. Consequently, *D. anteorbitalis* is placed in the synonymy of *D. adenomus*.

*Material examined.* Except for two specimens (132.0–139.0 mm SL) caught with an otter trawl at a depth of 600 m off Casablanca, Morocco, and kindly sent to me by Charles L. Brownell of the Institut des Peches Maritimes du Maroc, all of the material examined was collected by the National Marine Fisheries Service vessels *Oregon*, *Oregon II*, and *Silver Bay*. The available data for the latter are as follows: 50 (61.5–118.0 mm), *Oregon* sta. 3616, off

Nicaragua (Caribbean); 3 (121.0–181.0 mm), *Oregon II* sta. 10268, 12 March 1968, 11°26'N, 74°14'W, 315 fms, 71' shrimp trawl; 1 (147.0 mm), *Oregon II* sta. 10839, 12 July 1969, 17°37'N, 63°00'W, 360 fms, 40' shrimp trawl; 2 (89.5–97.0 mm), *Oregon II* sta. 11585, 10 March 1971, 29°15'N, 87°58'W, 160 fms, 71' shrimp trawl; 3 (134.0–155.0 mm), *Silver Bay* sta. 3500, northeast of Bahamas; 1 (72.0 mm), *Silver Bay* sta. 5161, 14 October 1963, 19°57'N, 71°05'W, 170 fms, 50' shrimp trawl.

The above material is deposited at the Natural History Museum of Los Angeles County (LACM).

### *Diaphus roei*, new species

#### Figure 2

*Holotype*. A male, 89.0 mm SL, National Marine Fisheries Service (NMFS) vessel *Oregon* sta. 5072, 17°20'N, 62°52'W, 3 September 1964, 1630 hrs, 305 fms, 40' shrimp trawl; USNM 210553.

*Paratypes*. A male, 89.0 mm SL, data as for holotype, LACM 33704-1; a male, 89.0 mm SL, Museum of Comparative Zoology, Harvard University, MCZ 49100, and a female, 104.0 mm SL, MCZ 49101, data for both as for holotype; a male, 89.0 mm SL, USNM 210554, and a female, 98.5 mm SL, USNM 210555, NMFS vessel *Silver Bay* sta. 5161, 19°57'N, 71°05'W, 14 October 1963, 1650 hrs, 170 fms, 50' shrimp trawl; two females, 94.0 and 103.0 mm, LACM 33705-1 and 33705-2, respectively, NMFS vessel *Silver Bay* sta. 5161, data as above.

Thirty-five additional specimens, 68.0–108.0 mm SL, were examined. These are deposited at the LACM.

*Diagnosis*. The high position of the PLO and SAO<sub>3</sub>, the absence of Ant, and the high gill raker count will separate this fish from its closest relative, *D. effulgens*.

*Description*. Counts are from 43 specimens. Proportional measurements, expressed in percent of SL, are based on 20 specimens, 68.0–104.0 mm SL; initial values are arithmetic means, values in parentheses represent the range of variation.

D. 15; A. 14 (13); P. 11 (12); V. 8; gill rakers on first arch 7 (6–8) + 1 + 15–16, total 23–24 (22–25); AO 6 + 5 (4–6), total 11 (10–12); lateral line scales 36.

Length of head 30.8 (29.4–32.0); depth of head 24.2 (23.0–25.0); length of upper jaw 21.9 (21.0–22.5); horizontal diameter of eye 10.8 (10.4–11.2).

Distance from tip of snout to: origin of dorsal fin 44.2 (43.0–45.0); origin of anal fin 66.8 (65.5–68.0); base of adipose fin 80.9 (79.4–82.0); base of pectoral fin 30.6 (29.0–31.5); base of ventral fin 45.8 (44.8–46.7).

A large *Diaphus*. Head large. Snout high, bluntly rounded and slightly overhanging mouth. Mouth large, oblique; length of upper jaw 1.3 to 1.4 in length of head and extending 0.6 to 0.8 of the diameter of eye behind vertical through posterior margin or orbit. Eye very large, its horizontal diameter 1.9 to 2.1 in length of upper jaw and 2.7 to 3 in length of head. Operculum tapering posteriorly to a point somewhat below PLO.

Origin of dorsal fin slightly in advance of base of ventral fin. Origin of anal fin behind end of base of dorsal fin. Pectoral fin not reaching base of ventral fin. Ventral fin reaching origin of anal fin in specimens smaller than about 90 mm SL, somewhat shorter in larger individuals. Base of adipose fin in advance of vertical through end of base of anal fin.

Dn very large, directed forward, its medial side in contact with median ethmoid crest, and extending higher than dorsal margin of orbit. Vn also very large and massive, occupying nearly entire lower half of snout, reaching ethmoid crest dorsad to olfactory organ, continuing along anteroventral border of orbit, terminating at or slightly behind vertical through anterior margin of pupil. Dn and Vn in contact with each other above olfactory organ. Ant absent.

PLO nearer to lateral line than to base of pectoral fin; distance between PLO and base of pectoral fin 2 to 3 times as long as that between PLO and lateral line. VLO midway between base of ventral fin and lateral line or a little lower. SAO on a straight or very nearly straight, subvertical line; SAO<sub>1</sub> well above and behind VO<sub>5</sub>; SAO<sub>3</sub> slightly in advance of vertical through origin of anal fin and immediately, or less than its own diameter, below lateral line. AOa forming a deep trough with first, fifth and sixth AOa elevated. Pol 1 to 1.5 times its own diameter below lateral line and nearly continuous with AOa. AOp behind base of anal fin, evenly spaced and level. Prc forming a gentle, ascending curve, with Prc<sub>1</sub>, 2 to 3 times its own diameter below lateral line.

A small luminous scale at PLO.

*Size.* The largest specimen found in the collections examined measured 108.0 mm SL and was one of two gravid females; the other was 104.0 mm SL, which indicates that in the North Atlantic this species spawns at a size considerably smaller than its apparently closest relative, *D. effulgens*.

*Range.* So far *D. roei* is known only from off the leeward islands of the Lesser Antilles, from northeast of Puerto Rico, and from off the north coast of the Dominican Republic.

*Name.* The species is named after Richard B. Roe of the NMFS, Southeast Fisheries Center, Pascagoula, Mississippi.

#### DISCUSSION

The two species discussed in this paper bring the total number of species of the genus *Diaphus* in the North Atlantic to 23. Of these, only six (*dumerili*, *lütkeni*, *lucidus*, *effulgens*, *mollis*, and *subtilis*) are known to be rather uniformly distributed across the ocean. Five (*splendidus*, *termophilus*, *fragilis*, *elucens*, and *brachycephalus*), though collected across the ocean, appear to be much more abundant in the western than in the eastern part; and six (*garmani*, *problematicus*, *bertelseni*, *minax*, *anderseni*, and *roei*) have so far been reported only from the western part of the North Atlantic. "Western part" is here considered the area of the ocean to the west of the mid-Atlantic ridge, including the Caribbean Sea and the Gulf of Mexico.

Of the remaining six species, two (*vanhoeffeni* and *holti*) are known only from the eastern North Atlantic, that is east of the mid-Atlantic ridge; two (*metopoclampus* and *rafinesquei*), though found across the ocean, are relatively more abundant in the eastern than in the western part; and two (*taaningi* and *adenomus*) occur as disjunct populations on both sides of the ocean. Finally, the eastern *holti* and the "mainly eastern" *metopoclampus* and *rafinesquei* are all found in the Mediterranean Sea.

It is obvious from the above data that there is a marked difference not only in the number of species but also in the relative abundance of a number of species between the western and the eastern North Atlantic. There are three times as many western as there are eastern species, and more than twice as many "mainly western" as there are "mainly eastern" ones. Studies currently in progress indicate that other myctophid genera show very much the same distributional pattern.

These faunal differences between the eastern and western North Atlantic may be attributed to a number of factors, primarily circulation, distribution of land masses, biology and vertical distribution of the animals involved, and more intensive sampling in the western part of the ocean than the eastern part. However, a serious attempt to explain the phenomenon must wait until we know a great deal more about the composition and distribution of the myctophid fauna in the South Atlantic.

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BACTERIAL LUMINESCENCE  
IN THE DEEP-SEA ANGLERFISH  
*ONEIRODES ACANTHIAS* (GILBERT, 1915)

By WILLIAM T. O'DAY



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*ONEIRODES ACANTHIAS* (GILBERT, 1915)<sup>1</sup>

By WILLIAM T. O'DAY<sup>2</sup>

**ABSTRACT:** The luminous organ (esca) of the deep-sea anglerfish *Oneirodes acanthias* (family Oneirodidae, suborder Ceratioidei, order Lophiiformes) has been studied by means of light and electron microscopical methods. The esca lumen contains numerous rodlike bacteria which are Gram-negative and without spores, capsules, or flagella. Ultrastructural features of the bacteria include a double-layered cell wall and mesosomal invaginations of the plasma membrane. Although the microorganisms grow on seawater nutrient broth or agar, no luminescence has been observed under these conditions.

INTRODUCTION

Adult female ceratioid anglerfishes, except *Caulophryne* and *Neoceratias*, bear a luminous organ called the esca at the distal tip of a modified first dorsal ray (Figs. 1 and 2). The name of the luminous organ, which means bait in Latin, evokes speculation about its use as a lure. Whether it attracts prey by mimicking some small luminous animal or whether it signals conspecific males remains an elusive problem; it might even serve both purposes in the life history of some anglerfishes (Bertelsen, 1951; Marshall, 1971; Pietsch, 1972).

That luminescence in anglerfishes involves symbiotic bacteria has been suspected since Dahlgren's (1928) elementary description of the esca in *Ceratias*. Nevertheless, Brauer (1908) concluded that only secretory granules were present and recently Haneda (1968) doubted that the luminescence of *Himantolophus groenlandicus* was bacterial, after he had observed the light and failed to culture microorganisms from the organ. Bassot (1966) stated that bacteria are present in the escas of *Linophryne* and *Gigantactis* [erroneously referred to as *Mancalias* in Bassot (1966) according to Hulet and Musil (1968)] on the basis of his own unpublished electron micrographs. Bassot (1966) also saw bacteria in histological sections of the escas of *Ceratias* and *Melanocetus*. The electron microscopical study of Hulet and Musil (1968)

<sup>1</sup>REVIEW COMMITTEE FOR THIS CONTRIBUTION

J. Woodland Hastings  
Robert J. Lavenberg  
N. B. Marshall

<sup>2</sup>Research Associate in Ichthyology, Natural History Museum of Los Angeles County; and Department of Biological Sciences, Allan Hancock Foundation, University of Southern California, Los Angeles, California 90007

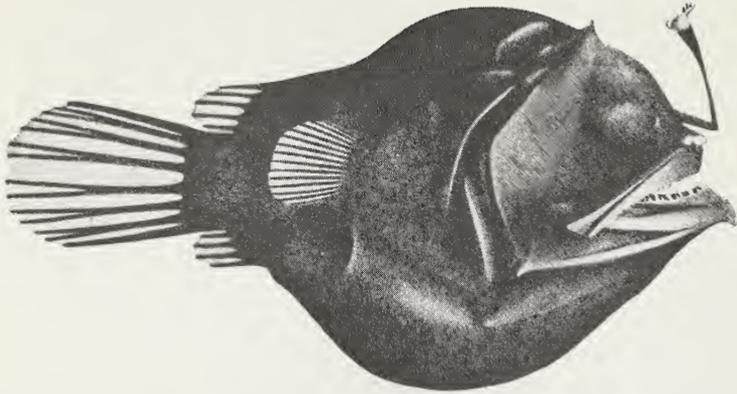


FIGURE 1. *Oneirodes acanthias*. From the original description by Gilbert (1915).

showed that there are bacteria in the esca of *Melanocetus murrayi* but the fixation limited the quality of ultrastructural detail. The results presented below confirm that bacteria are present in the esca of *Oneirodes acanthias* through bacteriological staining methods, light and electron microscopy, and growth of the microorganisms on artificial media.

#### MATERIALS AND METHODS

Fishes were collected in deep waters off southern California. Immediately after capture they were placed in a basin of cooled seawater and taken to the darkroom where their luminescence was observed. No emission spectra were recorded but the color appeared blue or blue-green to my eyes.

#### *Electron Microscopy*

Tissue from live specimens was fixed in 2.5% glutaraldehyde in phosphate buffer with added sodium chloride, pH 7.3-7.4, according to either Karlsson and Schultz (1965) or Millonig (1961) for one to one and one-half hours, rinsed in buffer, then postfixed in 1% osmium tetroxide in either of the two buffers just mentioned. Fixation was usually done at room temperature. Specimens were stored temporarily in the cold (about 5°C) on board ship, either in buffer or after being brought to 70% ethanol through a graded series of ethanol-water mixtures. After returning to the shore lab, dehydration was completed and the specimens were embedded in epoxy resin. Thin sections (500-1000 Å) were cut with a diamond knife on an MT-2 or LKB ultramicrotome. These sections were picked up on naked



FIGURE 2. Enlarged view of the esca of a specimen of *O. acanthias*. The esca bulb is partly covered with heavily pigmented skin of the illicium. A long, partially pigmented appendage extends anteriorly; a smaller unpigmented appendage is posterior. The scale equals one mm.

300-mesh grids and then stained in freshly prepared uranyl acetate (1-2% in 50% ethanol, filtered through a millipore before use) for thirty minutes at 40°C, followed by Reynold's lead citrate, also freshly prepared, for five to ten minutes. They were examined and photographed in an RCA EMU-3F electron microscope.

#### *Light Microscopy*

Sections one micron thick were cut from blocks prepared in the above manner and stained briefly in 0.1% toluidine blue in 1% borax. One esca, obtained from a museum specimen originally fixed in 10% formalin in sea-water and preserved in 40% isopropanol, was embedded in paraffin for serial sectioning. Another esca was embedded in glycol methacrylate (Feder and O'Brien, 1968). Paraffin and glycol methacrylate sections were stained with acid fuchsin and toluidine blue.

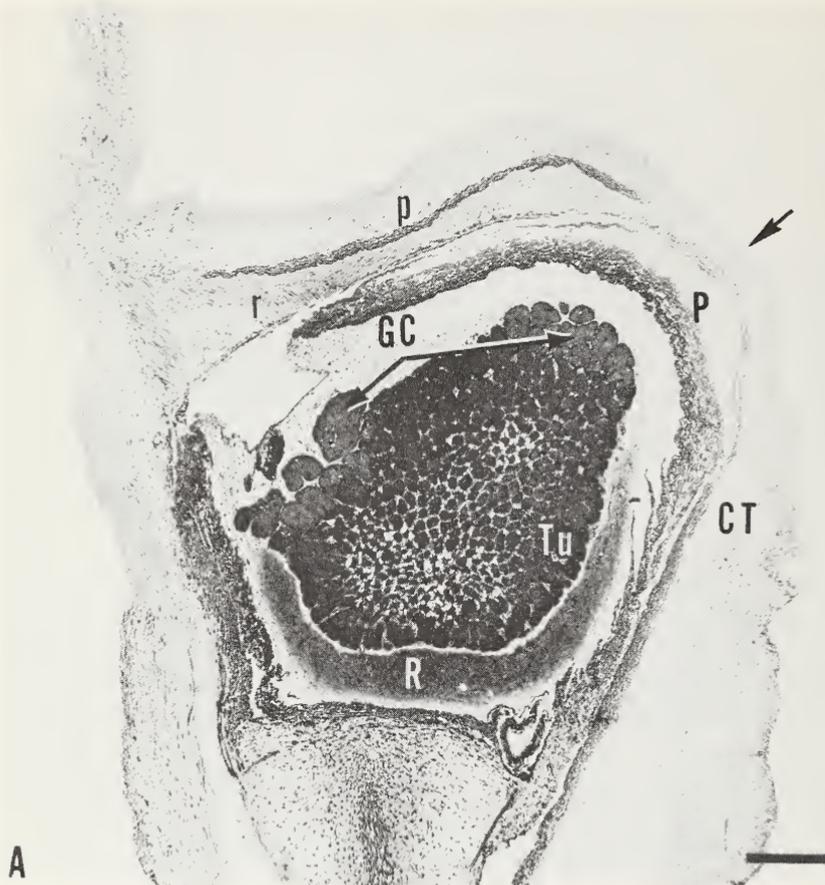


FIGURE 3A. (Above) Longitudinal section of the esca. This section does not pass through the pore which leads to the seawater but its location is indicated by an arrow on the posterior surface of the esca. B (Opposite page) The same section viewed through crossed polarizers, showing the birefringent crystalline reflectors. The scale for both figures equals 200 microns. Abbreviations: CT, connective tissue; GC, large gland cells; P, main pigment layer; p, accessory pigment layer; R, main reflector layer; r, accessory reflector layer; Tu, tubules lined with glandular epithelium and containing numerous bacteria.

### *Bacteriology*

Escal smears were prepared from live anglerfishes. The esca was rinsed briefly in 100% ethanol, then either pressed on a clean glass slide to extrude some luminal matter through the escal pore, or cut with a sterile razor blade to expose the lumen, the contents of which were then streaked on clean glass

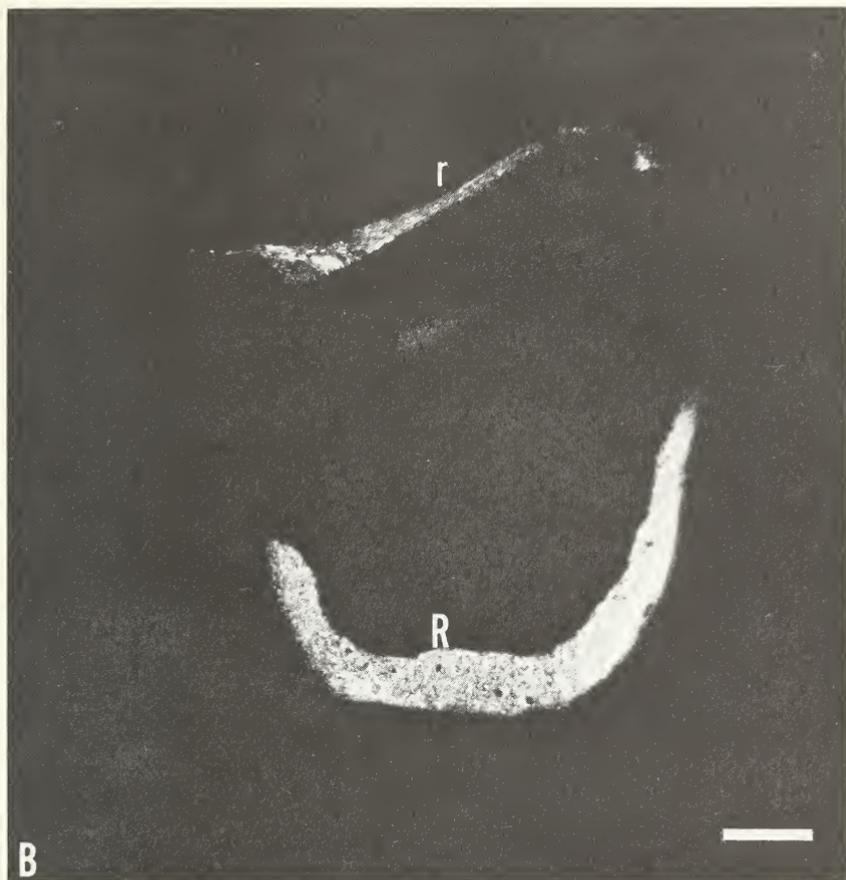


FIGURE 3B.

slides. The smears were dried on a warm hotplate. They were stained and examined right away or later in the shore lab, following a few days storage in the cold. The stains employed were the Gram stain (Lillie, 1965), Fontana's silver stain for flagella, Malachite green for spores, and Muir's stain for capsules (the latter three stains as described by Baker, 1967).

Whole bacteria were also examined by electron microscopy after drops of esca exudate had been allowed to evaporate on grids coated with collodion and stabilized with carbon. The specimens were then shadowed with platinum-palladium before examination.

To prepare a culture of the bacteria from the esca, the organ was first rinsed with sterile distilled water, then dipped in 70% ethanol for about ten

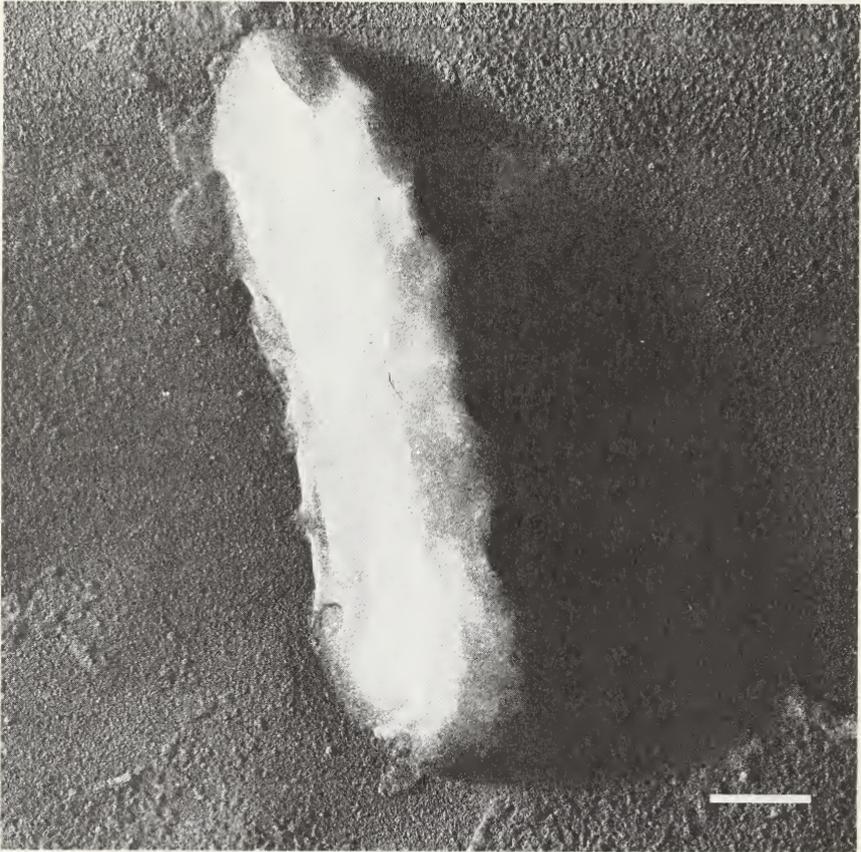


FIGURE 4. Electron micrograph of a whole bacterium from the esca of *O. acanthias*, shadowed with platinum-palladium. The scale equals one micron.

seconds. It was transferred to a sterile watchglass containing 0.5 ml sterile nutrient broth. The esca was pressed gently with a sterile pipette to extrude some material from the lumen. The inoculated nutrient broth was pipetted into several test tubes of sterile broth. Control tubes, which were not inoculated but were otherwise exposed to the same conditions as the inoculated ones, remained free of contamination. The culture was grown at room temperature. The medium used (Hastings and Mitchell, 1971) contained 8 g of nutrient broth (Difco) and 3 ml of glycerol per liter of seawater; it was sterilized by autoclaving.

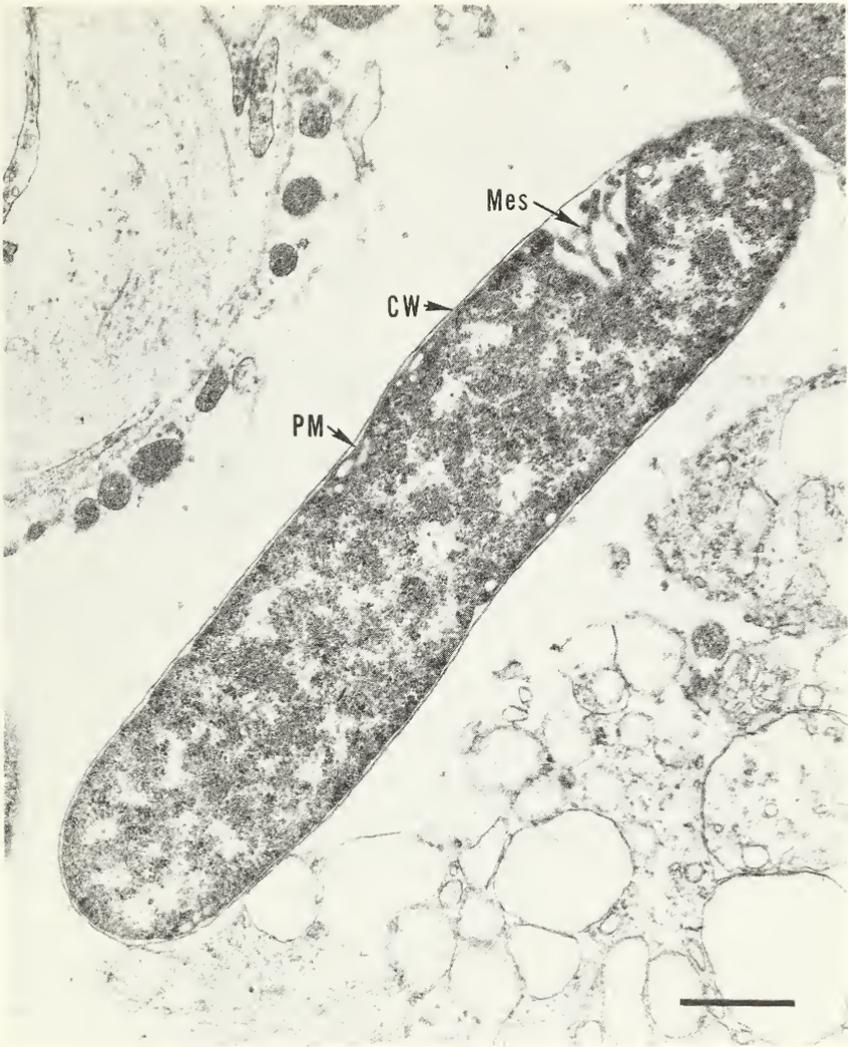


FIGURE 5. Electron micrograph of a longitudinally sectioned bacterium in the esca lumen. CW, cell wall; Mes, mesosome; PM, plasma membrane. The scale equals 0.5 micron.

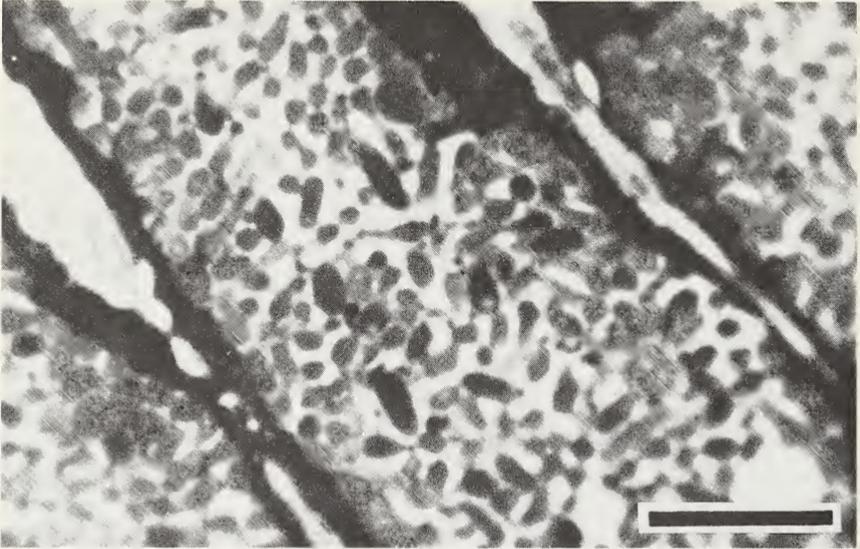


FIGURE 6. Light micrograph of portions of three tubules containing numerous bacteria. The scale equals 10 microns.

### *Specimens*

Eight specimens of *O. acanthias*, 21 to 118 mm in standard length (SL), were used. Observations of bioluminescence were made on seven of them; four were used for light and electron microscopy. The bacterial culture was isolated from a single specimen, 30 mm SL.

## RESULTS AND DISCUSSION

### *Histology*

The esca (Fig. 3) consists of the following arrangement of tissues: (1) a very thin external epithelium; (2) a thick layer of connective tissue which gives the esca its characteristic shape; (3) a layer of black pigment surrounding the esca bulb; (4) the main reflector, a cup-shaped layer of oriented crystals just internal to the layer of black pigment; (5) a smaller accessory reflector bordered distally by black pigment near the dorsal surface of the esca; (6) glandular cells, most of which line tubules which are continuous with the lumen of the esca bulb; (7) vascular supply; and (8) a central lumen containing numerous bacteria and communicating with the external environment by means of a pore. Although nerve branches occur in the peripheral connective tissue of the esca, they do not penetrate into the area where the glandular cells and bacteria are.

### *Staining Properties*

Smears from the esca of *O. acanthias*, dyed with selective stains for light microscopy, reveal numerous Gram-negative rods of varying length, some in the process of dividing, which lack capsules, spores, and flagella.

### *Fine Structure*

Studied with the electron microscope, whole bacteria shadowed with heavy metal appear to be aflagellate rods (Fig. 4), as expected from previous light microscopy. Thin sections reveal that the bacteria have a two-layered cell wall just external to the plasma membrane. Internally, ribosomes and a finely filamentous material which probably represents portions of the bacterial genome are present. A fairly common feature of bacterial structure in *O. acanthias*, a mesosome, is evident in Figure 5. The functional significance of these multiple infoldings of the plasma membrane remains uncertain, but it is possible that mesosomes increase the surface area of the cell membrane in order to facilitate such processes as cell division and spore formation and perhaps to provide additional sites for enzymatic attachment (Ryter, 1969; Bisset, 1970).

Many of the bacteria lie in the central lumen, together with a mass of irregularly shaped membranous bodies, most of which are unrecognizable but a few of which suggest degenerating mitochondria. Vesicles of varying shape can also be seen in the lumen. The membranous fragments and vesicles seem to be derived from apocrine secretion by the gland cells. Many other bacteria appear in the tubules lined with glandular epithelium (Fig. 6) or within deep invaginations into the glandular cells.

Vacuolar inclusions, apparently not enclosed by a membrane, occur in some of the bacteria. Similar structures were noted in the bacteria from *Melanocetus* by Hulet and Musil (1968) and they are evident in the electron micrographs by Haneda and Tsuji (1971) of symbiotic bacteria from the luminescent organs of *Photoblepharon* and *Anomalops*. They may represent dilute fluid or unsaturated lipid that was subsequently extracted from the specimen during processing.

### *Culture of the Bacteria*

The conclusive demonstration that bacteria are the source of luminescence requires that they be grown in a pure culture which luminesces. Although I have cultured bacteria from the esca of *O. acanthias*, I have not seen them luminesce. The moneran symbionts in the luminous fishes *Anomalops* and *Photoblepharon* reportedly grow on similar media as non-luminous forms only (Harvey, 1921, 1922, 1952; Haneda, 1943, as cited by Harvey, 1952). In their recent experiments on these fishes, Haneda and Tsuji (1971) obtained only a few colonies, none of them luminescent (Tsuji, personal communication).

Cultures of bacteria from certain other luminous fishes, on the other

hand, emit light readily. Such cultures have been reported from *Malacocephalus laevis* by Haneda (1938); *Physiculus japonicus* by Kishitani (1930); *Monocentris japonica* by Okada (1926); *Acropoma japonica* by Yasaki and Haneda (1936) and Haneda (1950); *Siphamia* spp. by Yoshida and Haneda (1967) and Haneda (1965); *Cleidopus gloria-maris* by Yoshida and Haneda (1967); and various species of Leionathidae by Haneda (1940, 1950) and Hastings and Mitchell (1971).

Perhaps the symbionts in *Oneirodes*, *Anomalops*, and *Photoblepharon* have lost the capacity to synthesize everything that the chemistry of their luminescence requires, so that they now depend on their hosts to complement their deficiencies. The fine structure of the esca in *O. acanthias* suggests that the bacteria obtain certain nutrients from the tissues of the host, with the possible exception of some dissolved salts and trace elements that might be extracted from seawater. The symbionts probably subsist on the secretory products of the glandular cells and the associated masses of degenerate membranous fragments which float freely in the lumen of the esca.

The existence of a pore leading to the seawater outside the esca satisfies several conditions for the successful long-term culture of any strain of microorganisms. It ensures that neither the tonicity nor the pH of the culture medium will vary and it allows continual removal of dead bacteria and cellular waste as newly formed bacteria and freshly synthesized cellular products take their place. Temperature hardly changes over hundreds of meters in the bathypelagic zone and at a particular depth it remains the same day after day, year after year. The bacteria, then, can depend on the constancy of the microenvironment inside the esca.

#### SUMMARY

The esca light organ of the deep-sea anglerfish *O. acanthias* contains numerous bacterial symbionts. These microorganisms are Gram-negative rods without capsules, spores, or flagella. Their ultrastructural features include a double-layered cell wall and mesosomes. Since the bacteria grow but do not luminesce in seawater nutrient broth, it appears that the host provides certain nutrients required for luminescence.

#### ACKNOWLEDGMENTS

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POSTCRANIAL ELEMENTS OF THE EXTINCT CONDOR  
*BREAGYPS CLARKI* (MILLER)

By HILDEGARDE HOWARD



CONTRIBUTIONS IN SCIENCE



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# POSTCRANIAL ELEMENTS OF THE EXTINCT CONDOR

## *BREAGYPS CLARKI* (MILLER)<sup>1</sup>

By HILDEGARDE HOWARD<sup>2</sup>

**ABSTRACT:** When the genus *Breagyps* was established, only the skull and tarsometatarsus were described. Other skeletal elements in the Rancho La Brea collections of the Natural History Museum of Los Angeles County are now assigned to *Breagyps* and are described in detail in comparison with bones of the two existing condor genera, *Vultur* and *Gymnogyps*. Contrasts with the smaller vultures are also noted. Resemblance is closest to *Vultur*, but distinctive generic characters are clear throughout.

### INTRODUCTION

*Breagyps clarki* was first described (Miller, 1910:11) under the genus "*Sarcorhamphus*" (= *Vultur*) in comparison with *Vultur gryphus*. The type, and only known element at that time, was a tarsometatarsus in the collections of the University of California, Museum of Paleontology, from the Pleistocene of Rancho La Brea (UCMP 12588). With the later assignment to this species of skull material in the Rancho La Brea collections at the Natural History Museum of Los Angeles County (LACM), the genus *Breagyps* was erected (Miller and Howard, 1938:171). At this time the tarsometatarsus was restudied and generic characters of this element, as well as the skull, were delineated.

A complete review of all condor bones in the LACM collections from Rancho La Brea has resulted in segregating eleven other limb and girdle elements as well as several vertebrae, all of which are distinguishable from specimens of the better represented California Condor, *Gymnogyps*. The elements form a homogeneous group of approximately 150 bones whose characters are compatible with those of the tarsometatarsus and skull of *Breagyps clarki*. Therefore, I have no hesitation in assigning them to this genus and species.

During study of these elements of *Breagyps*, all present-day cathartid genera were compared. Each of these was found to share one or more separate characters with one or another genus of the family. But differences also appear in each element, and the combination of characters is distinctive for each genus. This is true, as well, of *Breagyps*.

In order to simplify the description of the elements now to be described,

<sup>1</sup>REVIEW COMMITTEE FOR THIS CONTRIBUTION  
Pierce Brodkorb  
Alexander Wetmore  
David P. Whistler

<sup>2</sup>Chief Curator Emeritus, Natural History Museum of Los Angeles County, Los Angeles, California 90007

the detailed study of the fossil bones is confined to comparison with modern skeletal material of *Vultur gryphus* and *Gymnogyps californianus*. Comments concerning comparisons with the smaller vultures are included in the Discussion section.

#### MATERIAL AVAILABLE

All material is in the LACM collections except two modern skeletons of *Vultur gryphus*, which were loaned by the University of California at Los Angeles, Department of Zoology.

#### FOSSIL SPECIMENS

##### *Breagyps clarki*

(LACM catalog numbers)

STERNUM: six incomplete, B1517, B3071, B3372, B3783, B4554, B5669.

FURCULA: one symphysis, B6035; four clavicles, B2224, B2601, B8114, B8315.

CORACOID: nineteen nearly complete, B1499, B1638, B1739, B2311, B2644, B3242, B3424, B3821, B6188, B6320, B7067, B7124, B7479, B7699, B7743, B7847, B7914, B8039, B8376.

SCAPULA: one complete, B4450; ten articular ends, B1657, B1670, B1671, B1676, B2259, B3420, B3482, B4418, B6020, B6332.

HUMERUS: four nearly complete, B4847 + B5329, B7730, B7737 + B7739, B8002; five proximal ends, B1583, B2083, B2156, B4954, B5917; three distal ends, B2034, B5956, B7247.

ULNA: nine proximal ends, B1859, B1910, B3838, B4221, B4630, B6912, B6925, B7248, B8310; five distal ends, B3453, B5891, B6914, B7503, B7715.

RADIUS: one proximal end, B6782; one distal end, B7661.

CARPOMETACARPUS: fourteen nearly complete, B1075, B1755, B2168, B2632, B3154, B3271, B3625, B4160, B4375, B5331, B6395, B6712, B7608, J9402.

PELVIS: one nearly complete, B1082 + B1092; five incomplete, B1635, B3346, B6859, B6865, B7895.

FEMUR: eight nearly complete, B1404, B3358, B4989, B5580, B5693, B6259, B7493, B7803; two incomplete proximally, B2599, B6910; two proximal ends, B2257, B6372; six distal ends, B1437, B1574, B3388, B5950, B6620, B7460.

TIBIOTARSUS: three nearly complete, B4039, B5878, B6413 + B6414; one incomplete proximally, J9629; four proximal ends, B2115, B2314, B3361, B6404; nine distal ends, B1074, B1593, B2116, B3383, B5156, B6477, B7085, B7244, B8313.

CERVICAL VERTEBRAE: B3841, B3945, G9423, G9346 (atlas).

Additional specimens of these elements were used in the composite mount of *Breagyps clarki* now on exhibit at LACM: sternum B1428; furcula B8308 + B8309; coracoid B1495, H3837; scapula B4862, B7558; humerus B3246; ulna, proximal end B4458, K3353, distal end B592, B1665; carpometacarpus B2181, B2667; pelvis B4912 + B5165; femur B3379, B3576; tibiotarsus B7026, B7746. For an illustration of this mount, see Howard (1962: 29, fig. 12).

#### MODERN SPECIMENS

*Gymnogyps californianus*: 1 complete skeleton, 2 with wing bones only, 7 body skeletons.

*Vultur gryphus*: 2 complete skeletons.

*Sarcoramphus papa*: 1 complete, 1 body skeleton.

*Coragyps atratus*: 3 complete, 1 body skeleton.

*Cathartes aura*: 1 complete, 1 body skeleton.

As a further check on comparisons between genera of the family Cathartidae, Fisher's (1946) monograph on the comparative anatomy of this family was consulted.

DESCRIPTION OF ELEMENTS ASSIGNED TO *Breagyps clarki*

Sternum (Figure 1): Relatively broad across shield but short through costal row (see Table 1); anterior contour (viewed dorsally) broad and straight with lateral borders of dorsal lip of coracoidal sulcus protruding and tending to be square in outline; dorsal surface of shield deeply depressed close to anterior border on either side of a narrow central ridge; carina deep and ascending abruptly at level of last costal process; anterior border of carina depressed between central and lateral ridges; small, roughly triangular depression on ventral labial prominences, rimmed at lateral edge by rounded ridge and medially by external intermuscular line; ventral manubrial spine facing anterovertrally with long ridge rising to dorsal edge.

*Vultur* is generally similar in proportions and in anterior contour dorsally, but the carina is slightly lower and point of ascent farther posterior; the dorsal depression of the shield is less; the ventral labial prominences are

TABLE 1  
Measurements of Sternum  
(in millimeters)

	<i>Breagyps clarki</i> (3 bones)			<i>Gymnogyps californianus</i> (4 bones)			<i>Vultur gryphus</i> (2 bones)	
	max.	mean	min.	max.	mean	min.	max.	min.
Length from dorsal lip through last costal process	76.2	73.7	72.0	81.0	77.7	75.7	84.6	78.9
Length costal row	46.9	44.9	43.5	50.7	49.0	47.4	49.4	46.0
Breadth of shield back of second costal process	73.8	72.7	71.0	72.3	69.0	66.5	80.4	74.3
Breadth across ventral labial prominences	66.2	64.5	62.2	61.0	60.6	60.0	67.4	61.6
Ratio (in %) breadth shield to length from dorsal lip through last costal process	101.0	98.6	96.2	94.2	88.6	85.5	95.0	94.2
Ratio (in %) length costal row to breadth of shield	64.0	61.8	59.0	74.7	71.2	66.8	62.0	61.5

rounded ventrally, lacking the triangular depression found in *Breagyps*. In *Gymnogyps* the shield is relatively narrower, and anteriorly the contour is more curved; the carina is lower, with point of ascent well posterior to last costal process; the anterior surface of the carina slopes away laterally from the central ridge, with no lateral ridges; the depression on the ventral labial prominences is similar to that in *Breagyps* but somewhat longer. The ventral manubrial spine is more prominent in both *Vultur* and *Gymnogyps*, with a shorter ridge above.

Furcula (Figure 2D): Condorlike in the broad, gradual dorsal curvature of the clavicles; the arch is narrower and more abrupt in the other three cathartid genera. Externally, deep pneumatic fossa undercutting dorsal rim of clavicle as in *Gymnogyps*, but of less extent ventrally, stopping short of ventral border as in *Vultur*, but dorsal rim less undercut in *Vultur*. Area anterior to pointed scapular tip (externally) with shelflike expansion ventrally, narrowed abruptly dorsally with a large foramen between; unlike both *Gymnogyps* and *Vultur* in this character. (Although there is more expansion in *Gymnogyps* than in *Vultur*, it is gradual with multiple, small foramina, and the dorsal area is less narrowed.)

TABLE 2  
Measurements of Coracoid  
(in millimeters)

	<i>Breagyps clarki</i> (10 bones)			<i>Gymnogyps californianus</i> (8 bones)			<i>Vultur gryphus</i> (2 bones)	
	max.	mean	min.	max.	mean	min.	max.	min.
Length to sternal end mediad of angle	102.0	98.7	95.4	98.9	96.4	92.9	104.0	96.9
Breadth across triosseal canal	21.8	21.2	20.3	23.1	21.6	20.4	23.2	20.7
Breadth furcular facet	26.0	24.3	22.7	26.2	24.7	22.9	31.6	27.5
Height furcular facet	15.2	13.5	12.6	12.8	11.9	11.3	15.2	14.5
Ratio (in %) breadth triosseal canal to length of coracoid	22.2	21.3	21.0	23.5	22.4	21.0	22.2	21.4
Ratio (in %) breadth furcular facet to length of coracoid	26.6	24.6	23.7	26.5	25.6	23.5	30.3	28.2
Ratio (in %) height to breadth of furcular facet	58.6	55.6	51.6	51.5	48.2	45.5	52.7	48.1

Coracoid (Figure 2A,C): Head more prominently developed posteriorly than anteriorly, with diagonal groove through furcular facet emphasizing this unevenness; ligamental attachment on postero-external part of head short and deep, further increasing prominence of head posteriorly; neck well depressed; furcular facet high relative to breadth (see Table 2); anterior half of furcular facet narrowed and brachial tuberosity projecting anteriorly over deep fossa; fossa bordered externally by flange of bone, internally by sharply ridged edge of triosseal canal; lower margin of furcular facet concave near posterior edge, slightly overhanging triosseal canal.

The head is more evenly proportioned in the other two condors and the ligamental attachment on the postero-external part of the head is less prominent, the neck less depressed. In *Gymnogyps* there is a faint diagonal depression in the furcular facet, none in *Vultur*. The fossa below the brachial tuberosity is less developed in *Gymnogyps*, with the internal border of the triosseal canal rounded; the fossa is most markedly developed in *Vultur*, where the external flange of bone projects beyond the acutely bordered edge of the triosseal canal. The lower margin of the furcular facet is straight in both *Vultur* and *Gymnogyps*, with no overhang in *Gymnogyps*, a slight overhang in *Vultur*.

Scapula (Figure 2B): Acromion short and flaring abruptly from shaft, then markedly deflected mediad; dorsal contour of acromion (viewed externally) gradually rounded and, in proximal view, anterior projection of acromion broadly rounded; coracoidal articulation low; dorsal area between acromion and glenoid facet broadly depressed. See Table 3 for measurements.

The acromion rises gradually in *Gymnogyps* and is only faintly deflected; the dorsal contour is rounded but, as viewed proximally, the anterior projection is pointed; the coracoidal articulation is convex. In *Vultur* the acromion arises abruptly from the shaft but is less flared and is not deflected mediad;

TABLE 3  
Measurements of Scapula  
(in millimeters)

	<i>Breagyps clarki</i> (7 bones)			<i>Gymnogyps californianus</i> (8 bones)			<i>Vultur gryphus</i> (2 bones)	
	max.	mean	min.	max.	mean	min.	max.	min.
Breadth through acromion and glenoid facet	32.2	30.3	28.7	30.5	28.8	27.6	29.8	26.8
Length of acromion	23.3	22.1	21.5	22.0	21.0	20.2	24.3	24.0
Ratio (in %) length of acromion to breadth of scapula	75.4	71.8	68.5	75.0	72.9	68.5	89.5	81.2

in external view the dorsal contour is more angular and the anterior projection more prominently and acutely produced; the coracoidal articulation is low. In both *Gymnogyps* and *Vultur*, the space between the acromion and glenoid facet dorsally is narrower and less depressed than in *Breagyps*.

Humerus (Figures 3 and 5B): Bicipital crest broadly rounded; deltoid crest with even curvature, depressed medially (on anconal side) with raised, evenly contoured border; pectoral attachment widening gradually from a point proximal to level of distal border of bicipital crest; distal tip of pectoral attachment near edge of shaft; slightly pneumatic, shallow depression below head, palmar. Distally, deep pneumatic depression between internal condyle and attachment of anterior ligament and between external condyle and base of ectepicondylar prominence; ectepicondylar prominence broad and anconal border slightly concave.

*Vultur* resembles *Breagyps* in the shape of the bicipital crest, gradual widening and lateral termination of the pectoral attachment, and the shallow depression below the head; the bicipital crest is not as prominently protruded, however, and the pectoral attachment is narrower and does not extend as far proximally. *Gymnogyps* is distinct in all these features of the proximal end—the bicipital crest is less round especially at the distal terminus, the pectoral attachment broadens abruptly and its distal tip is medially to the edge of the shaft, and the depression below the head is deeper and more pneumatic. In neither *Vultur* nor *Gymnogyps* is the deltoid crest as medially depressed, and the rim is not raised in an evenly contoured border. Distally, the degree of pneumaticity in *Gymnogyps* closely parallels the condition in *Breagyps* and the ectepicondylar prominence is close in size but is less curved. This prominence is longer, narrower and more curved in *Vultur*.

Length is probably a significant character of this element in *Breagyps clarki*. Four complete bones average 10 mm shorter than the mean of four humeri of *G. californianus*, and the minimum is 13 mm less than the *G. californianus* minimum (see Table 4). In all other limb elements *B. clarki* exceeds *G. californianus* in length.

Ulna (Figure 4A,B): Brachial impression well depressed, with large pneumatic foramina, and area between impression and internal cotyla swollen; distally, external condyle short and broad and closely appressed to shaft. As there are no complete ulnae of *Breagyps*, the number of anconal papillae for attachment of the secondaries, and the total length of the element can only be estimated. See Table 5 for estimated length; the number of papillae is at least 17 and possibly 19.

In both *Vultur* and *Gymnogyps* the area proximal to the brachial impression merges more gradually towards the cotyla; distally the external condyle is narrower and in *Gymnogyps* it is of greater proximo-distal extent. The number of anconal papillae in *Vultur* is 17-19, *Gymnogyps* has fewer (15-16). The number is still less in the smaller vultures. The fossil appears to exceed both modern condors in ulnar length.

TABLE 4  
Measurements of Humerus  
(in millimeters)

	<i>Breagyps clarki</i> (6 bones) <sup>a</sup>			<i>Gymnogyps californianus</i> (4 bones)			<i>Vultur gryphus</i> (2 bones)	
	max.	mean	min.	max.	mean	min.	max.	min.
Greatest length	267.0	261.2	256.0	275.0	271.7	262.0 <sup>b</sup>	280.0	272.2
Greatest breadth proximally through bicipital crest	60.1	59.1	58.6	58.3	55.8	54.0	62.1	57.9
Greatest breadth distal end	49.2	48.1	46.7	47.8	47.1	46.2	52.3	49.5
Length deltoid crest to distal tip pectoral attachment	116.5	111.9	106.2	118.7	116.0	114.2	122.2	114.5
Ratio (in %) proximal breadth to length		22.0		20.6	20.0	19.6	22.0	21.3
Ratio (in %) breadth distal end to length	18.8	18.4	17.9	17.5	17.3	17.1	18.7	18.2
Ratio (in %) length deltoid crest to length humerus	43.5	42.7	41.6	42.7	42.5	42.3	43.6	42.0

<sup>a</sup>Measurement of length could be made on only 4 bones and ratio of proximal breadth to length on only one.

<sup>b</sup>Fisher's (1947:229) measurements on 11 humeri: 274-262, mean 267 mm.

Radius (Figure 5A,C): With only one proximal and one distal end of this element for *Breagyps*, any description is necessarily tentative. Based on variability as observed in the other cathartid genera, the following characters are probably valid: bicipital tuberosity clearly bordered and set well below (21.9 mm) the proximal articular facet; capital tuberosity prominent; distal end flaring abruptly from shaft and ulnar depression broad and deep.

In *Gymnogyps* the bicipital tuberosity is set higher (17-19 mm below facet), the capital tuberosity is less prominent, the distal end more gradually flared and the ulnar depression very shallow. *Vultur* is more like *Breagyps* proximally; distally the ulnar depression is also somewhat as in *Breagyps*, but the distal flare is more gradual.

Carpometacarpus (Figure 4C): Process of metacarpal 1 heavy and slightly upturned; proximal and distal symphyses short (see Table 6); proximal symphysis well depressed; tuberosity of metacarpal 3 (proximally) a prominent

TABLE 5  
Measurements of Ulna  
(in millimeters)

	<i>Breagyps clarki</i> <sup>a</sup>			<i>Gymnogyps californianus</i> (3 bones)			<i>Vultur gryphus</i> (2 bones)	
	max.	mean	min.	max.	mean	min.	max.	min.
Greatest length	365		341	320	315	312 <sup>b</sup>	354.0	330.0
Length to proximal cotylae	341		321	303.3	300.2	297.0	337.0	313.0
Breadth across proximal cotylae	31.7	30.7	30.0	33.0	31.5	30.6	32.6	30.5
Depth proximal end (externally)	26.8	26.3	25.9	25.5	24.9	24.4	28.5	26.7
Breadth distal end		25.5		22.7	22.5	22.2	25.0	22.3
Depth distal end externally		21.6		23.6	22.9	22.6	25.2	22.8

<sup>a</sup>No complete ulnae; measurements of length estimated; proximal breadth taken on 5 bones, distal breadth on only one.

<sup>b</sup>Fisher's (1947:229) measurements on 8 bones: 320-305, mean 313 mm.

tubercle; viewed posteriorly, internal trochlear crest narrowing abruptly distally on internal edge and joining shaft abruptly with ridge below; tuberosity of metacarpal 2 (distally) short but prominent, forming the median border of an anterior depressed area which is also heavily rimmed distally.

The process of metacarpal 1 is more anteriorly projected in the other condors but lower in proximal-distal dimension. Also, in the existing genera, the proximal symphysis is less depressed and the tuberosity of metacarpal 3 is less prominent. The length of the proximal symphysis is similar in *Vultur*, longer in *Gymnogyps*; distally the reverse is true, *Vultur* having a very long, flat symphysis. In both *Vultur* and *Gymnogyps* the internal trochlear crest is evenly rounded and lacks the abrupt narrowing as viewed posteriorly. Distally the tuberosity of metacarpal 2 is longer, less prominent and more ridgelike in *Vultur* and *Gymnogyps*. In *Vultur*, however, the anterior face of metacarpal 2 is depressed as in *Breagyps* and is heavily rimmed distally; *Gymnogyps* lacks the anterior depression but is more depressed internal to the tuberosity. See Table 6 for measurements.

Pelvis (Figures 6,7): With only one *Breagyps* pelvis even fairly complete, the characters of this element are indecisive. The following appear to be distinctive. Allied with condors in distinction to other cathartids in having three thoracic vertebrae attached to the synsacrum. Iliia not extending to anterior end of synsacrum; ilio-ischiatic surface deep with borders of ilia and ischia nearly parallel for a distance of about 30 mm posterior to acetabulum; iliac

TABLE 6  
Measurements of Carpometacarpus  
(in millimeters)

	<i>Breagyps clarki</i> (11 bones)			<i>Gymnogyps californianus</i> (2 bones)		<i>Vultur gryphus</i> (2 bones)	
	max.	mean	min.	max.	min.	max.	min.
Length from external trochlea to distal end metacarpal 2	145.9	141.1	134.5	136.1	135.8 <sup>a</sup>	143.5	136.7
Length proximal symphysis (to pisiform process)	30.8	28.6	26.9	31.3	31.1	28.0	26.3
Height process metacarpal 1	15.9	14.4	13.5	13.4	13.0	12.7	12.4
Length distal symphysis (to distal tip metacarpal 3)	17.7	15.5	13.3	15.7	15.6	21.3	20.7
Ratio (in %) length proximal symphysis to overall length	21.9	20.1	18.8	23.0	22.8	19.5	19.3
Ratio (in %) height process metacarpal 1 to overall length	11.2	10.1	9.6	9.8	9.5	9.1	8.8
Ratio (in %) length distal symphysis to overall length	12.3	11.1	9.2	11.6	11.4	15.1	14.8

<sup>a</sup>Fisher's (1947:230) measurements on three bones: 133-131 mm.

crest jutting out above acetabulum and ilio-ischiatic fenestra, the postacetabular ilia receding below the crest in the fenestral area; dorsal surface of shield moderately convex in midline, slightly depressed laterally and perforated with evenly spaced, fairly large pneumatic openings posteriorly, smaller openings farther forward; in ventral view, widest portion of synsacral caudal area posterior to acetabulum and flush with ventral surface of posterior ilia. See Table 7 for measurements.

*Vultur* resembles *Breagyps* in the extent of the anterior ilia; in *Gymnogyps*, the ilia extend only to the anterior border of the second synsacral thoracic vertebra. In both *Vultur* and *Gymnogyps*, the posterior ilia slope downward more rapidly and the borders of the ilio-ischiatic surface converge more noticeably than in *Breagyps*. In *Vultur*, the iliac crest recedes above the

TABLE 7  
Measurements of Pelvis  
(in millimeters)

	<i>Breagyps clarki</i> (3 specimens) <sup>a</sup>			<i>Gymnogyps californianus</i> (7 specimens)			<i>Vultur gryphus</i> (2 specimens)	
	max.	mean	min.	max.	mean	min.	max.	min.
Length synsacrum	146.4	143.6	141.5	152.3	142.0	134.5	163.0	139.6
Interacetabular width		55.8		57.0	53.8	49.8	61.2	55.8
Breadth across antitrochanters		82.4		83.0	79.8	74.6	92.8	85.8
Breadth across posterior iliac crests		79.1		85.9	82.9	80.7	84.1	77.9
Ratio (in %) interacetabular width to length synsacrum		39.2		40.6	38.0	33.8	42.5	37.5
Ratio (in %) breadth across posterior iliac crests to breadth across antitrochanters		96.3		108.1	103.9	102.1	90.8	90.6

<sup>a</sup>Only one pelvis measurable for dimensions other than length of synsacrum

acetabulum and the ilio-ischiatic fenestra; in *Gymnogyps* the crest is even more prominent than in *Breagyps*. The midline of the shield is narrower and more convex in *Gymnogyps* with greater depression laterally, but the perforations are similar to those of *Breagyps*; the reverse is true in *Vultur* (the midline is moderately convex as in *Breagyps*, but the perforations are fewer and smaller). In *Vultur* the point of greatest expansion of the synsacral caudal area (ventral view) is posterior to the acetabulum as in *Breagyps*, but a large pneumatic fenestra sets the synsacrum apart from the ventral surface of the ilia at this point; in *Gymnogyps* the expanded area is flush with the ventral surface of the posterior ilia as in *Breagyps*, but is farther forward.

Femur (Figure 8): Well flared proximal end, markedly protruding internally then narrowing abruptly in broad curve to slender shaft; shaft bowed anteriorly; trochanteric crest prominent, markedly deflected mediad and undercut by pneumatic foramina; obturator ridge sharply defined with deep depression adjacent internally below articular facet; attachment of round ligament (on head) deep and narrow; external intermuscular line forming sharp angle postero-externally at level of distal terminus of trochanteric crest. Distally, internal condyle protruding abruptly from shaft anteriorly; ligamental attach-

ment above fibular condyle large and facing proximally; rotular groove in line with shaft. See Table 8 for measurements.

The proximal flare is similar in *Vultur*, *Gymnogyps* is more columnar. However, in curvature of the shaft, *Gymnogyps* is more like *Breagyps*, *Vultur* is straighter. The trochanteric crest is less deflected in both the other condors although the arrangement of the foramina is similar in *Gymnogyps*; the obturator ridge is less sharply defined in *Vultur* and the adjacent depression shallower; in *Gymnogyps* the ridge is well defined but the depression tends to be narrower and deeper than in *Breagyps*. The attachment of the round ligament is broader but less deep, and the ligamental attachment above the fibular condyle is smaller and more posterior in position in both *Vultur* and *Gymnogyps*. The anterior contour of the internal condyle appears to be variable in *Gymnogyps*, so this may not be a valid character; it is, however, generally more abrupt than in *Vultur*. *Vultur* resembles *Breagyps* in placement of the rotular groove; the groove is more diagonally placed in *Gymnogyps* as a result of the mediad bending of the internal condyle.

Tibiotarsus (Figure 9): External cnemial crest longer than internal cnemial crest and having sharply compressed margin; internal crest (internal view) pinched in near proximal border; external proximal articular surface

TABLE 8  
Measurements of Femur  
(in millimeters)

	<i>Breagyps clarki</i> (9 bones)			<i>Gymnogyps californianus</i> (7 bones)			<i>Vultur gryphus</i> (2 bones)	
	max.	mean	min.	max.	mean	min.	max.	min.
Length from internal condyle to iliac facet	140.8	136.1	129.0	134.6	130.9	126.0	148.4	138.2
Greatest breadth proximal end	40.5	39.6	36.8	36.4	35.1	33.5	42.6	39.6
Greatest breadth distal end	39.0	37.5	35.3	36.2	34.8	33.7	39.5	38.1
Least dimension of shaft	16.5	15.5	14.5	16.8	15.7	15.0	16.7	15.7
Ratio (in %) breadth proximal end to length	30.1	29.2	28.2	27.0	26.8	26.3	28.7	28.6
Ratio (in %) breadth distal end to length	28.2	27.6	27.0	26.9	26.3	26.1	27.5	26.6
Ratio (in %) breadth of shaft to length	11.8	11.5	11.1	12.5	12.0	11.4	11.3	11.2

narrow and high. Distally, external condyle (anterior view) long and narrow with parallel sides and inclined so that proximal tip projects laterally, proximal contour of condyle blunt; ligamental attachment above external condyle well developed, somewhat triangular in shape with apex extending to level of upper edge of supratendinal bridge; lower margin of bridge tending to curl upwards resulting in large, unevenly shaped opening of tendinal canal. See Table 9 for measurements.

*Vultur* is similar to *Breagyps* in the character of the external crest, but the internal crest is more laterally deflected; distally, the external condyle in *Vultur* projects laterally but is broader; the ligamental attachment is smaller and the foramen more proximally placed. In *Gymnogyps* the external cnemial crest is shorter and less sharply compressed on the margin; the internal cnemial crest is less depressed near the proximal border; the external condyle is more vertically placed and tapers proximally; the ligamental attachment above the condyle is reduced. The proximal external articular surface is more broadly rounded and less raised in both *Vultur* and *Gymnogyps*, and distally the opening of the tendinal canal is more evenly oval.

Cervical vertebrae: The axis has been briefly described (Howard, 1969: 5-6) in connection with the discovery of a similar specimen in the Pleistocene deposits of Tequixquiac, Mexico. The characters distinguishing *Breagyps* from *Gymnogyps* and *Vultur* in this element are: the facets of the postzygapophyses are parallel, the posterior articulation of the centrum is broad and is directed posteriorly rather than dorsally, and the neural spine is broad and stubby. In both modern genera the facets of the postzygapophyses are aslant of the longitudinal axis of the vertebra, the posterior articulation of the centrum is narrower and faces more dorsally, and the neural spine is more slender.

The next *Breagyps* vertebra is either number 3 (immediately following the axis) or number 4. In this specimen, as in the axis, the facets of the post-

TABLE 9  
Measurements of Tibiotarsus  
(in millimeters)

	<i>Breagyps clarki</i> (4 bones)			<i>Gymnogyps californianus</i> <sup>a</sup>			<i>Vultur gryphus</i> (2 bones)	
	max.	mean	min.	max.	mean	min.	max.	min.
Greatest length	233est	223	214	213	210	208	251	236
Length to proximal articulation	225est	216	209				244	230
Breadth distal end	25.7	24.4	23.7	25.5	24.3	23.3	26.2	25.4

<sup>a</sup>Measurements as given by Fisher (1947:234). Length assumed to be greatest length but not so stated. Single available LACM specimen measures 218 mm greatest length, 213 mm to proximal articulation, breadth distal end 23.5 mm.

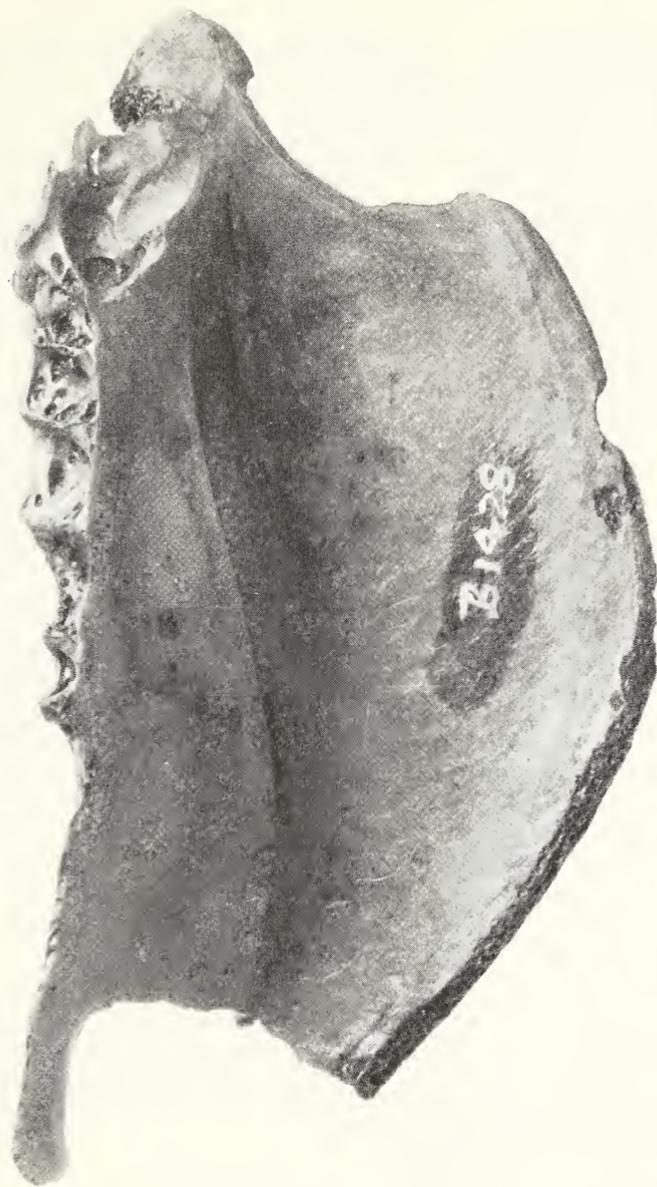


FIGURE 1. *Breagyps clarki*, sternum, B1428 (now in mounted skeleton on display). X 1.

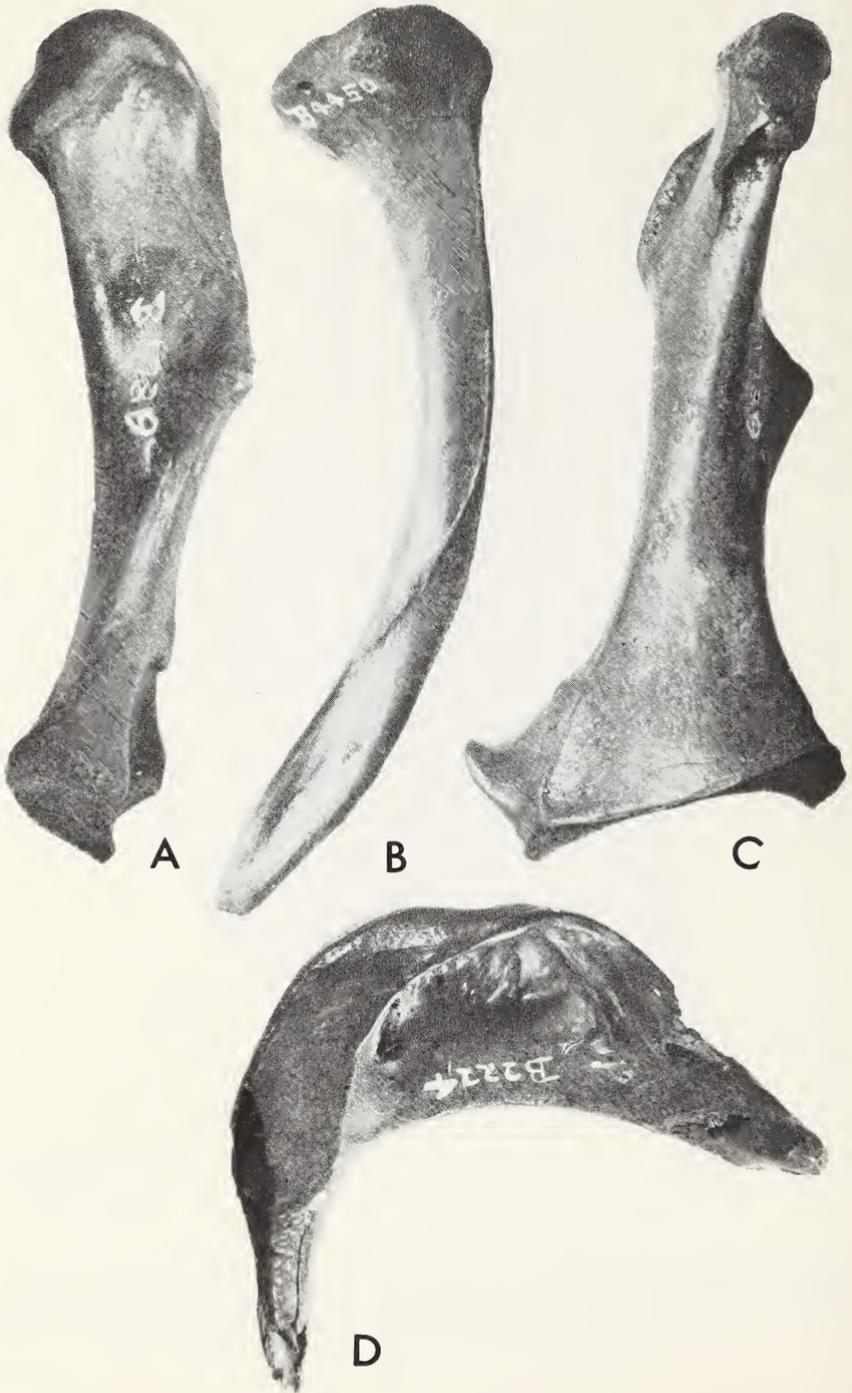


FIGURE 2. *Breagyps clarki*. A. internal, and C. anterior views of right coracoid, B1739; B. right scapula, B4450, ventral view; D. left clavicle, B2224, external view. X 1.

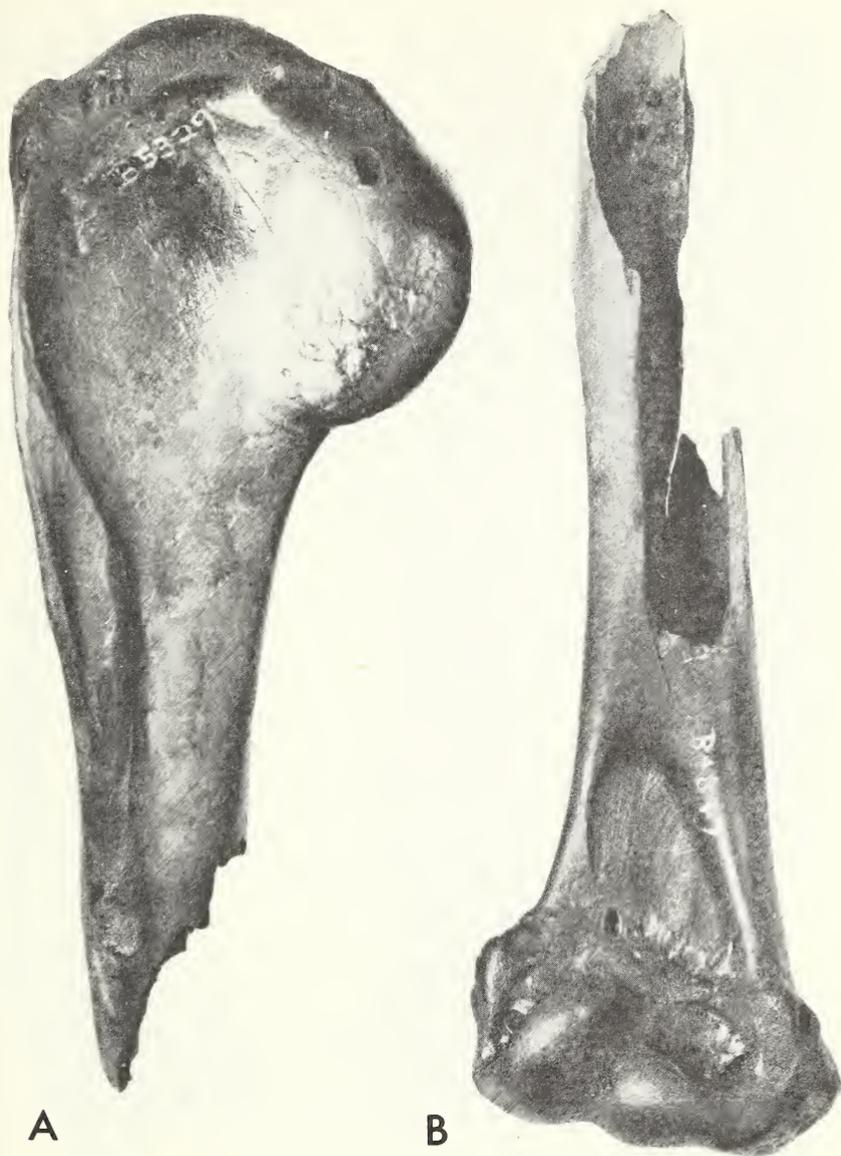


FIGURE 3. *Breagyps clarki*, right humerus. A. proximal (B5329), and B. distal (B4847) ends of same bone, palmar view. X 1.

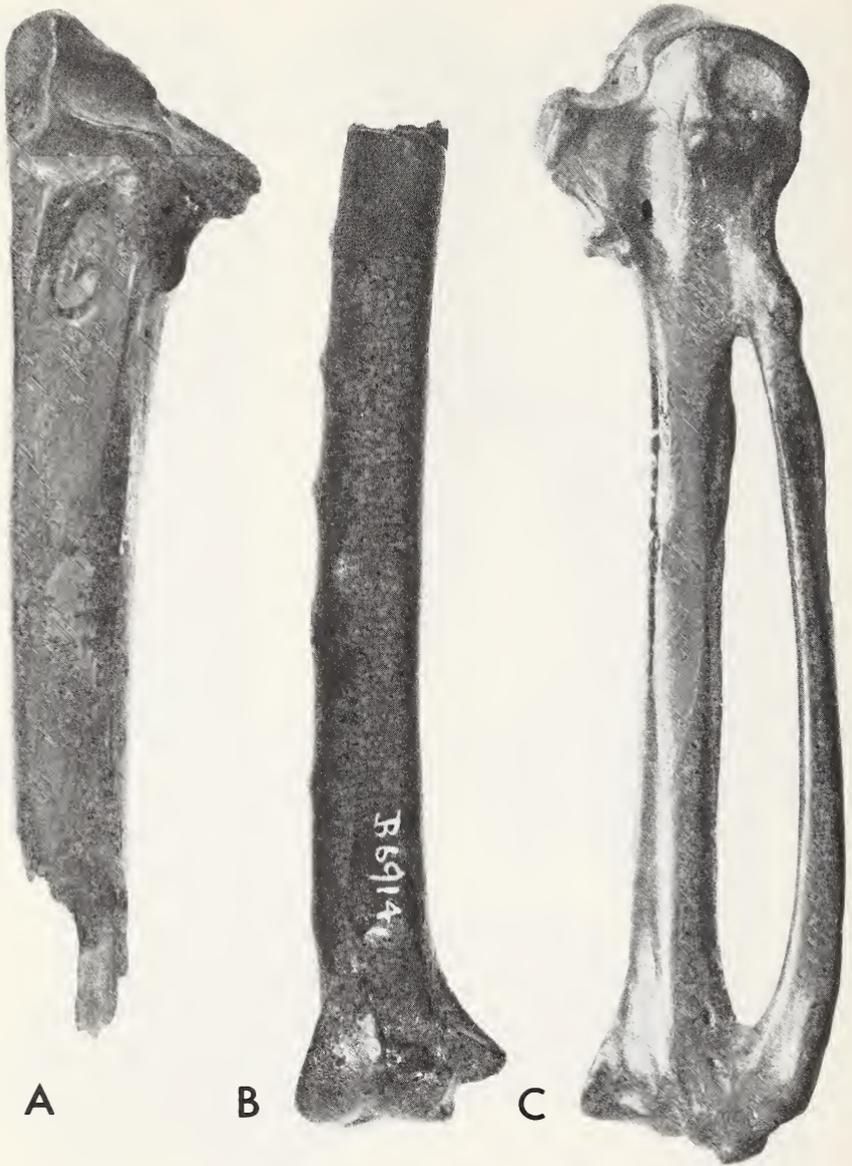


FIGURE 4. *Breagyps clarki*. A. proximal end of left ulna, B8310, internal view; B. distal end of left ulna, B6914, internal view; C. right carpometacarpus, J9402, internal view (previously figured (Miller, 1925) as *Cathartornis gracilis* and later (Miller and Howard, 1938) assigned to *B. clarki*).

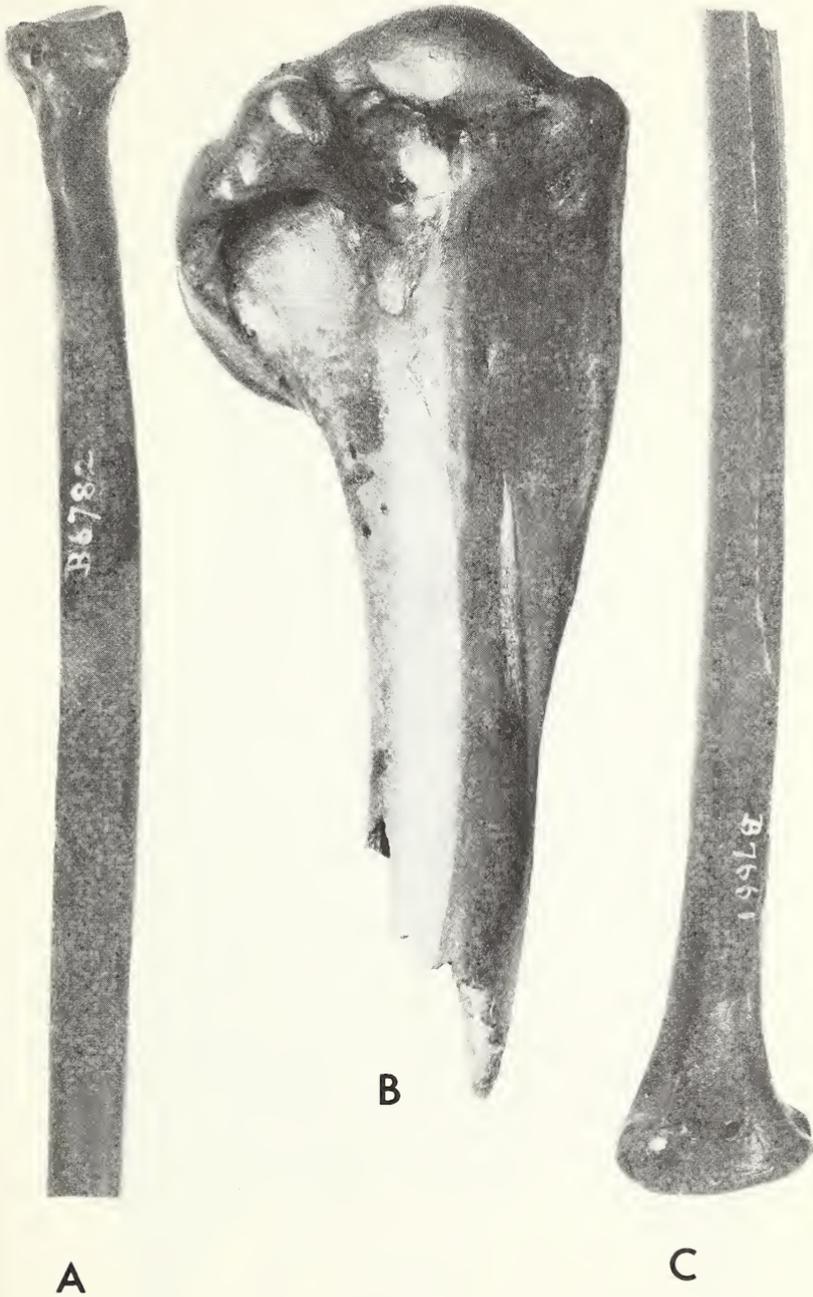


FIGURE 5. *Breagyps clarki*. A. proximal end of right radius, B6782, external view; B. proximal end of right humerus, B5329, anconal view; C. distal end of right radius, B7661, palmar view. X 1.



FIGURE 6. *Breagyps clarki*, pelvis, B1082+B1092, dorsal view. Approx. X 1.



FIGURE 7. *Breagyps clarki*, pelvis, B1082+B1092, lateral view. Approx. X 1.



FIGURE 8. *Breagyps clarki*, left femur, B5580. A. anterior view; B. external view. X 1.

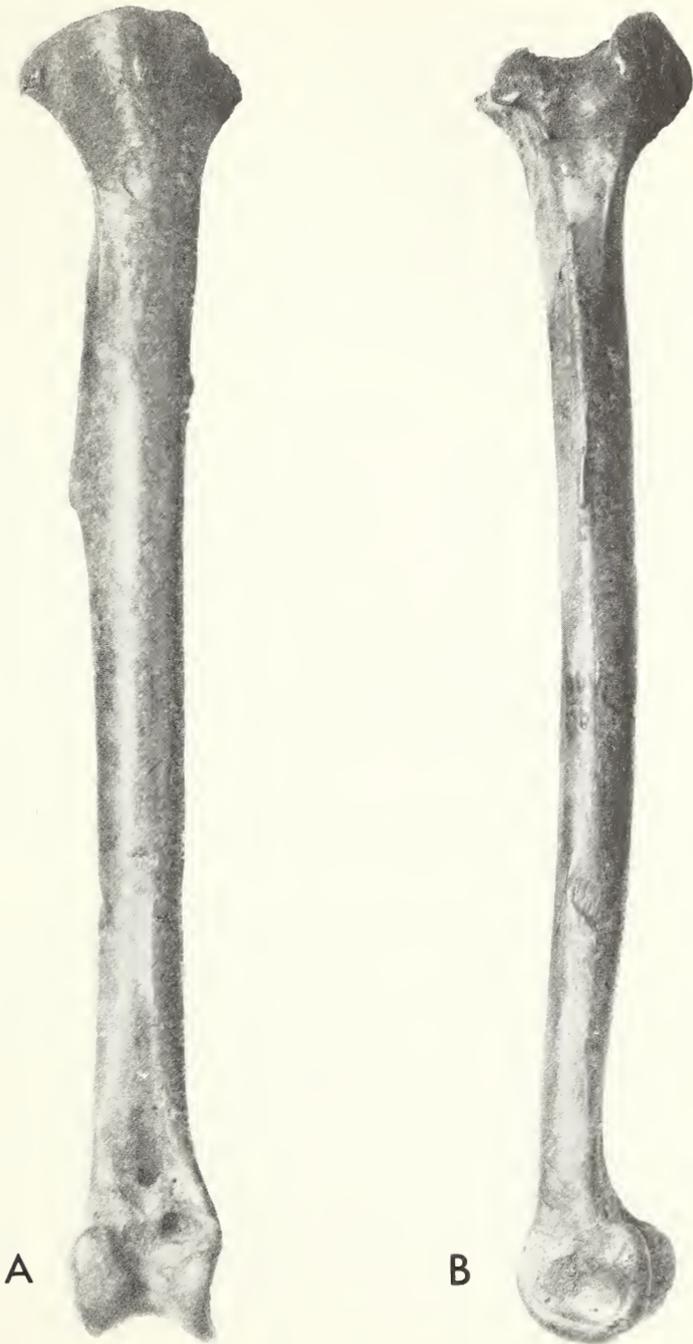


FIGURE 9. *Breagyps clarki*, right tibiotarsus, B5878. A. anterior view; B. external view. Approx.  $\times \frac{3}{4}$ .

zygapophyses are parallel in position and the posterior articulation of the centrum faces more posteriorly than dorsally. Also, as in the axis, the neural spine is broad and stubby. These characters distinguish the *Breagyps* vertebra from the cervicals of either modern condor genus.

The other two vertebrae resemble cervical number 6 of *Gymnogyps* in the deep V-shaped posterior contour which separates the postzygapophyses, but they differ from this element in *Gymnogyps* in that the facets of the prezygapophyses face more anteriorly. In this respect they more closely resemble cervical number 5 of *Vultur*, though the posterior contour in this latter is less acutely V-shaped. The neural spine on the fossil specimens is more nearly centered (in antero-posterior direction) than in the specimens of either of the other condors. In these latter, the spine is more anteriorly placed.

#### DISCUSSION

As previously noted, *Breagyps* shares some separate characters with other cathartid genera but may be clearly differentiated by the combinations of its characteristics. The foregoing section has demonstrated these points with respect to comparison with *Vultur* and *Gymnogyps*. There appear to be more areas of similarity with the former. In summary, the most notable points of resemblance to *Vultur* are found in the general shape of the sternum, humerus, radius and femur and in the details of the cnemial crests of the tibiotarsus. But even in these elements, detailed differences exist. The most notable distinctions, however, are found in the furcula, scapula, ulna and carpometacarpus.

Although marked differences from *Gymnogyps* occur in all elements, resemblance is noted in a few detailed characters: triangular depression on ventral labial prominences of sternum, deep pneumatic fossa undercutting dorsal rim of furcula, rounded dorsal contour of acromion of scapula, degree of pneumaticity of distal end of humerus, curvature of femoral shaft and projecting posterior iliac crests of pelvis.

Areas of resemblance to the smaller vultures are given below.

The sternum of *Coragyps* resembles that of *Breagyps* in the broad, straight anterior contour and the shape of the carina. In *Coragyps*, however, the point at which the carina ascends is more posterior, the dorsal area of the shield less depressed, the ventral labial prominences lack the triangular depression, and the ventral manubrial spine is more prominent. The coracoid of *Coragyps* resembles that of *Breagyps* in the protruding brachial tuberosity and angular border of the fossa beneath, but the furcular facet is narrower, the ligamental attachment on the external side of the head less prominent and the neck less depressed. In the pelvis, *Coragyps* resembles *Breagyps* in the depth of the ilioischiatric area, the prominence of the posterior iliac crests and the condition of the synsacral caudal area. The shield, however, is set lower with respect to the ilia and is flatter and more perforated; also there are only two synsacral thoracic vertebrae.

The ulnae of both *Coragyps* and *Sarcoramphus* have the area between the

brachial impression and the internal cotyla swollen as in *Breagyps*, but the area is much more pneumatic in *Coragyps*, and, in *Sarcoramphus*, the brachial impression is more deeply depressed adjacent to the heavy, abruptly flared anconal border. Furthermore, in both *Coragyps* and *Sarcoramphus*, the internal contour of the proximal end from olecranon to cotyla is more nearly straight, the olecranon less clearly defined than in *Breagyps*. Also, these smaller vultures have fewer anconal papillae for the secondaries and, distally, both have a longer, narrower external condyle.

In *Sarcoramphus* the bicipital crest of the humerus is rounded as in *Breagyps* and the distal tip of the pectoral attachment is laterally placed. Other characters of the humerus described for *Breagyps* are, however, different in *Sarcoramphus*. The femur of *Sarcoramphus* resembles that of *Breagyps* in the mediad deflection of the trochanteric crest and in the anterior contour of the internal condyle, but is otherwise distinct.

Even *Cathartes*, which is least like *Breagyps* throughout the skeleton, shares one character of the humerus not found in any of the other genera, namely the bordering rim and mediad depression of the deltoid crest. The contour of the crest, however, is more flared and angular.

Distinctive detailed characters of *Breagyps*, not found in any of the other genera, are:

**Sternum:** Dorsal area of shield more deeply depressed back of heavy anterior swelling; apex of carina at level of last costal process.

**Furcula:** Deep pneumatic fossa undercutting dorsal rim of clavicle but ending above its ventral border; abrupt expansion back of pointed scapular tip with foramen above.

**Scapula:** Short, abruptly flared acromion with marked mediad deflection dorsally.

**Coracoid:** Uneven contour of head with marked diagonal groove through furcular facet.

**Ulna:** Short, heavy external condyle.

**Radius:** Abruptly flared distal end.

**Carpometacarpus:** High, more upturned process of metacarpal 1; marked depression of proximal symphysis and short, prominent tuberosity of metacarpal 2.

**Femur:** Large ligamental attachment above fibular condyle facing proximally, and deep, narrow attachment of round ligament.

**Tibiotarsus:** Blunt external condyle projecting laterally.

With respect to size, *Breagyps clarki* averages generally larger than *Gymnogyps californianus* and is notably broader and deeper chested. Greater wing length is gained through the distal segments; the four complete fossil humeri are all shorter than the four available of *G. californianus*. Although ulnar length can only be estimated for *Breagyps clarki*, the very smallest estimate exceeds the maximum for *G. californianus* by 18 mm. The carpo-

metacarpri average 5 mm greater than the larger of the two available *G. californianus* specimens.

The larger of the two comparative skeletons of *Vultur gryphus* exceeds *Breagyps clarki* in nearly all measurements. The smaller skeleton, however, falls within the range of the fossil bones in many areas. In general, compared to this minimum *Vultur* specimen, the fossil species averages slightly narrower, though deeper through the chest, the wings slightly longer and differently proportioned, the legs shorter in all elements though proportionately longer in the femora. (See tables).

#### ACKNOWLEDGMENTS

The loan of two skeletons of *Vultur gryphus* by the Department of Zoology, University of California at Los Angeles, is gratefully acknowledged. All other material, Recent and fossil is contained in the collections of the Natural History Museum of Los Angeles County. My continuing thanks are extended to that Museum, and particularly to the Section of Vertebrate Paleontology, for providing the facilities for my research.

The photographs were made at the Museum by the late H. Wm. Menke (figures 1; 2A,B,C; 3; 4C; 5B; 8; 9) and by Lawrence Reynolds (figures 2D; 4A,B; 5A,C; 6; 7).

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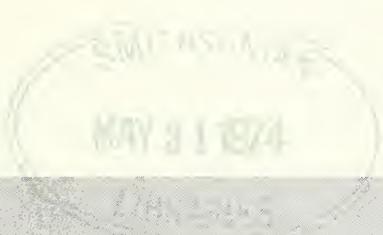


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REDUCTION AND LOSS OF THE  
PELVIC GIRDLE IN *GASTEROSTEUS* (PISCES):  
A CASE OF PARALLEL EVOLUTION

By MICHAEL A. BELL



CONTRIBUTIONS IN SCIENCE



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REDUCTION AND LOSS OF THE PELVIC GIRDLE IN  
*GASTEROSTEUS* (PISCES): A CASE OF PARALLEL EVOLUTION<sup>1</sup>

By MICHAEL A. BELL<sup>2</sup>

**ABSTRACT:** The structure of the pelvic girdle of *Gasterosteus* from a Recent population in Paxton Lake, Texada Island, British Columbia and a fossil assemblage from the Pliocene Truckee Formation, Hazen, Nevada is described. Ecological conditions inferred from the geology and paleontology of the Truckee Formation are consistent with the ecological requirements of living *Gasterosteus*. Based on paleoclimatological, ichthyofaunal and independent paleontological evidence, the fossil sticklebacks probably entered Nevada through the Death Valley region.

The structure of the pelvic girdle varied similarly in both samples from normally developed to entirely absent, with intermediate structures. In the fossil sample, specimens with normally developed pelvic girdles tended to be stratigraphically segregated from those with reduced pelvic structures. In both samples, specimens with developed pelvic girdles have more dorsal spines than those with reduced pelvic structures. The fossils lack lateral plates, but Recent specimens have 0 to 7, and specimens with developed pelvic girdles tend to have more than those with reduced structures. Other correlations with pelvic structure were found.

While there is a suite of correlated characters common to both samples, details of their variation differ. Differences between the two samples include the shape of pelvic vestiges, the arrangement of dorsal spines on predorsal radials, presence of lateral plates, the number of dorsal spines and the range of some other meristic characters. Based primarily on zoogeographic considerations, the two samples are believed to represent independent phyletic lines. Morphological similarity is due to parallelism and not convergence.

Variation in pelvic structure and other characters correlated with pelvic structure do not indicate that either the Recent or fossil sample is composed of more than one species. *Gasterosteus apodus* Mural (1973) is regarded as a junior synonym of *Gasterosteus doryssus* (Jordan, 1907). *Gasterosteus doryssus* should be maintained until the status of living populations of *Gasterosteus* with reduced pelvic structures can be evaluated according to the biological species concept.

Reduction of the pelvic girdle and dorsal spines similar to that reported for *Gasterosteus* in this study have been reported previously for two other gasterosteid genera, *Pungitius* and

<sup>1</sup>REVIEW COMMITTEE FOR THIS CONTRIBUTION

Theodore Cavender  
Robert J. Lavenberg  
Joseph S. Nelson

<sup>2</sup>Museum Associate in Ichthyology and Vertebrate Paleontology, Natural History Museum of Los Angeles; and Department of Biology, University of California, Los Angeles, California 90024

*Culaea*. There has been parallelism within and between these three genera. Although evidence concerning the selective mechanism is not presented in this paper, considerable evidence exists that predator selection of those structures reduced in these genera is very important.

Selection is probably responsible for the production of parallel phenotypes in widely dispersed samples of *Gasterosteus* and is probably the most important factor in its geographic variation. This phenomenon is very common among all organisms. Similar parallelisms within three gasterosteid genera lend support to Vavilov's theory of homologous series in variation. Ubiquitous parallelism poses a serious problem for systematists and zoogeographers working at the species level.

#### INTRODUCTION

Parallelism is a common feature among many groups of organisms. This phenomenon is generally believed to be a consequence of adaptation to similar environments. Within the sticklebacks (*Gasterosteidae*) parallelism is probably responsible for an unusual distribution pattern of phenotypes of species in at least three genera. *Gasterosteus*, *Pungitius*, and *Culaea* populations are occasionally found which tend to lose or reduce the normally strong pelvic girdle. Variable presence or absence of the pelvic girdle in sticklebacks was first reported by Day (1878) who described it in the ninespine stickleback, *Pungitius pungitius* (Linnaeus), from Ireland. Nelson (1971a) has since described populations of *P. pungitius* from Ireland and Canada, and Coad (1973) reported additional populations from Canada, in which the pelvic girdle may be normally developed, reduced to a vestigial plate or absent. Such variation was also reported by Nelson (1969) and Nelson and Atton (1971) in Canadian populations of the brook stickleback, *Culaea inconstans* (Kirtland). Penczak (1965) described pelvic girdles of White Sea *Gasterosteus aculeatus* Linnaeus in which the ascending branch of the pelvic girdle is short. *Gasterosteus* populations in which the pelvic girdle may be reduced or absent have been mentioned (Hagen and McPhail, 1970; Nelson, 1971a, 1971b; Nelson and Atton, 1971) and Moodie and Reimchen (1973) have discussed such a population from the Queen Charlotte Islands, British Columbia. However, pelvic variation in populations of *Gasterosteus* in which the pelvic girdle tends to be reduced has not been described in detail.

The fossil stickleback, *Gasterosteus doryssus* was originally described as *Merriamella doryssa* by Jordan (1907) who considered it to be an atherinid (silversides). He was misled by the absence of the characteristic *Gasterosteus* pelvic girdle and spine from his specimens. One month later, Hay (1907) described other fossils of the same species as *Gasterosteus williamsoni leptosomus* based on specimens from the same locality as Jordan's type. One of Hay's specimens had a normal pelvic girdle but in the others, it was incompletely developed. Although Hay described the variation in pelvic structure in his small sample, he did not comment on its significance. Jordan (1908)

made no mention of the pelvic girdle and he attributed differences between his material and Hay's to incomplete preservation. Mural (1973) interpreted these differences in pelvic structure to indicate the presence of two species, *G. doryssus* with normal pelvic structure and a new species, *Gasterosteus apodus*, with vestigial or no pelvic structures.

I have examined the pelvic girdles in a large series of fossils of the nominal species *G. doryssus* and *G. apoda* and found that differences in the pelvic structure between Jordan's and Hay's specimens represent morphological variation and not the state of preservation of the fossils. I have also examined a sample from a population of similar sticklebacks from Paxton Lake, Texada Island, British Columbia. The purpose of this study is to describe variation in the structure of the pelvic girdle in these samples and the relationship of pelvic structure to other morphological features.

#### MATERIALS AND METHODS

Fossil *Gasterosteus doryssus* in the collections of the following institutions have been examined: Natural History Museum of Los Angeles County, Section of Vertebrate Paleontology (LACM); California Academy of Sciences, Department of Geology (CAS); and University of California, Berkeley, Museum of Paleontology (UCMP). Several unnumbered specimens were received from C. A. Repenning of the U. S. Geological Survey, Menlo Park, California.

Specimens of *G. doryssus* come from near Hazen, Lyon County, Nevada. LACM Material is from LACM vertebrate paleontology locality LAV 6663 (=UCMPV 66146). This locality is in secs. 9 and 10, T. 19 N, R. 25 E (approximately N 39°32', W 119°10'), Two Tips Quadrangle, Nevada. The CAS specimens are also from this locality. The locality is a commercial diatomite quarry situated on the northeast slope of the Virginia Range and is reached by dirt road beginning at the east end of the Fernley Farm District Road and winding southward. The matrix at this locality and others in the Middle Truckee Formation is a very pure, finely laminated diatomite with occasional laminae of sand and tuff. The dip of the beds seems generally to conform to the surface topography. The UCMP specimens come from localities UCMPV 1034, 5613, and 6998. Repenning's specimens were collected in sec. 17, T. 19 N, R. 26 E, at a distance of about 8 km from LAV 6663.

Fossil specimens examined were LACM 17439 to 17475, 17924 to 17945, and 28090 to 28126; CAS 50033 to 50054 from locality LAV 6663 UCMP 9372 (type of *Merriamella doryssa*), 9374 and 9375 from locality UCMPV 1034; UCMP 58565 from locality UCMPV 5613; and Repenning's unnumbered specimens. All of these specimens are skeletons preserved on slabs of laminated diatomite of the Middle Member of the Truckee Formation. UCMP 99674 from locality UCMPV 6998 (Brady Pocket, MacDonald, 1956) consists of isolated elements from the Lower Member of the Truckee Formation.

The fossil fish were found by splitting the laminated diatomite along the bedding planes with a knife. This procedure usually split the fish skeletons and sometimes individual bones down their centers so that portions of the skeleton were represented on both slabs resulting from the cleavage of the rock. Thus, preparation to improve the quality of the specimens was impractical. Specimens discovered by this method were collected or discarded depending on their state of preservation and the abundance of their morphological type among previously collected specimens. Specimens with well developed pelvic structures or more than one dorsal spine were usually retained regardless of condition, but specimens with vestigial pelvic girdles or fewer than 2 dorsal spines may have been discarded. Thus, the frequency of pelvic structures or individuals with different numbers of dorsal spines is not considered *per se* without taking this bias into account. Specimens LACM 28090 to 28126 form a series of specimens in which all fossils were retained. With the exception of this collection, the fossils studied in this report do not represent a random sample of those fossils available in the deposit. Some specimens were partially or entirely covered with matrix after splitting and were prepared further by removing the matrix with needles. The fish fossils were sprayed with acrylic aerosol following preparation to harden their surfaces.

Specimens of Recent *Gasterosteus* from a population in which the pelvic girdle may be normal or reduced were supplied by J. D. McPhail and D. Hay of the Institute of Animal Resource Ecology, University of British Columbia. This collection is from Paxton Lake, Texada Island, British Columbia. The lake is occupied by two populations of *Gasterosteus*, one benthic and the other pelagic. The sample I studied is the benthic form (D. Hay, pers. comm.). Texada Island was subjected to postglacial marine submergence, so the habitat is probably less than 5,000 years old (J. D. McPhail, pers. comm.). The sample I received has been deposited in the Ichthyology collection of the LACM and catalogued LACM 32008-1 (202 specimens).

Recent specimens of *Gasterosteus aculeatus* from southern and central California were examined to determine the frequency of individuals with different number of dorsal spines. The following specimens from the Ichthyology collection of the LACM were examined (number in parentheses are the number of specimens examined): LACM 30899-1 (316), Alamo Creek, Santa Barbara County; 30922-1 (310), Twitchell Reservoir, San Luis Obispo County; 30943-1 (60), Santa Clara River, Los Angeles County; 30946-1 (341), Ventura River, Ventura County; 31420-1 (103), Los Berros Creek, San Luis Obispo County; 31421-2 (79), Arroyo Grande Creek, San Luis Obispo County; 31422-1 (177), San Antonio Creek, Santa Barbara County; 31423-1 (350), Santa Ynez River, Santa Barbara County; 31424-2 (305), Salsipuedes Creek, San Luis Obispo County; and W71-10 (148), Big Pico Creek, San Luis Obispo County.

All specimens in LACM 32008-1 were stained with alizarin to allow inspection of bony elements near the body surface. Sixty-seven specimens

were selected for pelvic structure and cleared and stained using the Taylor (1967) technique.

Standard measurements (outlined below) were made on the cleared and stained specimens in LACM 32008-1 and 115 fossil specimens LACM 17439 to 17475, 17924 to 17945, 28090 to 28126, and CAS 50033 to 50054. The pelvic condition and number of lateral plates and dorsal spines were determined in all specimens in LACM 32008-1.

The standard measurements were devised to compare the fossil assemblage with the Recent population, to determine whether correlations between pelvic structure and other structures exist, and to measure as many structures as possible which could be seen on most of the fossils. The measurements were made following the procedures of Hubbs and Lagler (1964) except as noted below:

1. Standard length (SL).
2. Total number of vertebrae.
3. Predorsal radials; the number of proximal radials (but possibly including predorsal bones of Smith and Bailey, 1961) anterior to and including the radial normally bearing the last dorsal spine in *Gasterosteus aculeatus* (see Lindsey, 1962, Fig. 1).
4. Number of dorsal spines.
5. Number of dorsal fin rays; the last two rays were counted separately.
6. Number of anal fin rays; the last two rays were counted separately.
7. Number of lateral plates; all plates were counted on both sides regardless of plate size. All specimens counted were greater than 25 mm SL, the length at which all plates have appeared (Hagen and McPhail, 1970).
8. Length of dorsal spines; measured from the top of the proximal radial to the tip of the spine with an ocular micrometer.
9. Pelvic girdle structure; classified as developed, vestigial or absent.
10. Predorsal radial and spine arrangement; the notation of Penczak (1960) in which the radial or predorsal element is represented by a Roman numeral and the position of the dorsal spines by Arabic numeral superscripts on the appropriate Roman numeral was used.

The data obtained from the standard measurements were grouped according to pelvic morph and the grouped data were plotted in histograms (Fig. 5) or their means were calculated (Table 1). The distributions shown in Fig. 5 were examined using the Kolmogorov-Smirnov Test (Tate and Clelland, 1959) to determine if there were statistically significant differences at the 0.05 confidence level in the distribution of character states between pelvic classes. The distribution of ranked dorsal spine lengths were also examined in this manner.

Skeletal elements were drawn using a camera lucida attachment on a

dissecting microscope. Figures were photographed by L. S. Reynolds, staff photographer of the LACM.

#### STRATIGRAPHY

The Truckee Formation was originally described by King (1878). The original description contained misleading and incorrect information according to Axelrod (1956) who redescribed the type section. Axelrod recognized three members in the formation totaling about 760 m (2500 ft), but Ruben (1971) indicated that the Truckee Formation is 1021 m (3350 ft) thick. The Lower Member of the Truckee Formation is composed of basalt tuff overlain by sedimentary breccia primarily composed of reworked basalt tuff. This is overlain by limestone rich in mollusks, followed by blue-grey sandstone, thin diatomite and basalt tuff. This member of the formation totals 43 to 49 m (140 to 160 ft) thick. The middle member is primarily nearly pure diatomite generally occurring in beds up to 0.3 m thick but much thicker in the quarries. Pumice beds scattered throughout the section range from a few centimeters to about a meter thick and there are local 8 to 10 cm thick blue-grey sandstones. The Middle Member of the formation is about 460 m (1500 ft) thick. The upper member is characteristically slabby grey limestone ranging from a few centimeters to 9 m (30 ft) thick. The limestones are regularly interbedded with grey sandstones, paper-thin lenses of diatomite, and black and red basalt pebble conglomerates. This member is at least 260 m (850 ft) thick, but Axelrod did not see the top of the formation.

Axelrod (1956) mapped the Truckee Formation in the area northeast of Brady's Hot Springs, Churchill County, about 35 km (23 miles) northeast of locality LAV 6663 near Hazen. His map shows outcrops of the middle member of the formation scattered over an area of about 16 sq. km. Middle Truckee rocks abruptly disappear due to faulting to the southeast and they are overlain by younger sediments and alluvium to the west, north and east. The beds generally dip to the northwest at 12 to 35° except at the southern extremity of the outcrops where they dip to the southeast at the edge of a fault. The area of deposition of Middle Truckee sediments in the Brady Hot Springs region must have been greater than that exposed, but the area of the lake in which deposition took place was not necessarily as large at any time as the basin in which the Truckee Formation was deposited. The lake may have occupied and deposited sediments in different portions of the basin at different times. Ruben (1971) has suggested that the Truckee Basin contained several interconnected lakes in the Pliocene. Confusion of the names applied to Tertiary formations in west-central Nevada makes difficult more precise statement of the aerial extent of Middle Truckee rocks or the size of the lake inhabited by *Gasterosteus*.

#### AGE OF FOSSIL DEPOSITS

With the exception of UCMPV 6998, which is in the Lower Member of the formation, all localities for fossil *Gasterosteus* are in the Middle Member

of the Truckee Formation as defined by Axelrod (1956). Ruben (1971) reviewed the age of the Truckee Formation indicating that it extends from Early to Middle Pliocene, basing his interpretation on correlations of Stirton (1939). The presence of numerous fossil fish (Stirton, 1939) indicates that Stirton's fossils were from the Middle Member of the Truckee Formation. Buwalda (1914) had reported a proboscidean tooth from the Truckee Formation considered to indicate an age no greater than Middle Miocene. MacDonald (1950 and 1956) reported fossil mammals from the Lower Member of the Truckee Formation that indicate an Early Pliocene age.

Age determinations of specimens of *G. doryssus* have been rather confused. Following Merriam's advice, Jordan (1907) stated that his material was probably Miocene. Hay (1907) mistakenly believed that the sticklebacks he studied came from the Pleistocene Lahontan Beds. This error was perpetuated, notably by Jordan (1908) and Hubbs and Miller (1948), until it was corrected by La Rivers (1953) who recognized that the fossil sticklebacks came from the Pliocene Truckee Formation. Axelrod's (1948 and pers. comm.) "Hazen flora" which is Middle Pliocene, came from the type locality of *G. doryssus* (UCMPV 1034). On the basis of information supplied by Axelrod, Miller (1955) concluded that specimens of *Fundulus nevadensis* (Eastman, 1917) which occur with *G. doryssus* were of Early Pliocene age. Uyeno and Miller (1963) accepted this conclusion. Axelrod (pers. comm.) has also tentatively suggested an age of Early Pliocene for locality LAV 6663 based on a few plant remains which I sent to him.

Yen (1950) believed that mollusks from the type section of the Lower Member of the Truckee Formation represent a Pliocene assemblage even though a Miocene species is present. (Yen did not give the stratigraphic position within the Truckee Formation of his collections, but Axelrod (1956) stated that they came from the lower member of the formation.) On the basis of a characteristic Miocene diatom (*Melosira granulata*) identified by G. D. Hanna, M. Ghiorso (pers. comm.) considers locality LAV 6663 to be Late Miocene.

Correlations to determine the age of assemblages of *G. doryssus* based on mammalian, higher plant, diatom, and mollusk fossils tend to produce conflicting results. This inconsistency may be due to the deposition of *G. doryssus* and the Middle Member of the Truckee Formation over a long period of time. Perhaps the earliest record of *G. doryssus* is from the Late Miocene. It persisted through the Early Pliocene to the Middle Pliocene at which time it was deposited with the Hazen flora. Based on Axelrod's (1948, 1957, 1958) estimates that the deposits are Clarendonian to Hemphillian and the conclusions of Everden, et al. (1964), the deposits in which *G. doryssus* occurs are probably at least 10 million years old.

#### PALEOECOLOGY

Axelrod (pers. comm.) has inferred from fossil plants at locality LAV

6663 and his Hazen flora (Axelrod, 1948) some of the climatic conditions in which *G. doryssus* lived. There was an equable climate with warm but rarely hot summers and mild winters. There may have been occasional light frosts. Average yearly rainfall was at least 38 to 44 cm (15 to 18 inches) but may have been greater. Summer rainfall is also indicated.

Yen (1950) made paleoecological inferences based on mollusk assemblages which came from the Lower Member of the Truckee Formation. He believed that the diversity of the assemblages which came from the Lower Member of the Truckee Formation indicates deposition in a large body of water. The considerable distance between localities for *G. doryssus* (about 8 km) and between the type section of the Truckee Formation and fossil localities also tends to support this view. There were muddy and stony shores. Variation in size, sculpture, and height of the shells possibly indicates a variety of water velocities and pH. Abundant rissoid and planorboid snails indicate a habitat rich in aquatic filamentous algae and leafy plants. Fresh-water limpets, which feed on algae and diatoms and prefer rocky bottoms with still water, are also present.

It is, of course, difficult to evaluate the relevance of Yen's inference to the paleoecology of the middle member of the formation. By Middle Truckee times, water condition may have changed and much sedimentation had occurred. Ruben (1971) discussed Middle Truckee paleoecology. He believed that the diatomites were deposited in quiet water near shore. The lake water was slightly saline and part of a larger basin and range system. Ruben suggested that the presence of encysted diatoms indicates extreme seasonal dry conditions, but this suggestion is inconsistent with Axelrod's inferences on climatic conditions and encystment could have resulted from other adverse conditions.

Living *G. aculeatus* inhabit very diverse habitats. This species is found in waters of varying salinity, temperature, color, depth and velocity, over substrates of varying particle size and vegetation type. None of the inferences on the paleoecology of the Middle Member of the Truckee Formation is inconsistent with these broad ecological tolerances. It is interesting that the only fish genera known from the Truckee Formation, *Gasterosteus* and *Fundulus*, have distributions centered in coastal marine and brackish water and low gradient coastal streams. Seasonal drying resulting in elevated salinity suggested by Ruben (1971), may account for the presence of only these two euryhaline fishes.

There is evidence that *G. doryssus* was subject to predation. One snake reported to be a *Coluber* has been described with *G. doryssus* as stomach contents (Ruben, 1971). Coprolites produced by animals apparently large enough to eat *Gasterosteus* are common in Middle Truckee beds, although they contain no stickleback bones. Bell (1973a) has reported coprolites from the Pleistocene Bautista Formation containing recognizable stickleback spines. Their absence from coprolites in the Truckee Formation may indicate that

sticklebacks were not the prey. A cormorant in the LACM vertebrate paleontology collection (H. Howard, pers. comm.) has been collected from Middle Truckee rocks and cormorants feed exclusively on fishes. However, there is no evidence that the fossil specimen preyed on sticklebacks. No piscivorous fishes (Uyeno and Miller, 1963) or other potential predators on *G. doryssus* have been reported from the Truckee Formation. Hagen and Gilbertson (1972) found that *Gasterosteus* that are preyed upon by other species of fishes tend to have longer fin spines and a modal number of seven lateral plates. Thus, one would not expect from the morphology of *G. doryssus* (plate-less, pelvic-less, and reduced dorsal spines) that it was preyed upon by other species of fishes.

#### ZOOGEOGRAPHY OF FOSSIL GASTEROSTEUS

Neither the phylogenetic relationships nor the geographic origins of the Gasterosteidae are well understood. Sticklebacks do not appear in the fossil record until the Early Pliocene or possibly very late in the Miocene. Only the modern genera *Gasterosteus* (Bell, 1973a) and *Pungitius* (Schtylco, 1934; Berg, 1965) are known as fossils. *Pungitius haynesi* David (1945) is a *Gasterosteus* (Bell, 1973b). The five gasterosteid genera are very distinct and their interrelationships are poorly understood (Nelson, 1971b). Although the family is composed of widespread amphiboreal species, its distribution seems to be centered in the North Atlantic. According to Durham (1950) and Axelrod and Bailey (1969), there has been progressive cooling throughout the Tertiary with only minor fluctuations. Wolfe (1971) has suggested more dramatic Tertiary climatic fluctuations, but these were not of sufficient magnitude to allow *Gasterosteus* to enter the Pacific Ocean by dispersing along the southern coast of North America. Regardless of where *Gasterosteus* arose, it must have entered the Pacific ocean from the north through the Bering Straits area.

Modern *Gasterosteus* are peripheral freshwater fish (Darlington, 1957). Such fishes belong to groups restricted to freshwater adjacent to the sea or so recently derived from marine ancestors that their present distribution is the result of dispersal through the sea. The distribution and physiology of living *Gasterosteus aculeatus* conforms to this definition (Münzing, 1963). Thus, there have been two potential routes for southward movement of the ancestors of *G. doryssus*: along the coast in marine water as trachurus populations or over land in fresh water as leiurus populations. The names trachurus and leiurus have been applied to modal anadromous and freshwater *Gasterosteus* phenotypes respectively. The taxonomic status of these names is presently a point of contention (Hagen and McPhail, 1970; Miller and Hubbs, 1969).

Based on the present range of the completely plated, anadromous form of *G. aculeatus* (Miller and Hubbs, 1969), the trachurus type, breeding populations seem to be restricted in California to waters where the mean

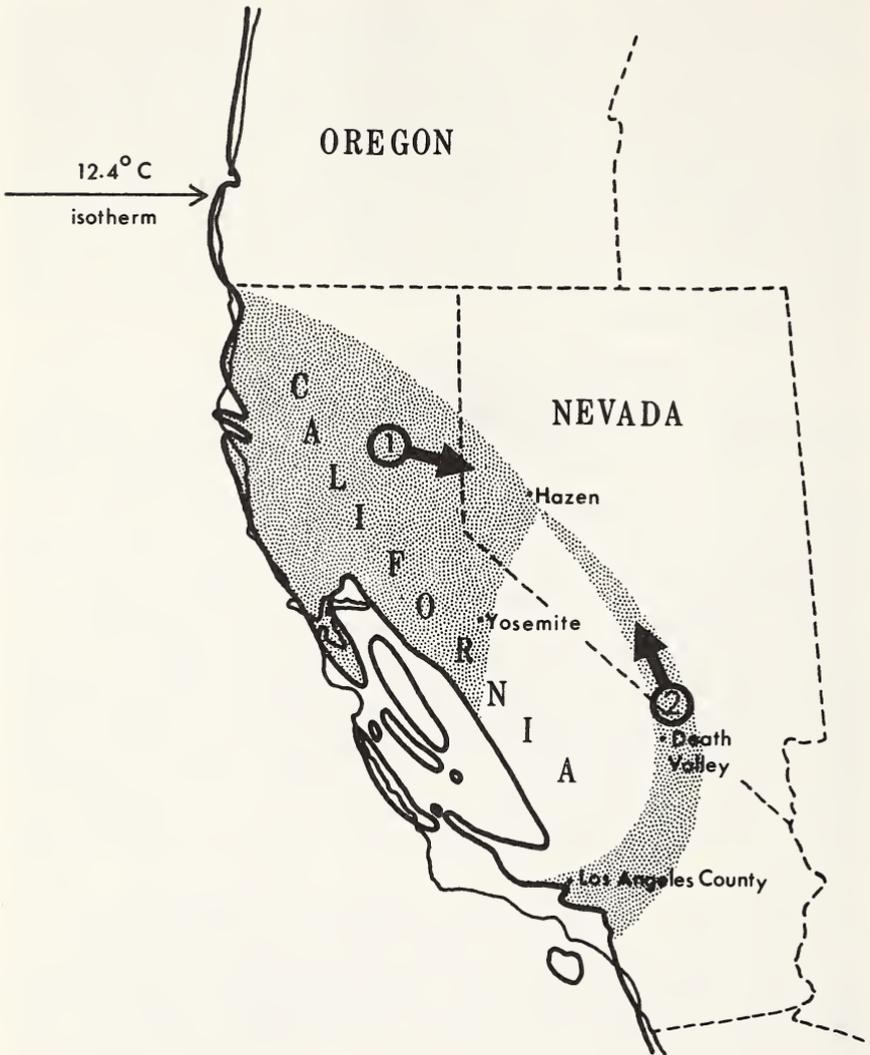


FIGURE 1. Map of the possible invasion routes (stippled), 1, the northern and 2, the southern, by which the ancestors of *Gasterosteus doryssus* could have entered Nevada. The heavy line represents the shore line in the Late Miocene and the light line the present coast. The latitude in the Miocene of the minimum water temperature inhabited by extant marine (trachurus) breeding populations of *Gasterosteus aculeatus* in California is indicated by the horizontal arrow.

February surface temperature exceeds 12.4°C. This isotherm would have intersected the shoreline at about 43°N (Fig. 1) in the Late Miocene according to Durham's (1950) Fig. 3. However, even short term temperature declines would have allowed *Gasterosteus* to move a great distance southward along the coast. Hubbs (1948) reported northward range extensions of tropical fishes of hundreds of miles in the 1850's. The presence of the salmonid, *Smilodonichthys rastrosus* Cavender and Miller (1972) in the Early Pliocene, marine Capistrano Formation in Orange County, California (L. Barnes, pers. comm.) indicates that marine waters had cooled sufficiently to allow cold water fish species to move into southern California. Thus, it is not surprising that *Gasterosteus* has been reported from the Pliocene Ridge Formation in Los Angeles County (David, 1945; Bell, 1973b). *Gasterosteus* had reached at least as far south as Los Angeles County by the Pliocene and could have entered fresh water anywhere north of this point to reach the site of deposition at Hazen, Nevada (about 39°N). The establishment of partially plated, freshwater or leiurus type populations from trachurus populations could have easily taken place because leiurus populations have been established repeatedly from marine stocks (Hagen, 1967; McPhail and Lindsey, 1970; Münzing, 1959, 1963).

The terrain across which the freshwater ancestors of *G. doryssus* dispersed was very different from that of western North America today. At the end of the Miocene, the present position of the Sierra Nevada was occupied by a broad ridge with the summit at about 900 m (about 3000 feet) elevation, gradually increasing to about 1500 m (about 5000 feet) in the south and decreasing to about 300 m (about 1000 feet) to the north (Axelrod, 1957 and 1962a). Three to 6 km (about 2 to 4 miles) wide valleys crossed the Sierran ridge north of Yosemite (Axelrod, pers. comm.) at elevations of 600 to 750 m (about 2000 to 2500 feet) (Axelrod, 1957). These valleys contained rivers with their headwaters in western Nevada at an average elevation of about 600 to 750 m (Axelrod, 1957 and 1962b). Axelrod (1958) noted that the Truckee Formation includes sediments carried eastward from the region of the Sierra, but this fact does not preclude drainage of the basin to the Pacific Coast. The rivers north of Yosemite are one possible route (route 1, Fig. 1) by which *Gasterosteus* may have invaded Nevada.

There is considerable zoogeographical and paleontological evidence for a more southerly route (route 2, Fig. 1) of invasion. Miller (1958) reviewed the similarities of the fish faunas of the Lahontan Basin (within which the Truckee Formation is located) to other basins and found similarities to the Death Valley, Klamath, Columbia, and Bonneville River systems. Miller (1958) believed that the connection between the Lahontan Basin and the latter three river systems existed no earlier than the Middle Pliocene. He suggested that fossil sticklebacks reached the Lahontan Basin through the Death Valley region in Late Miocene or Early Pliocene times. Hubbs and Miller (1948) pointed out that most of the 8 fish species endemic to the Lahontan

Basin are lowland forms not capable of crossing an elevated divide. This would necessitate access to the Lahontan Basin through the area south of the Sierran ridge. Miller (1946) gave evidence which supports this view. *Siphatales* is known as either a Recent or fossil occupant of both the Death Valley and Lahontan Basins. The presence of *Empetrichthys* in Pahrump Valley also supports his view. The Owens River stock of *Catostomus* is most closely related to and probably derived from *C. tahoensis* of the Lahontan Basin. In 1958, Miller added evidence for the Tertiary connection between the Death Valley and Lahontan Basins. The fossil killifishes, *Fundulus curryi* and *Fundulus eulepis*, similar to *Fundulus nevadensis* of the Truckee Formation, occur in Late Tertiary deposits of Death Valley (Miller, 1945). *Pantosteus santaeannae*, which probably reached the Pacific coast in the Pliocene, is most closely related to Great Basin forms. Thus, there is considerable faunal evidence to indicate a Late Tertiary connection between the Death Valley and Lahontan Basins through which *Gasterosteus* could have dispersed.

#### RESULTS OF MORPHOLOGICAL STUDIES

##### *Pelvic Variation*

Variation in the pelvic structure is very similar in the Recent and fossil collections of *Gasterosteus*, ranging from normal development to entire absence. However, it is useful to recognize 3 pelvic classes. The different classes in the Recent and fossil materials can be discussed together.

*Developed:* Twenty-four fossil specimens ranging from 34.0 to 73.3 mm SL and 23 Recent specimens ranging from 34.1 to 57.2 mm SL were examined. The developed pelvic girdles of the Recent sample and the fossils conform to the description by Nelson (1971b) except that the anterior margin of the pelvic girdle is incised, forming a strong anterior process (Fig. 2a; 3a, b, c). In the Recent specimens, the pelvic spines are denticulated. The ascending branch of the pelvic girdle may be forked or unforked but is usually fairly bilaterally symmetrical. When forked, a lateral plate generally lies between the forks. In the fossils, the ascending branch of the pelvic girdle is not forked to accommodate a lateral plate because lateral plates are lacking. The pelvic spine of the fossils, unlike that of most *Gasterosteus*, is undenticulated (the dorsal spines are also undenticulated). However, *Gasterosteus* has been reported with undenticulated spines previously (Penczak, 1962a, 1964). *Gasterosteus* fin spines from the Lower Member of the Truckee Formation (locality UCMP 6998) are denticulated. Pelvic spines are recognizable by enlarged denticles along the ventral margin.

*Vestigial:* Sixty-seven fossil specimens ranging in size from 24.4 to 68.1 mm SL and 25 Recent specimens ranging from 33.7 to 63.2 mm SL were examined. Only one vestige is found in 21 of the fossil and 4 of the Recent specimens examined. Pronounced bilateral asymmetry is common (Fig. 2c, d, e, h; 4b, e), especially in the Recent sample. The fossil and Recent materials differ

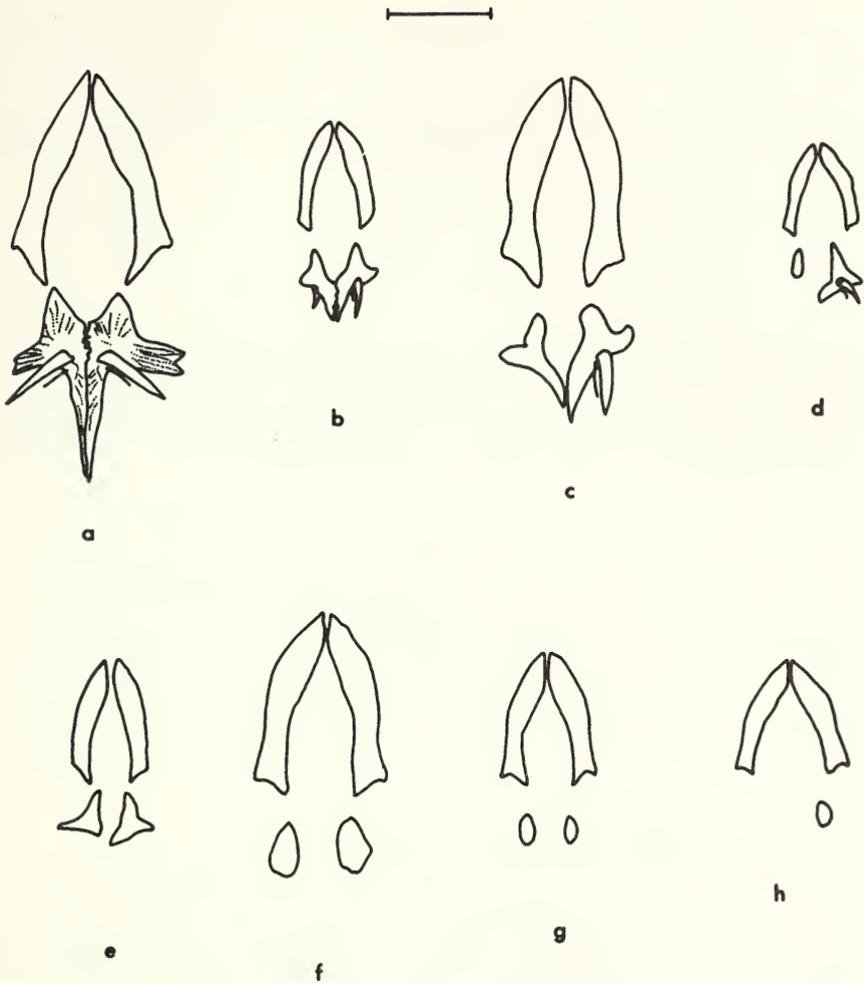


FIGURE 2. Camera lucida drawings of pelvic girdles (with the ectocoracoid above for orientation) of Recent *Gasterosteus* (LACM 32008-1): *a* is normally developed and *b* through *h* is a series of vestiges in order of decreasing development. The pelvic spine denticles are not shown.

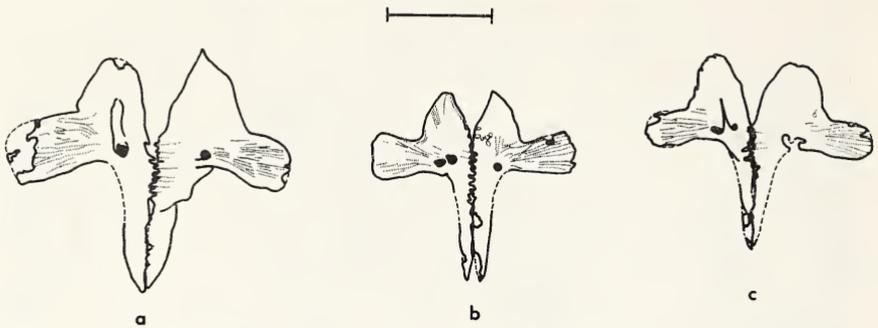


FIGURE 3. Reconstructions from camera lucida drawings of normally developed pelvic girdles of *Gasterosteus doryssus*: a, LACM 17442; b, 17452A; and c, 17452B. The pelvic girdle was flattened during preservation so that its ventral and lateral surfaces shown here lie in the same plane. The pelvic spines are not shown. Broken lines are estimates of the bone margins covered by other elements or which have been broken and are represented by impressions in the matrix.

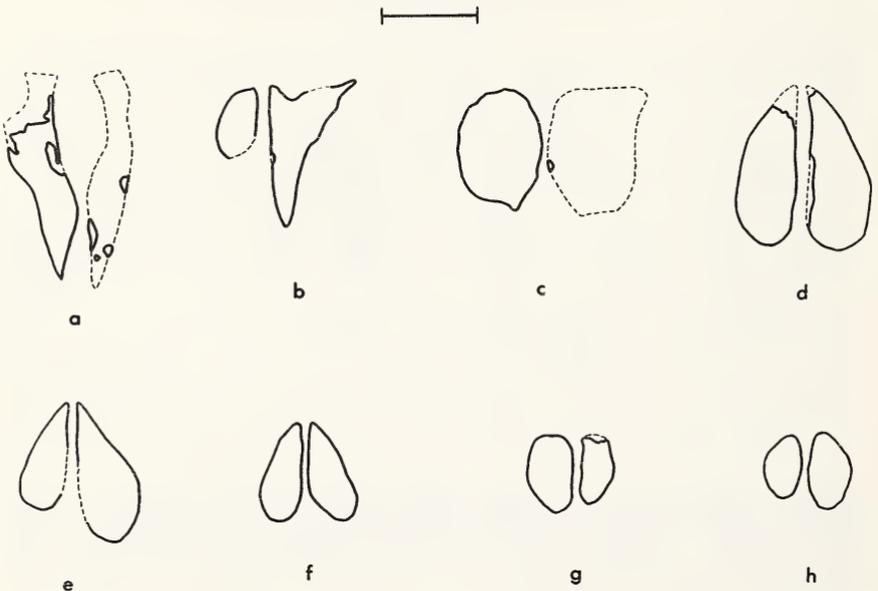


FIGURE 4. Reconstructions from camera lucida drawings of pelvic vestiges of *Gasterosteus doryssus* in order of decreasing development: a, LACM 17452C; b, 17944A; c, 17940A; d, 17941A; e, 17461; f, 17463; g, 17944B; and h, 17474A. Broken lines are estimates of the bone margins covered by other elements or which have been broken and are represented by impressions in the matrix.

in that the tear-drop shaped vestige shown in Fig. 4d to f is very common in the fossils. In the fossils, very small vestiges tend to be irregularly shaped (Fig. 4g, h). There are also some rather large vestiges which have shapes intermediate between those of the developed and vestigial classes (Fig. 4a, b). The pelvic girdle of CAS 50046 is much reduced in size but resembles the normal pelvic girdle, complete with spines. In LACM 17944A (Fig. 4b), one of the pelvic vestiges is the typical tear-drop shape and the other has the form of the developed pelvic bone but is smaller, flat, and lacks the spine. Jordan's (1907) type of *Merriamella doryssa* (UCMP 9372) and other specimens labeled as type, cotype or paratype (UCMP 9374 and 9375), all from the type locality (UCMPV 1034), and UCMP 58565 (from locality UCMPV 5613) have intermediate shaped pelvic vestiges. Pelvic vestiges of Recent specimens are relatively variable in shape (Fig. 2b to h), but smaller vestiges tend to be roughly tear-drop shaped. Nine of the 25 specimens with pelvic vestiges have a reduced spine on one or both vestiges. Such spines are denticulated.

*Absent:* No sign of the pelvic girdle is found in 24 of the fossil specimens ranging in size from 24.2 to 64.4 mm SL and 19 Recent specimens ranging from 33.1 to 63.1 mm SL. It is possible that some of the smaller specimens had unossified pelvic vestiges which would have ossified if they were older, because the pelvic girdle develops relatively late in ontogeny (Nelson and Atton, 1971; Swarup, 1958). However, many of the specimens are large. It is also possible that pelvic vestiges in the fossils could have been lost prior to burial, but all of these specimens are otherwise well preserved, and there is no reason to believe that the pelvic vestiges were selectively lost when all other structures are in place.

#### *Stratigraphic Distribution of Fossil Classes*

The distribution of the pelvic classes through time is difficult to determine from available data. Fossil sticklebacks occur from at least Early Pliocene to Middle Pliocene. Most of the material available for this study was collected from Early Pliocene portions of the Middle Member of the Truckee Formation. Unfortunately, most of the fossils were collected from loose rubble or are without field data. Thus, their relative stratigraphic positions cannot be determined.

UCMP 99674 from the Lower Member of the Truckee Formation includes isolated pelvic spines which are well denticulated. At least some Lower Truckee sticklebacks had normally developed pelvic girdles.

LACM 28090 to 28126 were collected *in situ*. These specimens have a vestigial pelvic girdle or no girdle. None has a developed pelvic girdle. One of the specimens collected *in situ* has two dorsal spines, and the remainder have one.

Another source of information is slabs with two or more specimens. LACM 17452 includes 3 specimens, 2 of which have developed pelvic girdles (Fig. 3b,

c) and the third of which has a girdle intermediate between the developed and vestigial classes (Fig. 4a). On LACM 17452, the specimens with developed pelvic girdles have 1 and 3 dorsal spines, and the specimen with the intermediate girdle has 2. CAS 50044 has 2 specimens with developed pelvic girdles, but the dorsal spines could not be counted. LACM 17944 has 4 specimens, 1 of which has 1 vestigial pelvic element and 1 intermediate between developed and vestigial (Fig. 4b) whereas the remainder all have typical pelvic vestiges. One of the latter specimens lacks dorsal spines, and the remainder have 1. LACM 17440 (2 specimens), 17469 (2 specimens), 17474 (2 specimens), 17937 (2 specimens), 17940 (2 specimens), and 17942 (8 specimens) have only fish with vestigial pelvic girdles. All but 2 of these slabs (LACM 17474 and 17940) have fish with differing numbers of dorsal spines (either 0 and 1 or 1 and 2) and LACM 17942 has fish with 0 to 2 dorsal spines. Two slabs, LACM 17941 (3 specimens) and LACM 17943 (4 specimens) have fish with either vestigial or no pelvic girdles. All of these specimens have one dorsal spine. No slabs were found on which all fish lack the pelvic girdle.

Analysis of the stratigraphic distribution of fossil sticklebacks has limitations. Specimens occurring on one slab or which were collected *in situ* within a restricted section of the formation generally do not come from precisely the same layer of diatomite and must have been deposited at different times. Even if two specimens occur on precisely the same layer, they were not necessarily sympatric. They may have come to rest in the same area following death. Conversely, incomplete sampling may result in the erroneous impression that two classes are isolated from each other stratigraphically.

The effect of such limitations on this analysis is minimal because the sample size is fairly large, and different classes of sticklebacks seem to be segregated, eliminating the first two limitations. Thus, the distribution pattern is relatively easy to interpret. Fish with the developed pelvic girdle tend to be segregated from those in which the pelvic girdle is reduced. The only exception to this general pattern is LACM 17452 as noted above. Sticklebacks with vestigial and no pelvic girdle occur together as fossils but may not have been sympatric. The apparent segregation of the developed class from other classes may be the result of geographic or temporal separation.

The earliest known sticklebacks from the Truckee Formation are from the Lower Member. Some of these had normal pelvic girdles with denticulated spines. From my series it is impossible to determine if sticklebacks with vestigial pelvic girdles occur in the Lower Member of the formation. Locality LAV 6663, where all three pelvic morphs occur, penetrated only a restricted portion of the Middle Member of the Truckee Formation so all pelvic morphs occur in the Early Pliocene part of the Middle Member of the Truckee Formation. Jordan's (1907) and Hay's (1907) Middle Pliocene type material had varying pelvic structures. There are two possible explanations for this distribution pattern. These specimens may have come from polymorphic populations with varying proportions of the pelvic classes, or there may have been two

biological species of *Gasterosteus*. If there were polymorphic populations, they would probably have consisted primarily of individuals with developed pelvic girdles or primarily of the vestigial and absent classes. This polymorphism must have persisted from Early to Middle Pliocene. Fish with different numbers of dorsal spines were probably less segregated from each other than were those with developed pelvic girdles from ones with vestigial and no pelvic girdles.

#### *Characters Correlated With Pelvic Structure*

The number of dorsal spines, dorsal fin rays, predorsal radials, anal fin rays, total vertebrae and the length of the last two dorsal spines expressed as a per cent of standard length (SL) were examined in the fossil and Recent material to determine whether any were correlated with pelvic structure. The number of lateral plates was also compared between the different pelvic classes in the Recent sample. Means of the spine lengths were calculated using only individuals of 40 to 60 mm SL to minimize the effect of allometric growth, known to take place throughout life in *G. aculeatus* (Bertin, 1925; Hagen and Gilbertson, 1972). Mean spine lengths are shown in Table 1. The distributions of character states within the range of variation of meristic characters for the

Table 1. Mean spine lengths of the different pelvic classes: DEV, developed; VEST, vestigial and ABS, absent. Numbers in parentheses are sample sizes.

TABLE 1			
Mean Dorsal Spine Lengths			
Fossil	DEV	VEST	ABS
Second dorsal spine	8.37 (9)	6.60 (5)	2.38 (1)
Third dorsal spine	3.90 (9)	2.96 (30)	2.56 (10)
Recent			
Second Dorsal spine	6.97 (18)	6.66 (20)	6.50 (13)
Third dorsal spine	2.26 (18)	2.17 (20)	2.30 (13)

different pelvic classes are shown in Fig. 5. The Kolmogorov-Smirnov Test (Tate and Clelland, 1959) was used to compare the distribution of character states between different pelvic classes within the two samples. Statistically significant results of analysis of the data shown in Fig. 5 and data the means of which are presented in Table 1 are presented in Table 2. Comparisons between the length of the second dorsal spine in fossils of the absent class and the other two classes were not made because the sample size was too small.

#### *Arrangement of Predorsal Radials and Dorsal Spines*

In normal three-spined individuals of *Gasterosteus*, the first two dorsal spines are anterior to and free from the soft dorsal fin. The smaller third spine is also anterior to but contiguous with the soft dorsal fin. The arrangement of

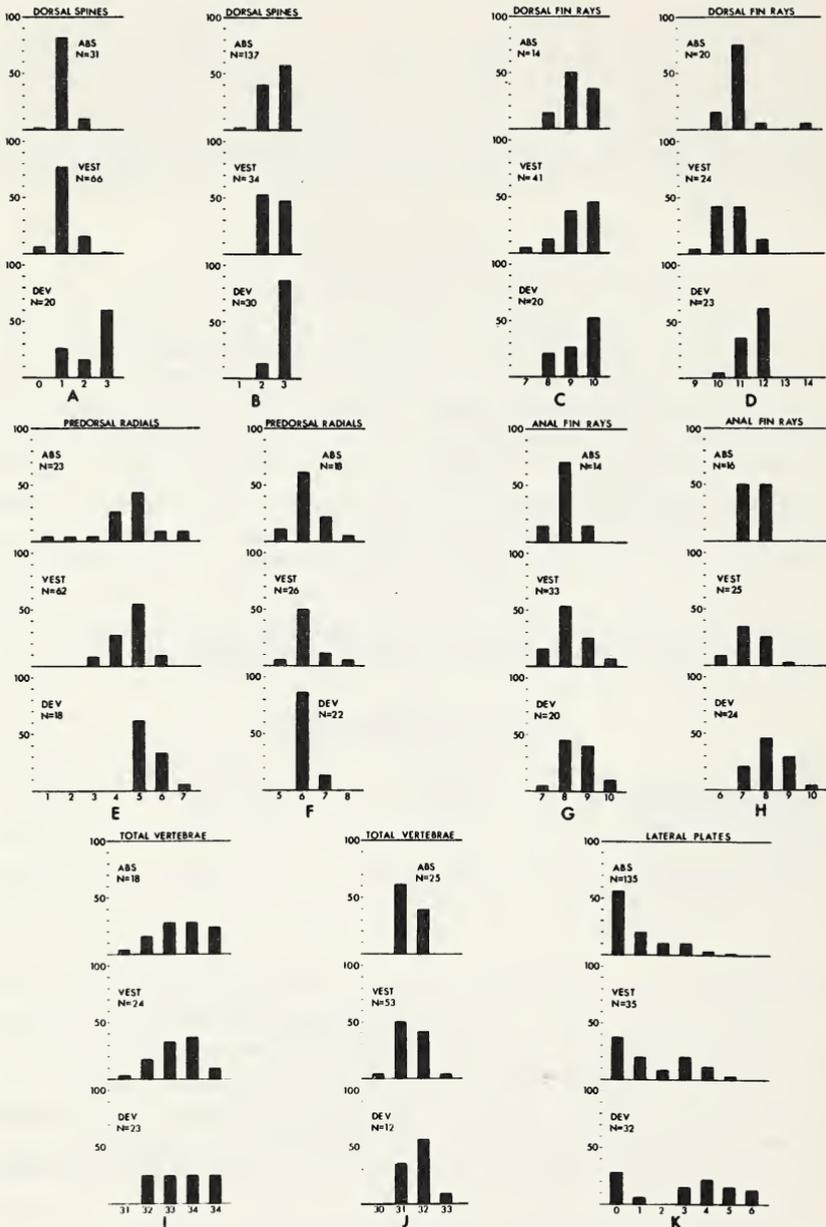


FIGURE 5. Histograms of the distributions of character states of meristic characters in the different pelvic morphs of *Gasterosteus* which tend to reduce or lose the pelvic girdle. A, C, E, G, and I are data for fossils and B, D, F, H, J, and K for Recent, benthic sticklebacks from Paxton Lake. The vertical axes are frequency (%) and the horizontal axes are the number of elements in the meristic series. DEV, developed; VEST, vestigial; ABS, absent pelvic class and N, sample size.

Table 2. Statistically significant results (at the 5% confidence level) of Kolmogorov-Smirnov Test of data presented in Fig. 5 and distributions of dorsal spine lengths, the means of which are presented in Table 1. *D*, maximum cumulative difference in frequency (%) of character states between two pelvic classes,  $\alpha$ , confidence level at which the null hypothesis has been rejected; and Fig., where the data are plotted in Fig. 5.

TABLE 2  
Statistically Significant Results of Comparisons of Pelvic Classes

Sample	Character	Classes compared	<i>D</i> (%)	$\alpha$	Fig.
Recent	number of dorsal spines	DEV:VEST	36.37	0.05	5B
		DEV:ABS	27.60	0.05	5B
Fossil	number of dorsal spines	DEV:VEST	61.16	0.01	5A
		DEV:ABS	66.31	0.01	5A
Recent	number of dorsal fin rays	DEV:VEST	48.87	0.01	5D
		DEV:ABS	50.34	0.02	5D
Fossil	number of predorsal radials	DEV:VEST	36.50	0.05	5E
		DEV:VEST	37.57	0.05	5K
Recent	number of lateral plates	DEV:ABS	37.71	0.01	5K
		DEV:ABS	88.89	0.05	—
Fossil	length of third dorsal spine	VEST:ABS	50.00	0.02	—

predorsal radials and dorsal spines forms a complex pattern because the number of both radials and spines varies. I have assumed for the purpose of analysis that the dorsal spines are invariably associated with the same radial and that variation in position is due to addition or loss of radials not bearing spines. Fig 5E and F shows the frequency of different numbers of predorsal radials in different pelvic morphs in the fossil and Recent samples respectively.

Among the fossils, the number of predorsal radials varies from 7 to 1 (Fig. 5E). The modal number of predorsal radials is 5 in developed (61.1%), vestigial (54.8%) and absent (43.5%) pelvic classes. However, 5 is the minimal number of radials for specimens with the developed pelvic girdle, but only 11.8% of specimens with a vestige or lacking the pelvic girdle have greater than 5 predorsal radials. A specimen with 7 radials and 3 spines has the following arrangement:

I II<sup>1</sup> III<sup>2</sup> IV V VI VII<sup>3</sup>

Two-spined specimens (regardless of the number of predorsal radials) lack the spine at II; one-spined specimens lack the spines at II and III; and specimens with no dorsal spines lack the spines at II, III and VII. Specimens with 6 predorsal radials lack IV, V or VI. Those with 5 predorsal radials lack I and IV, I and V, I and VI, IV and V or V and VI. Specimens with fewer than 5 radials could not be analyzed because they have 1 or no dorsal spines. Specimens in the sample with 7 predorsal radials have 0, 1 or 3 dorsal spines; those with 5 or 6 radials 1 to 3 dorsal spines; those with 3 or 4 radials have 0 or 1 spine and those with 1 or 2 radials have 1 spine.

Among the Recent specimens, the number of predorsal radials varies from 5 to 8 (Fig. 5F), but 72.7% of all specimens have 6 predorsal radials. In striking similarity to the fossils, all specimens with a developed or a pelvic girdle intermediate between the typical vestigial and developed pelvic girdle (as in Fig. 2b to e) equal or exceed the modal number of radials (6 or 7) while specimens lacking the pelvic girdle or with only a vestige vary from 5 to 8 predorsal radials. Specimens with 8 predorsal radials and 3 dorsal spines have the following arrangement:

I II III IV<sup>1</sup> V<sup>2</sup> VI VII VIII<sup>3</sup>

Two-spined specimens lack the spine on radial IV. Specimens with 7 radials may lack II or VI. Those with 6 radials may lack II and III or II and VI. Specimens with 5 radials lack I, II and VI or II, III and VI.

The greater variability of the fossils may be due to poor preservation, since the predorsal radials are delicate structures, easily destroyed in preparation. However, the arrangement of radials and spines in the two samples is fundamentally different.

#### CONCLUSIONS

##### *The Nature of the Samples*

The fossil and Recent samples are very different. The Recent sample is from one population. The fossils came from a series of beds probably representing a span of hundreds of thousands or millions of years. Since the generation time in living freshwater *G. aculeatus* is only one or two years (see Mullen and Vlugt, 1964, for a review of generation time), the fossil collection may represent millions of generations. Thus, the fossil sample of less than 150 specimens represents a very small sample from a very large number of successive related populations. Comparisons of fossil specimens are, in effect, interpopulation comparisons with very small sample sizes. Comparisons of the Recent population are intrapopulation comparisons. Characters correlated with pelvic condition in the fossils may represent correlations of the mean state of the characters in the population to which that individual belonged. The degree to which these characters were correlated within one individual is obscured because the variability of the character in the population to which the individual belonged is unknown. Characters correlated with the pelvic condition in the Recent sample must be due to mechanisms which result in their association in one individual of a population. Possible mechanisms include genetic linkage, strong mortality of phenotypes in which both of the characters are not present, subdivision of the sample into small breeding units (Tabachnick and Underhill, 1972) and pleiotropy. Such mechanisms need not be invoked to explain correlations with pelvic structure of the fossils because they do not represent one population, but such mechanisms may be involved.

*The Polyphyletic Origin of Pelvic-less Gasterosteus*

The range of variation of the pelvic girdle, lateral plates and the dorsal spines is very similar in the Recent sample from Texada Island and the fossil assemblage from Hazen, Nevada. While there seems to be a suite of correlated characters common to both of the samples, the details of their variation are different. The pelvic structure varies from fully developed to absent with similar vestigial intermediates in both samples. However, fossils with pelvic vestiges tend to have tear-drop shaped vestiges and rarely (1 specimen) have spines. In the Recent sample, pelvic vestiges vary in shape and often have spines.

The number of dorsal spines varies differently in the two samples, although, spines drop out sequentially from first to third in both. In the Recent sample, fewer than 2% of specimens had only one dorsal spine and all had at least one. Fossil specimens with no or one dorsal spine constituted nearly 70% of the sample, even though collecting was biased in favor of specimens with two or 3 dorsal spines. Even in fossils with developed pelvic girdles (which tend to have more dorsal spines, see Fig. 5d), a quarter of the specimens examined had only one dorsal spine. Although lateral plates are reduced in both samples, about 59% of the Recent sticklebacks have 1 to 7 lateral plates on at least one side of the body, but none of the fossils examined had any lateral plates.

The number of predorsal radials and the placement of dorsal spines on the radials differs between the two samples. The maximum number of predorsal radials in the Recent specimens exceeds that of the fossils by one, and the minimum number in the fossils exceeds that of the Recent sticklebacks by 4, although extremely low counts among the fossils may be due to poor preservation. The fossils and Recent specimens that have the same number of predorsal radials always have the dorsal spines at different positions. Predorsal radial and dorsal spine patterns analyzed by Bertin (1925) and Penczak (1962b, 1962c) by techniques similar to those used in this study, differ from the Recent and fossil samples. There is apparently considerable interpopulation and intrapopulation variation in the arrangement of these elements.

Some other differences between the Recent and fossil specimens are, respectively: vertebrae, 30 to 33 ( $\bar{x}=31.54$ ) and 31 to 35 ( $\bar{x}=33.32$ ); dorsal fin rays, 9 to 12 ( $\bar{x}=11.06$ ) and 7 to 10 ( $\bar{x}=9.03$ ); and anal fin rays, 6 to 10 ( $\bar{x}=8.56$ ) and 7 to 10 ( $\bar{x}=8.22$ ). Serial elements of fossils can easily be miscounted because of poor preservation, but this generally results in a lower count than actually existed. The greater maximum of total vertebrae and minimum anal fin rays must represent real morphological differences.

The significance of these morphological differences for the phyletic relationship of the fossil and Recent sticklebacks is difficult to assess. Differences in the number of meristic elements may not have a genetic basis as several are known to be altered by environmental variables such as temperature and salinity (Lindsey, 1962; Lindsey and Harrington, 1972). It seems likely that

differences in the relationship of dorsal spine number and size to pelvic structure, the placement of dorsal spines on the predorsal radials, the form of pelvic vestiges, and the total absence of lateral plates in the fossils represent underlying genetic differences. These morphological differences do not preclude the possibility that the reduction and loss of the pelvic girdle is monophyletic in *Gasterosteus* because random genetic effects such as the founder principle and drift influence subsequent selection, and selection is not a deterministic process.

Whether pelvic loss in *Gasterosteus* has a monophyletic or polyphyletic origin can not be determined on the basis of only morphological criteria, but zoogeography tends to support the latter possibility. Texada Island, according to McPhail (pers. comm.) was subject to postglacial marine submergence about 5000 years ago. It is reasonable to assume that physiological attributes associated with the trachurus and leiurus phenotypes have been established for a long time because freshwater fossil *Gasterosteus* are all leiurus and the relationship between the physiological and morphological phenotype generally is the same where ever they occur. Thus the sticklebacks on Texada Island must have arrived as the trachurus type. Subsequent selection on the island has produced the pelvic-less phenotype. The fossil sticklebacks are from the Pliocene and were deposited more than 10 million years ago. The absence of low elevation passes from the Lahontan Basin westward to the Pacific Ocean, the ichthyofaunal relationships of the basin, and the presence of *Gasterosteus* in southern California in the Pliocene indicate that the fossil sticklebacks probably entered Nevada via river systems draining through southern California before the beginning of the Pliocene. The two samples are separated from each other by great gaps in time and space. The most parsimonious model for the evolution of the lines represented by the fossil and Recent sample is that their advanced features have arisen independently.

#### *Convergence and Parallelism*

If the morphological similarities between *Gasterosteus* from Texada Island and the Pliocene fossils are independently derived, they may be due to convergence or parallelism. Simpson (1961) has defined the terms parallelism and convergence, and Marshall (1971) has discussed them with respect to the radiation of some teleost fishes. Simpson defines parallelism as “. . . the development of similar characters in two or more lineages of common ancestry and on the basis of or channeled by characteristics of that ancestry.” and convergence as “. . . the development of similar characters separately in two or more lineages without a common ancestry pertinent to the similarity but involving adaptation to similar ecological status.” The definition of parallelism implies that very similar genetic systems which have been inherited from a common ancestor are those that are being selected to produce the parallel phenotypes.

I believe that the close morphological similarity between the fossil and

Recent samples reported in this study represents a case of parallelism. Morphological variation in the two samples is similar and they are relatively closely related. Determination of the genetic basis of the similarity could be achieved only by making genetic crosses, and this is impossible in this case.

#### *Model For Evolution of Gasterosteus Phenotypes*

Another population of *Gasterosteus* that tends to lose the pelvic girdle has been reported from the Queen Charlotte Islands, British Columbia (Moodie and Reimchen, 1973; Hagen and McPhail, 1970; Nelson, 1971b; Nelson and Atton, 1971) and it was probably also independently derived. The Queen Charlotte population also tends to have reduced dorsal spines (T. Reimchen, pers. comm.). Fig. 6 is a very simplified graphical model

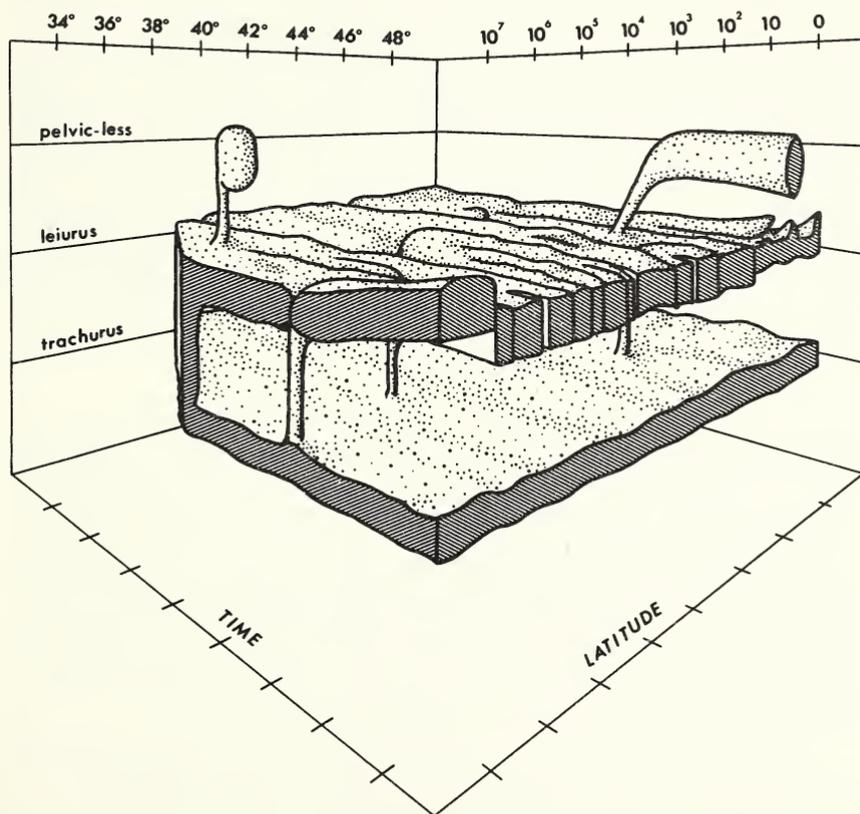


FIGURE 6. Simplified diagrammatic three-dimensional plot of the distribution of different *Gasterosteus* phenotypes through time (in years ago) and space (in degrees N latitude). The time axis is logarithmic and the vertical axis is morphological with the primitive phenotype at the bottom. Note that the multiple transitions between structural grades have been limited for clarity and in reality must be much more numerous. The Queen Charlotte Islands population of pelvic-less *Gasterosteus* is not shown.

showing phyletic relationships between *trachurus*, *leiurus*, and pelvic-less structural grades of *Gasterosteus*. Parallelism is probably the dominant mechanism underlying the amphiboreal distribution of *G. aculeatus* with different phenotypes (Băcescu and Mayer, 1956 cited in Münzing, 1963; Hagen and Gilbertson, 1972; McPhail and Lindsey, 1970; Münzing, 1963). Lindsey (1962) reached the same conclusion from studies of the genetic variability of meristic characters in *G. aculeatus*.

Morphological variation upon which selection can act to produce parallel phenotypes is abundant in *leiurus* populations. *Leiurus* populations from southern and central California frequently have individuals with reduced numbers of dorsal spines. The maximum frequency of two-spined specimens in *leiurus* samples examined was about 5%. One sample (LACM 30922-1) with about 5% two-spined individuals also had one one-spined and one four-spined specimen. In the samples in which two-spined individuals were at a high frequency, specimens with the first dorsal spine small and incapable of locking into the normal defensive posture (Hoogland, 1951) were also present in similar abundance. Two, four, and five-spined specimens have been reported from Europe by Penczak (1966). Two-spined specimens are apparently very rare in many European populations (Penczak, 1965). Lindsey (1962) obtained two, three, and four-spined offspring from crosses of three-spined parents. Variation in the number of lateral plates is very well documented in *Gasterosteus* (e.g., Rutter, 1896; Münzing, 1963; Miller and Hubbs, 1969; Hagen and Gilbertson, 1973). Substantial reduction of pelvic structure has rarely been reported (Penczak, 1965).

### Taxonomy

Determination of the taxonomic categories to which the Texada Island and fossil samples belong is a difficult problem. Mural (1973) assigned the fossil sticklebacks from the Truckee Formation to two species based primarily on pelvic structure, although, he did not describe variation in the pelvic girdle in detail. He believed that Jordan's (1907) type specimen had a normally developed pelvic girdle and restricted *Gasterosteus doryssus* to include only specimens with developed pelvic girdles. He described *Gasterosteus apodus* as a new species of fossil stickleback characterized by vestigial or absent pelvic girdles and reduced numbers of dorsal spines and lateral plates. His data, based in part on specimens used in this study, are largely consistent with my data, but his description of a new species is unwarranted.

Mural suggested several characters to separate the two species of fossil sticklebacks. Individuals with reduced pelvic structures also tend to have fewer dorsal spines than those with a normal pelvic girdle. My data confirm this tendency (Fig. 5A) but this trend is also present in the Recent sample (Fig. 5B) which consists of conspecifics. He also noted that sticklebacks in the University of Michigan Museum of Paleontology collection with normally developed pelvic girdles had ". . . occasionally several lateral plates. . . ." while

those with reduced pelvic structures had “. . . lateral plates only rarely noted. . .” His conclusion that differences in the frequency of individuals with lateral plates between sticklebacks with different pelvic structure constitute a species character is unjustified. In my Recent sample, individuals (from one population) with reduced pelvic structures were found to have fewer lateral plates (Fig. 5K).

Mural stated that pelvic vestiges in *Gasterosteus apodus* are always leaf shaped, bilaterally symmetrical, and lack spines. It is true that leaf (tear-drop) shaped vestiges are very common among the fossils, but intermediate pelvic structures occur. Mural examined LACM 17452 which includes 3 individuals and assigned them to *G. apodus*. These specimens have either developed pelvic girdles (Fig. 3b, c) or a structure intermediate between developed and vestigial (Fig. 4a). LACM 17944A which he considered to be *G. apodus* has one typical vestige and an intermediate structure (Fig. 4b). Mural also examined Jordan's type specimen (UCMP 9372) and UCMP 9374 and concluded that they have normally developed pelvic girdles. My examination of these two specimens indicated that their pelvic structure closely resembles the intermediate structure of LACM 17944A. Bilateral asymmetry in the size and shape of pelvic vestiges is also present (Fig. 4b, e) and only one pelvic vestige was found in 21 of 67 specimens with vestigial pelvic girdles. CAS 50046 had a much reduced pelvic girdle with spines.

Mural's failure to recognize the degree of pelvic variation in his sample, and his lack of a Recent *Gasterosteus* population, in which the pelvic girdle may be reduced, with which to compare the fossil sample led him to two incorrect conclusions. He concluded that pelvic variation in his sample differed from intrapopulation variation in *Gasterosteus*, *Pungitius* (Nelson, 1971), and *Culaea* (Nelson and Atton, 1971) which tend to reduce the pelvic skeleton. He believed that the uniform leaf shape structure which he thought characterized pelvic vestiges in his sample constituted a species character. He also concluded that correlations between pelvic structure and dorsal spine and lateral plate number could not occur within one species. These conclusions are refuted by the variability actually displayed among the pelvic girdles of fossils (Fig. 4) and intrapopulation correlation between pelvic structure and dorsal spine and lateral plate number in the Recent *Gasterosteus* reported in this study (Fig. 5B, K, Table 2). Thus, no evidence has been presented by Mural which would warrant specific separation of fossil sticklebacks with reduced pelvic structure from those with normally developed pelvic girdles. The nominal species, *Gasterosteus apodus*, is a junior synonym of *Gasterosteus doryssus*.

The nominal species, *Gasterosteus doryssus*, should be retained until more data are available on extant populations of *Gasterosteus* which tend to lose or reduce the pelvic girdle. Nelson (1971b) did not believe that pelvic reduction in *Pungitius* warranted taxonomic recognition. The criteria of the biological species concept (Mayr, 1963) should be applied to the Paxton Lake

and Queen Charlotte Islands populations. The validity of *G. doryssus*, a species polymorphic for pelvic structure and other features, may be inferred by analogy with morphologically similar living populations of *Gasterosteus*.

#### DISCUSSION

##### *Parallelism Within the Gasterosteidae*

Within the Gasterosteidae, there are three genera, *Gasterosteus*, *Pungitius*, and *Culaea*, which normally have well developed pelvic girdles with an ascending branch and a strong pelvic spine (Nelson, 1971b). In all three genera, there are populations reported with individuals with reduced and missing pelvic girdles. Nelson and Atton (1971) have reported *Culaea* populations ranging over a wide area in Alberta and Saskatchewan, Canada in which the pelvic girdle tends to be reduced or absent. Although it is possible that these widespread populations represent a monophyletic group dispersed by disruptions of drainage patterns, it is more likely that the unusual morphological attributes of at least several of these populations were independently derived. They occur in different drainages dispersed among normal populations, and postglacial invasion of the area was probably from more than one refugium (Nelson and Atton, 1971).

*Pungitius* populations in which the pelvic girdle tends to be absent were first reported from Ireland by Day (1878). Nelson and Atton (1971) mentioned populations of *Pungitius* from Alberta in which about one-third of the individuals had incomplete pelvic girdles. Nelson (1971a) has discussed populations of *Pungitius* from Ireland and central Canada in which the pelvic girdle tends to be reduced or absent. Coad (1973) reported additional populations in which pelvic reduction occurs at low frequencies (about 5%) from eastern and central Canada. Obviously, parallelism is responsible for at least some of this distribution pattern.

In *Gasterosteus* reported in this study there is a clear relationship between the condition of the pelvic girdle and the state of several characters. In both samples, there tend to be more dorsal spines in specimens with normally developed pelvic girdles. In the fossils, the third dorsal spine is shorter in sticklebacks lacking the pelvic girdle than in the other two morphs. The second and third dorsal spine may tend to be shorter in fossils with reduced pelvic structures but significant differences were not established. Dorsal spines are about the same length in all Recent specimens. The fossils lack lateral plates but in the Recent sample, specimens with developed pelvic girdles have more lateral plates than those with reduced pelvic structures. Among the fossils, specimens with developed pelvic girdles have more predorsal radials than those with vestiges.

Nelson and Atton (1971) have examined *Culaea*, and Nelson (1971a) has examined *Pungitius* to determine if the number of dorsal spines is correlated with the pelvic structure in populations with reduced pelvic girdles. In *Culaea*, Nelson and Atton (1971) believed that no clear relationship emerges

in interpopulation comparisons between the frequency of reduced pelvic girdles and the frequency of individuals with various numbers of dorsal spines. However, Nelson (1969), studying populations of *Culaea* with normal pelvic girdles, found that the lengths of the pelvic and dorsal spines were positively correlated. He found that this correlation was stronger between populations than within populations and that the area of pelvic-less populations is where dorsal and pelvic spines tend to be shortest. Nelson (1971b) reported no clear association was found in *Pungitius* between the condition of the pelvic girdle and the number or size of dorsal spines in interpopulation and intrapopulation comparisons, but pelvic spine length was somewhat shorter in the area of loss of the pelvic girdle in Canada. Day (1878) noted that pelvic-less specimens of *Pungitius* in Ireland frequently had extreme numbers of dorsal spines. The relationships of the development of these structures in *Gasterosteus* and of the pelvic girdle and spines in *Pungitius* and *Culaea* may indicate that they are responding to a common selection pressure because they may form a complex of defensive structures (Hoogland, et al., 1957).

#### *The Genetic Basis of Parallel Phenotypes of Gasterosteids*

Regardless of the selective mechanisms involved in producing the pelvic-less phenotype, a certain set of circumstances has apparently elicited a very similar phenotypic response independently in the genera *Gasterosteus*, *Pungitius*, and *Culaea* since at least the beginning of the Pliocene. The similarity of the normal pelvic structure and of the reduction of the pelvic girdle and dorsal spines in *Gasterosteus*, *Pungitius*, and *Culaea* may indicate that very similar genetic systems involving homologous genes in these genera control the tendency for failure of these structures to develop normally in populations with reduced structures. The portion of the genome upon which selection acts to produce the pelvic-less phenotype has probably been stable since at least the Pliocene and has endured the radiation of the Gasterosteidae. (Genetic homology may also be responsible for the widespread systematic variation in the number of lateral plates of *Gasterosteus* (Hagen and Gilbertson, 1972)). However, subtle differences in the manner in which the spines and pelvic girdles are reduced in the Recent and fossil samples studied in this paper tend to indicate that there are many genes involved in the formation of defensive structures. Thus, their normal development could be prevented through allelic substitutions at one or more of many loci. Subtle differences in these structures may also indicate the involvement of nonhomologous genes. Rigorous proof of genetic homology in these cases requires that genetic crosses be made. Rarely are such rigorous proofs provided in alleged cases of parallelism. Thus, while the distinction between parallelism and convergence is an interesting one, it is in practice, a difficult one to rigorously demonstrate. It is with this reservation that I apply the term parallelism to variation of defensive structures in the Gasterosteidae.

The degree of genetic homology could be determined by performing interpopulation crosses of congeneric populations and intergeneric crosses between members of the three genera with different pelvic structures. Schwartz (1972) has listed the attempted hybridizations of fishes. He did not list any attempted hybridizations involving *Culaea*, but he did list several for *Gasterosteus* x *Pungitius*. Leiner (1957) was able to produce adult hybrids of *Gasterosteus* x *Pungitius*, so it may be possible to cross members of these genera with different pelvic structure. It may also be possible to perform crosses involving *Culaea* because *Apeltes* (Moenkhaus, 1911) and *Spinachia* (Appellöf, 1894) have been crossed with *Gasterosteus*. Genetic plasticity probably underlies differences in other populations of *Gasterosteus* characterized by unusual behavioral and morphological adaptations discussed by Hagen and McPhail (1970), McPhail (1969), Moodie (1972a, 1972b), Semler (1971), and Moodie and Reimchen (1973).

#### *Natural Selection For Reduction of Defensive Structures*

The selection mechanism for the reduction of defensive structures of gasterosteids is unknown. Nelson and Atton (1971) felt that a disproportionate number of the 20 *Culaea* populations that they examined which had reduced pelvic structures were less subject to predation than populations with normal pelvic girdles. Hagen and Gilbertson (1972), in a detailed study of the relationship or morphology in *G. aculeatus* to several environmental variables, found that stickleback populations with a modal number of 7 lateral plates and greater mean pelvic and dorsal spine length were associated with the presence in the habitat of predators on *Gasterosteus*. Coad (1973) mentioned unpublished studies which yielded the same findings for *G. aculeatus* in Quebec. Moodie, et al. (1973) found that in the laboratory under winter conditions (short photoperiod and cold water) 7 plated sticklebacks were less subject to predation by salmonids than sticklebacks with 4, 5, 6, 8 or 9 lateral plates. Moodie (1972b) reached a similar conclusion based on stomach content analysis of predatory fishes. Thus, evidence is accumulating that predators act as strong selective agents on spine length and lateral plate number in sticklebacks.

Nelson (1969) has speculated that a reduced number of alternate prey species for predators on *Culaea* may alter selective pressure on a population because the spines would not discourage predators from exploiting the only available prey. Hoogland, et al. (1957) showed that stickleback spines act as a deterrent to predators, which soon learn to avoid them in favor of alternate prey species. Consequently, alternate adaptations such as streamlining of the body for swifter escape would be selected over increased spination. This hypothesis seems to be applicable to the loss of lateral plates, dorsal spines and pelvic girdles of other sticklebacks. The elucidation of the mechanisms by which predation affects stickleback genomes awaits further research.

### *Parallelism In Other Groups*

Parallelism is responsible for much of the morphological similarity found in sticklebacks in widely scattered but similar habitats. This phenomenon is widespread among organisms. Hubbs (1943) has discussed the case of the Johnny darter, *Etheostoma nigrum*, which occurs in the Great Lakes and Mississippi River basins. Two subspecies, *E. n. nigrum* and *E. n. eulepis* have been recognized. *E. n. nigrum* is wide-ranging and ubiquitous, occurring over sandy bottoms in open water. It is slender and smooth-bodied. *E. n. eulepis* has a restricted distribution and occurs in water congested with vegetation. It is stout and rough-bodied. *E. n. eulepis* occurs in pockets of the appropriate habitat within the range of the other subspecies, *E. n. nigrum*. These pockets of *E. n. eulepis* are apparently products of selection on *E. n. nigrum* populations which have invaded weed choked habitats. Lagler and Bailey (1947) have shown that characters used to separate the two subspecies have a genetic basis in the populations they studied. The phenotypes of the two subspecies are believed to be adaptive for predator avoidance in their normal habitat.

Another interesting example of parallelism in similar but disjunct habitats was discussed by McPhail and Lindsey (1970). *Myoxocephalus quadricornis* is a circumpolar species of sculpin which tends to become isolated in fresh water. Compared to the marine form, the freshwater isolates known as *M. q. thompsoni*, have a shorter preopercle spine, lack spines on the head and shoulder girdle and lack tubercles below the lateral line. The degree of divergence in the different characters from the condition in the marine form is always about the same. The transition from marine to fresh water has taken place independently on Arctic islands, in Eurasia and North America (Johnson, 1964). The adaptive significance and genetic basis of the freshwater phenotype is apparently not known.

Hubbs (1940) has mentioned several genera of fishes including *Catostomus*, *Pantosteus*, *Gila*, *Richardsonius*, *Lepidomeda*, *Rhinichthys*, *Cottus*, and *Salmo*, which tend to have parallel isolates.

Kabata and Cousens (1972) studied the structure of the attachment organ, the bulla, of parasitic copepods in the family Lernaeopodidae and found that parallelism has been a dominant feature of the radiation of this group. They recognized three types of bullae: type I of parasites on freshwater teleosts and acipenseriforms, type II of parasites on marine teleosts and type III of parasites on elasmobranchs and holocephlans. They prepared a phyletic dendrogram for the family based on details of development. The type I bulla occurs in only one group of the family but type II occurs in two independently derived groups plus one early offshoot. Type III bulla also occurs in two distinctive groups. The parallel attainment of the same bulla structure repeatedly has resulted from the responsiveness of bulla structure to host type. The adaptive significance of bulla morphology, the authors speculate, is related to osmotic stress placed on the parasite by the osmolarity of the host tissues and that of the environment.

Mosquin and Small (1971) reported parallel development of autopolyploidy in *Epilobium angustifolium* and *E. latifolium*, members of the primrose family. In both species, diploids occur in more northern and Alpine areas of Eurasia and north America while polyploids occupy warmer, southern regions. Polyploids of both forms closely resemble the diploids except that there is an increase in extra pores in the pollen grains. The two species are closely related and the authors speculated that genetic characteristics of the common ancestral species preadapted them to give rise to autopolyploids. Autopolyploids may have arisen repeatedly within both species.

Geographic variation in the coat color of *Peromyscus* and some other rodents has been shown to be correlated with substrate color (Blair, 1947a, 1947b; Dice, 1939a, 1939b, 1940). Many of these studies included experimental crosses which indicate that coat color is genetically determined. Dice (1947) showed that mice which most closely match the substrate were least subject to predation by visually orienting predators under laboratory conditions. There is strong evidence in some of these studies that coat color has been independently selected to match the substrate in different populations (Blair, 1943, 1947b; Dice, 1939a, 1939b). Many other examples could be cited for the rodents.

Many other cases of parallelism are scattered through the literature. Parallelism for size and shape in the frog genus *Hyla* (Jameson and Richmond, 1971), pigment pattern polymorphisms in the snail *Caepea* (Jones, 1973), and biochemical products in the lichen-forming fungus, *Parmelia*, (Culbertson and Culbertson, 1973) are a few additional examples. The general pattern that emerges from studies on a heterogenous group of organisms is that phenotypes in a given locality are rather precisely matched by natural selection of existing phenotypes to fit the local environment. Thus, when similar environments are encountered, similar phenotypes for a given species are frequently seen. An alternative explanation for a disjunct distribution of phenotypes is that dispersal has taken place between similar habitats or that populations in these habitats are relicts of a former widespread range. In some cases, parallelism is the only acceptable hypothesis. The distribution of pelvic-less sticklebacks, *Pungitius* (Nelson, 1971a) and *Gasterosteus* are particularly convincing examples of the role that parallelism can play in the distribution of organisms with very similar phenotypes in geographically or temporally separated but ecologically similar habitats. The possibility of parallelism must be considered as a reasonable alternative hypothesis to dispersal or relicts to account for the disjunct distribution of phenotypes within the range of a species. Behnke (1972) did not seriously consider the possibility of parallelism to explain the presence of cisco (*Coregonus pollan*) in Ireland which he believed were not sufficiently different to warrant subspecific separation from the Arctic cisco (*C. autumnalis*) that is not found west of the Menzen River of the eastern White Sea Basin. He concluded that the only explanation for this distribution pattern is that the Irish *C. pollan* populations are relicts of a

widespread postglacial distribution of *C. autumnalis*. This paper contains numerous references to allegedly relictual salmonid populations to explain similarly disjunct distributions of phenotypes. In addition, systematists must be very careful lest they describe as single taxa a series of phyletically unrelated populations which are independently adapted to similar environments. Hubbs, as early as 1929, noted this possibility for *Gasterosteus* and this problem continues to be a source of controversy in this genus (Hagen and McPhail, 1970; Miller and Hubbs, 1969).

#### *The Law Of Homologous Series In Variation*

If parallelism is an important factor in the distribution of phenotypes within species and closely related species have similar ecological requirements, one would expect to find parallel populations of closely related taxa often in the same areas. This phenomenon was discussed by Vavilov (1922) who termed it the law of homologous series in variation. He gave abundant examples of such series from cultivated plants such as grains, beans, cotton, squash and mellons. He concluded that in general, closely related species have similar and parallel series of varieties. The more consanguinous the species are, the more precise is the similarity of the variants. Vavilov believed that a consequence of the law is that one could predict unknown phenotypes from a knowledge of variation in closely related species. Hovanitz (1947) recognized this pattern of parallelism among mosquitoes, fruitflies, and butterflies, and also noted the tendency for parallelism to be more precise among more closely related taxa. The law of homologous series in variation is pertinent to the Gasterosteidae.

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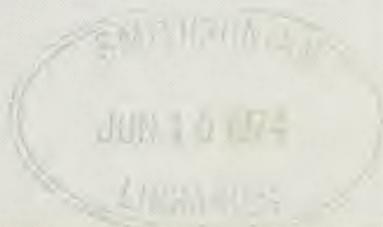
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A HEMPHILLIAN LOCAL FAUNA CONTAINING A  
NEW GENUS OF ANTILOCAPRID  
FROM SOUTHERN CALIFORNIA

*By* WADE E. MILLER and THEODORE DOWNS

CONTRIBUTIONS IN SCIENCE



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# A HEMPHILLIAN LOCAL FAUNA CONTAINING A NEW GENUS OF ANTILOCAPRID FROM SOUTHERN CALIFORNIA<sup>1</sup>

WADE E. MILLER<sup>2</sup> and THEODORE DOWNS<sup>3</sup>

**ABSTRACT:** The Kinsey Ranch local fauna was collected from fluvial deposits (upper Peace Valley beds and lower Hungry Valley Formation) of middle Pliocene (Hemphillian) age, located in the northwest corner of Los Angeles County, California. Faunal components, mostly ungulates, indicate a predominantly grassland condition in the studied area.

A new genus and species of antilocaprid, *Ottoceros peacevalleyensis* Miller and Downs, is described and is the most significant and well represented constituent of the local fauna. Although the exact position of this new taxon in the antilocaprid phylogeny is not known, its closest affinity appears to be with *Sphenophalos*.

The structural grade of the *Pliohippus* and the rhinocerotid together with cf. *Tanupolama* suggest a Hemphillian age for the Kinsey Ranch local fauna.

## INTRODUCTION

A relatively small local fauna has been recovered from the Hungry Valley-Peace Valley area of southern California, and can be dated as Hemphillian (traditionally Middle Pliocene).

Fossil vertebrates were first recorded from Hungry Valley by Chester Stock (in Crowell 1950:1638). This area is located in the northwestern corner of Los Angeles County, California (Fig. 1).

In August of 1952, Howard T. Anderson of Standard Oil Company of California brought to the Natural History Museum of Los Angeles County, the original slab of sandstone containing the diagnostic parts of the new genus of Antilocapridae to be described in this paper. This material was discovered by William P. Davidson of the above mentioned company on the G. E. Kinsey Ranch in the Hungry Valley area. Further investigations were made at the site in 1952, and 1953, by Theodore Downs with Howard Anderson, Steven Anderson and Jon Szati all of Standard Oil Company, resulting in the discovery of more material representing the new genus. Collections of other vertebrates from this area were made previously by personnel from the California Institute of Technology (CIT). These collections are now in the

### <sup>1</sup>REVIEW COMMITTEE FOR THIS CONTRIBUTION

DONALD E. SAVAGE

RICHARD H. TEDFORD

DAVID P. WHISTLER

<sup>2</sup>Research Associate, Section of Vertebrate Paleontology, Natural History Museum of Los Angeles County, and Departments of Zoology and Geology, Brigham Young University, Provo, Utah 84602

<sup>3</sup>Chief Curator, Earth Sciences Division, Natural History Museum of Los Angeles County, Los Angeles, California 90007

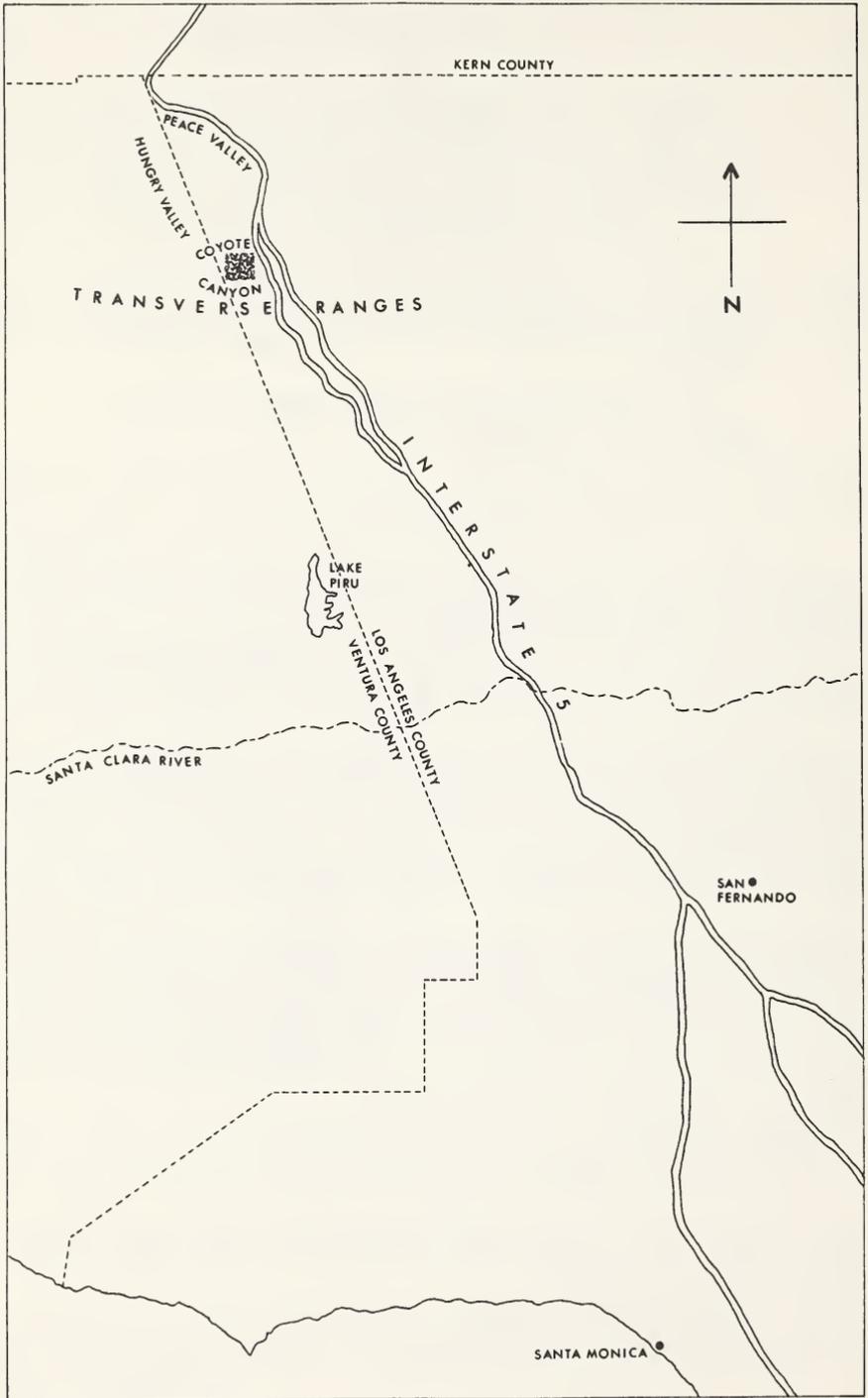


FIGURE 1. Generalized locality map, Hungry Valley-Peace Valley area (Kinsey Ranch local fauna shown in shaded portion of map).

Natural History Museum of Los Angeles County (LACM). From March, 1970, to June, 1971, Wade E. Miller made several field trips with students and associates to the area in an attempt to recover more faunal material (with moderate success) and to relocate previous CIT sites.

#### ACKNOWLEDGEMENTS

We are grateful to Mr. G. E. Kinsey of Los Angeles for granting permission to collect and prospect for fossils on his property. We are especially indebted to William P. Davidson who discovered *Ottoceros* and Howard T. Anderson (of Standard Oil Company of California); the latter recognized the significance of the remains of *Ottoceros* and arranged to have the material deposited in the Natural History Museum of Los Angeles County. Others who were helpful in the recovery of fossils and information include John Szati, Kurt Camp, Clarence Aschbrenner, and Steven Anderson. We have particularly benefited from opinions and information provided by R. H. Tedford, D. E. Savage, M. C. McKenna, B. Taylor, the late R. A. Stirton and S. David Webb. Material for comparison was made available by the late R. A. Stirton and D. E. Savage of the Museum of Paleontology, University of California, Berkeley, and C. B. Schultz of the University of Nebraska State Museum, B. H. Brattstrom made the original reptile identifications. John S. Babel and Laurie Bryant Macdonald assisted in measurements of skeletal material. D. E. Savage, David P. Whistler, R. H. Tedford and L. G. Barnes kindly reviewed the manuscript.

The unusual skill of William J. P. Otto is especially appreciated; all the preparation of the highly indurated matrix enclosing *Ottoceros* and the restorations were successfully accomplished by Mr. Otto while he was associated with the California Institute of Technology and the Natural History Museum of Los Angeles County. The illustrations were prepared by Mary Butler and the photography was done by Howard K. Johnson and the late George Brauer. The several drafts of the manuscript were typed by Carolyn Chadburn of Brigham Young University and by Linda L. Wilson and Marjorie Travis of the Natural History Museum of Los Angeles County. Assistance in curation of the material from Kinsey Ranch was done by Richard L. Reynolds and Paul Langenwalter, both of the Natural History Museum of Los Angeles County. Part of the financial assistance was made possible through funds from the National Science Foundation (GB 33585X).

#### GEOGRAPHIC AND STRATIGRAPHIC SETTING

The Kinsey Ranch local fauna was collected from the northwest corner of Los Angeles County about seven miles south of the town of Gorman (Black Mtn quadrangle, California, 1958). The fossil sites comprising this locality trend north-south along a low mountainous ridge of the Transverse Ranges just west of Peace Valley and Interstate Highway 5 (Fig. 1). Elevations of these sites vary from about 3,000 to 3,300 feet. This area is drained

by numerous intermittent streams which trend roughly northwest to southeast. The climate is semiarid with vegetation consisting largely of chaparral, sage and scattered oak trees. Numerous ravines are sparsely vegetated, resulting in widespread areas of exposed rock.

Pleistocene disturbances largely responsible for the present structure of the Transverse Ranges are evidenced in this area by incised stream beds with accompanying elevated floodplains and open folding of rock units. Beds yielding the fossils strike roughly north-south and dip westward from  $20^{\circ}$  to  $45^{\circ}$ . Although faults are known in the general area, none were detected within the area of the present study.

Two geological units are exposed in the area of study, the Peace Valley beds and the conformably overlying Hungry Valley Formation, both of which yield vertebrate fossils. These Pliocene beds were described in detail by Crowell (1950). He stated that the Peace Valley beds in this area are probably underlain by a quartz monzonite of unknown age. They are reported to be about 4,000 feet thick (Crowell, 1950). They vary from shales to coarse sandstones in exposed areas, with colors grading through gray, to brown. Subrounding of the larger clasts, relatively poor sorting and arkosic sediments are suggestive of limited stream transport. Occasional cross-bedding and asymmetrical ripple marks also support a fluvial origin of the sediments. The site yielding the majority of antilocaprid specimens (LACM locality 1092) is located in the Peace Valley beds in the southernmost part of the study area adjacent to Coyote Canyon. The bones were found just-posed in a steeply dipping flaggy sandstone unit which rests on a sandy, silty, shale. The remainder of fossil sites in the Peace Valley beds are north of Hungry Valley.

In thickness the Hungry Valley Formation is roughly equivalent to the Peace Valley beds (Crowell, 1950); the mode of accumulation is probably similar also. Although some of the sediments are coarser in the Hungry Valley Formation, varying from shaly silts to pebbly sands, a fluvial origin is indicated by cross-bedding, scour marks and rounded to subrounded clasts. Only the lower portion of this unit, that conformably overlies the Peace Valley beds, is present in the area of investigation.

## SYSTEMATIC DISCUSSION

### Class Reptilia

#### Family Testudinidae

##### *Clemmys* cf. *C. marmorata*

*Material*—shell and carapace fragments (LACM 27956, 27976, 27961, 27965, 28469).

The above specimens show great similarity to the living western pond turtle, *Clemmys marmorata*. However, the fossil specimens do not seem sufficiently diagnostic to allow a positive identification at the species level.

cf. *Geochelone*

*Material*—carapace fragments (LACM 27933, 27994, 27975, 27963 28470).

A large tortoise is included in the present collection as indicated by the size and configuration of the carapace fragments (they are heavier and thicker than in *Gopherus*). The material most closely approximates *Geochelone*.

Class Mammalia

Order Carnivora

Family? Felidae

## Figure 2

*Material*—questionable P<sup>3</sup> of a felid (LACM 28340).

A nearly complete tooth (the anterior root is missing) of a moderately large carnivore is the only evidence for this order in the present local fauna (Fig. 2). This tooth resembles both a right P<sup>3</sup> of a moderately large (puma-sized) felid and a left P<sub>4</sub> of a large canid. The similarity between these teeth in certain felids (P<sup>3</sup>) and canids (P<sub>4</sub>) is striking. We (Miller and Downs, 1971) previously identified this tooth questionably as *Osteoborus* Stirton and Vanderhoof but further study and review indicate it could be felid.

P<sup>3</sup> in the jaguar appears different than the tooth from the present carnivore by possessing an accessory cusp anterolingual to the principal cusp and by lacking a well-developed posterior cingulum which is evident on the tooth from Kinsey Ranch. In the latter form this cingulum is strongly upturned posteriorly and is developed into a third cusp. In several Pleistocene and Recent mountain lions observed, this cingular cusp is present but not as dis-

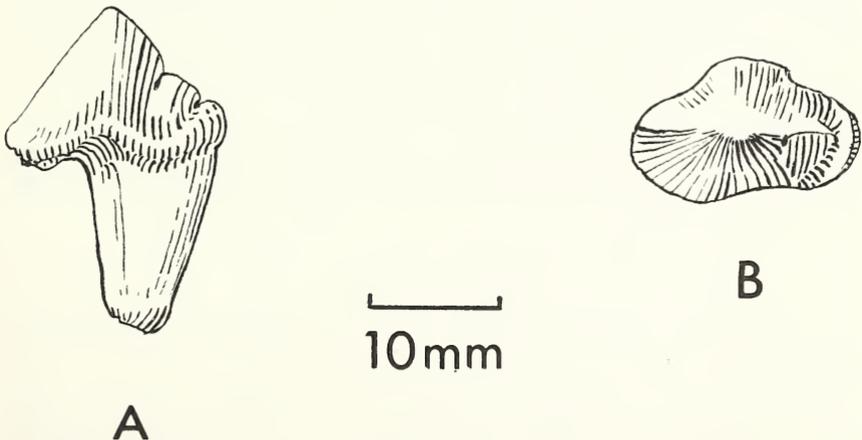


FIGURE 2. ?Felidae, right P<sup>3</sup>, LACM 28340; a. lateral view, b. occlusal view.

tinct. However, it is distinct in *Felis studeri* from Cita Canyon in Texas (Savage, 1960). *F. studeri* evinces a P<sup>3</sup> that strongly resembles the Kinsey Ranch tooth in many respects. It does differ, though, by possessing a flattening or shelf on the lower half of the anterior edge of the principal cusp which the present specimen does not show. Several Recent and fossil *Felis concolor* specimens also have this shelflike structure. The Kinsey Ranch tooth also differs from *Felis studeri* in the configuration of the posterolateral border. This border is slightly concave in the first-named form and convex in the latter. The tooth from the present local fauna has a distinct ridge trending dorsoventrally along the anterior edge of the principal cusp which is similar to that in canids. In cats, including *Felis studeri*, this ridge is present but is directed more medially.

Comparisons of the fossil tooth with numerous specimens and illustrations of *Osteoborus* P<sub>4</sub>s show that the configuration of the crown bears strong similarities. It was noted, however, that the shape of *Osteoborus* P<sub>4</sub> crowns is quite variable. The major difference between the crown of the Kinsey Ranch specimen and that in the P<sub>4</sub> of *Osteoborus* is the slightly narrower posterior than anterior width of the tooth. The posterior width of P<sub>4</sub> in *Osteoborus* is almost always greater than the anterior width (however, a few specimens seen had a posterior width about equal to the anterior one).

The root of the Kinsey Ranch tooth resembles a felid more than *Osteoborus* in being laterally rather than anteroposteriorly compressed. An exception to this condition was observed in a specimen of *Osteoborus*, *O. orc*, from Florida (University of Florida, UF 14781) in which the P<sub>4</sub> root was elongate anteroposteriorly rather than transversely. The tooth row was not characteristically crowded in this individual. It seems that the typically anteroposteriorly compressed roots of P<sub>4</sub> and other teeth in *Osteoborus* is a result of tooth crowding. If a tooth is not crowded, it evidently develops a laterally compressed root. Another characteristically felid trait of the carnivore from the present local fauna is the distinctly larger posterior than anterior root. Although the anterior root is missing in the studied tooth, it could not have been as large as the posterior one. The two roots are generally subequal in canid P<sub>4</sub>s.

Until or unless additional material of this carnivore is found that can help resolve the present uncertainties, the familial as well as generic designation will be in doubt.

#### Order Proboscidea

*Material*—A mastodont tooth fragment, LACM 28339; a tusk fragment, LACM 27955; a cuboid, LACM (CIT) 4010; and limb fragments, LACM 28000.

The nature of the collected material is not sufficiently diagnostic to allow even a positive familial identification with available reference specimens and illustrations. The cuboid, however, might be identified to family when suffi-

ciently complete and positively identified carpal material representing Gomphotheriidae and Mammutidae becomes available.

### Order Perissodactyla

#### Family Equidae

#### *Pliohippus* Marsh

#### Figures 3-4

*Material*— $P_3$  and  $P^4$ , LACM (CIT) 3924;  $P^2$ , LACM 27978;  $M^2$ , LACM 27951 and LACM (CIT) 2925; incomplete upper cheek teeth, LACM 27959, 28341, 27982, 27990, 27977, and 27962; jaw symphysis, LACM (CIT) 4009; jaw fragment, LACM 28344;  $P^2$ , LACM 28346; lower molars, LACM 27966 and 28342; incomplete lower cheek teeth, LACM 27989, 27968 and 28453; incisor, LACM 27952; incisor fragments, LACM 28455 and 28546; distal radius epiphysis, LACM 27967, radii fragments, LACM 27949 and 27974; patella, LACM 27964; distal portion of tibia, LACM 27991; incomplete calcanei, LACM 27988 and 28345; external cuneiform, LACM 28349; distal end of metapodial, LACM 27957; two incomplete phalanges (1st), LACM 28347 and 27972; 2nd phalanx, LACM 28468; sesamoid, LACM 28464; and splint bone, LACM 28465.

Stock (*in* Crowell, 1950) commented on the few specimens of equid from the Hungry Valley area known at that time. Since then several additional specimens have been collected. It appeared to Stock that two species of horse were represented as based on size of the teeth. The present study shows that all existing dental material is within the size limits of one species.

Stock's comparisons were made with *Plesippus francescana* (Frick) from the Coso Mountains of California (Blancan age) and with *Pliohippus* cf. *P. spectans* (Cope) from the Kern River fauna of California (Hemphillian age). He noted that the Kinsey Ranch horse was slightly smaller than the former and larger than the latter. His description implies that it was intermediate between the two named species based on dental characteristics. Although he stated that the Kinsey Ranch equid was slightly smaller than *P. francescana*, we have found that it coincides in size of teeth with smaller individuals of that species. However, the present species is markedly smaller in all its represented postcranial elements. While dental characters do show some similarities between the Kinsey Ranch horse and *P. francescana*, the former exhibits characters more like *Pliohippus* (Figs. 3 and 4). These characters include lack of a protoconal heel, distinct curvature of cheek teeth, moderate degree of hypsodonty and well rounded, subequal metaconid and metastylid. The Kinsey Ranch *Pliohippus* has teeth that are distinctly larger and less curved than *Pliohippus* cf. *P. spectans* from the Kern River fauna and, as Stock observed, the protocone of the former horse is flatter along its lingual border. Surprisingly, all postcranial material of the present form is somewhat smaller than *P. cf. spectans*. The very simple enamel pat-

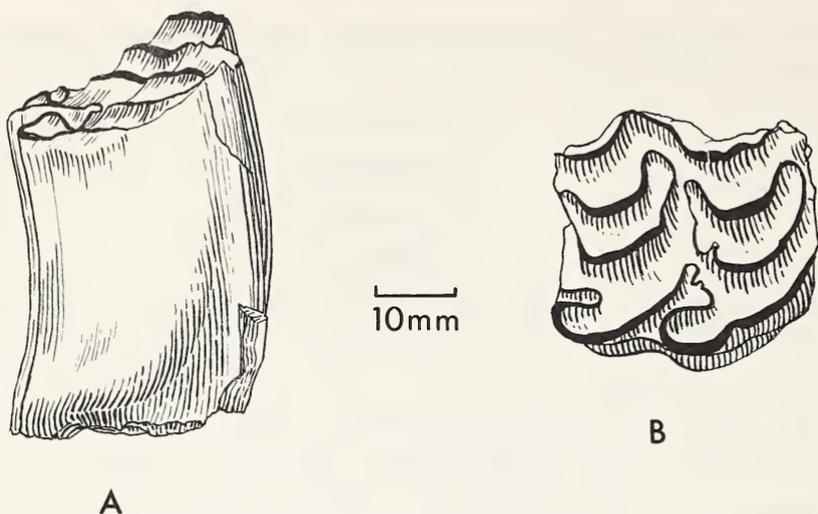


FIGURE 3. *Pliohippus* sp., right P<sup>3</sup>, LACM (CIT) 3924; a. anterior view, b. occlusal view.

terns in the teeth, the nearly equal size of the metaconid and metastylid, and the unrestricted opening of the metastylid are indicative of *Pliohippus* rather than *Dinohippus* as described and figured by Quinn (1955). Also, the metastylid has an unrestricted opening as opposed to the restricted opening in *Dinohippus*. Although it is possible that two species of equid exist in the Kinsey Ranch local fauna, one known only from dental and the other from postcranial material, it seems unlikely.

The stage of dental development suggests that the Kinsey Ranch horse is a slightly more advanced form than the one from the Kern River fauna. It compares closely with the *Pliohippus* from the Mt Eden fauna (Hemphillian age) of California. The only differences are the slightly smaller tooth size and very slightly greater tooth curvature of the Mt Eden species. Frick (1921) named two new species of *Pliohippus* from the Mt Eden fauna; the type of each was a single upper cheek tooth. *Pliohippus osborni* Frick is a supposed larger species with an incipient protoconal heel, and *P. edensis* a smaller

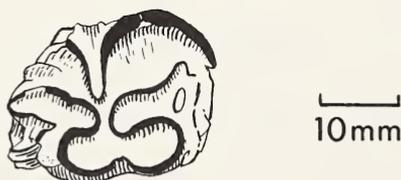


FIGURE 4. *Pliohippus* sp., occlusal view of lower cheek tooth, LACM 28453.

species without a protoconal heel. However, the intraspecific variation known in equid teeth could reasonably include the known Mt Eden specimens in one species. Illustrations in Frick's (1921) paper show a gradation from teeth with no protoconal heel to ones showing a modest development of one. It does not appear that *P. osborni* and *P. edensis* represent two distinct species.

#### Family Tapiridae

##### *Tapirus* Brännish

*Material*—scaphoid, LACM (CIT) 4005; lunar, LACM (CIT) 4006; and two median phalanges, LACM (CIT) 4007 and 4008.

The above listed specimens were found in close association and probably represent one individual. Bone density and complete epiphyseal fusion of the phalanges indicate the represented tapir was either mature or nearly so. Examination of large numbers of Pleistocene *Equus* median phalanges revealed that the proximal epiphysis does not completely fuse to the diaphysis until a nearly adult size is reached. It is postulated that this condition is possibly similar in the tapir.

The tapir in the Kinsey Ranch local fauna is about one-third the size of the extant *Tapirus terrestris* (Linnaeus) and one-half that of *T. pinchaque* Roulin. Both carpals and phalanges from the fossil tapir resemble the modern *Tapirus* available for study and specimens figured by Radinsky (1965). Apparently only one genus, *Tapirus*, is recognized for all North American Pliocene through Recent tapirs.

#### Family Rhinocerotidae

##### ? *Aphelops* Cope

*Material*—tooth fragment, LACM (CIT) 4012.

Although the tooth fragment, an ectoloph from M<sup>2</sup>, cannot be identified with certainty, its size and configuration most closely approximate *Aphelops*. LACM (CIT) 4012 is a hypsodont tooth (slightly worn) and for that reason *Peraceras* Cope can probably be eliminated from serious consideration. Matthew (1931) observed that *Peraceras* remained subbrachyodont whereas *Aphelops* tended toward hypsodontology in Pliocene time. The dentitions of *Teleoceras* Hatcher studied exhibit a greater degree of hypsodontology than does the Kinsey Ranch specimen. In his review of the rhinoceroses, Matthew (1932) noted that *Teleoceras* by Middle Pliocene time was very high-crowned, while *Aphelops* was only moderately so. A study of sufficient amount of comparative material may show the present specimen to be definitely outside the variable limits of *Teleoceras*. However, until such a comparative study can be made, the Kinsey Ranch rhinocerotid will questionably be assigned to *Aphelops*.

## Order Artiodactyla

Family Camelidae  
cf. *Tanupolama Stock*  
Figure 5

*Material*—P<sup>4</sup>, LACM (CIT) 3957; M<sub>2</sub>, LACM (CIT) 3958 and LACM 28459; metapodial fragments, LACM (CIT) 3961 and LACM 2857; astragalus, LACM (CIT) 2962; astragalus fragments, LACM 28343 and 28458; and a navicular, LACM (CIT) 3960.

The above material is representative of a slenderly built camel. Of the smaller Pliocene camelids the present specimens appear more closely allied to *Tanupolama* than to either *Procamelus* or *Protolabis*. According to Webb (1969), the mandible, and in particular the length and width of the cheek teeth, is most widely used in taxonomic identifications of *Procamelus*. This might also apply to other genera such as *Protolabis*. In the above paper Webb gave dental and other measurements of eight specimens of *Procamelus grandis*. The variation in anteroposterior basal length of M<sub>2</sub> was 26.5 to 31.4 mm and the maximum width 18.8 to 20.9 mm. The Kinsey Ranch camel M<sub>2</sub> (LACM 3958, Fig. 5) which shows only a modest amount of wear, measures 22.7 mm and 14.3 mm in basal length and maximum width respectively (greatest anteroposterior length 27.5 mm). Both measurements on this last specimen are significantly less than any measurements seen for species of *Procamelus* or *Protolabis*. An unworn M<sub>2</sub> from the present local fauna (LACM 28459) is also smaller than corresponding teeth in these two genera. This tooth has a basal anteroposterior length of 22.8 mm and a transverse

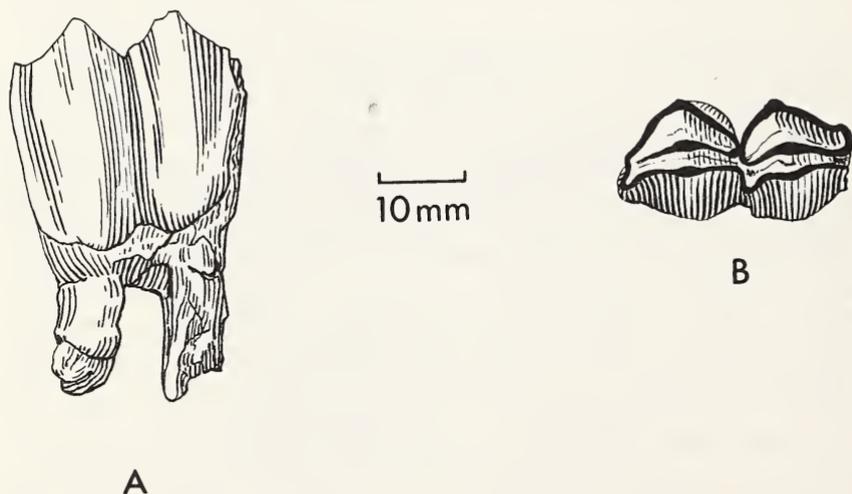


FIGURE 5. cf. *Tanupolama*, left M<sub>2</sub>, LACM (CIT) 3958; a. lingual view, b. occlusal view.

width of approximately 14 mm (greatest anteroposterior length, 26 mm). Average larger size, poorly developed (if at all) llama buttresses and flatter lingual molar walls characterize *Pliauchenia* in contrast with the present camelid.

Comparison of the Kinsey Ranch slender camelid to *Tanupolama* was made and a close correspondence was noted. Although the present fossil form has cheek teeth narrower in transverse width than *Tanupolama stevensi* (Merriam and Stock) from McKittrick, California, the disparity is not as great as when compared to *Procamelus* or *Protolabis* and probably falls within the variable limits of the first-named genus. The basal anteroposterior length of the known cheek teeth, while a little less than the average for *Tanupolama stevensi* specimens, does apparently fall within the limits of that species. LACM (CIT) 3958 ( $M_2$ ) while closely approaching the same tooth in the above species, does differ by possessing more distinct ribs and a less pronounced llama buttress. LACM (CIT) 3957 ( $P_4$ -basal length is 13.5 mm, maximum width is 14.0 mm), and LACM 28459 ( $M_2$ ) also evidence more distinct ribs than do corresponding teeth from the McKittrick *Tanupolama*, and the  $P_4$  shows development of an anterior and posterior cingulum, discontinuous along the lingual border. No cingula are present on the two specimens of *Tanupolama* possessing  $P_4$  from McKittrick, California. However, two Pliocene specimens of *Tanupolama* from the University of Florida (unnumbered) show cingular development somewhat similar to the Kinsey Ranch specimens. The lingual surface of both the present  $M_2$ s is not as flat as in *Procamelus* or *Protolabis* but is similar in this regard to *Tanupolama*, where there is a distinct step between tooth moieties. Although the llama buttress is better developed in *Tanupolama stevensi*, it is distinct in the present species and essentially lacking in the other two named genera.

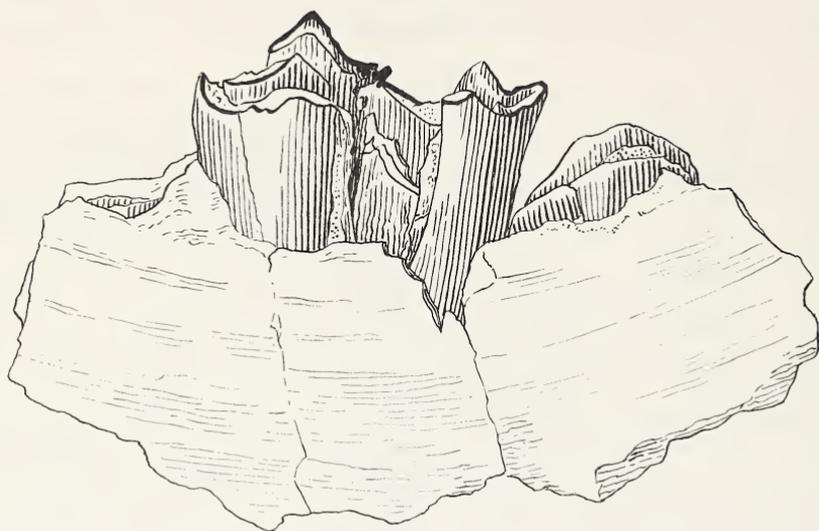
The relatively small and slender limb bones and other postcranial specimens from Kinsey Ranch, tentatively referred to *Tanupolama*, are essentially indistinguishable from *T. stevensi* except for a slightly smaller size. While there is insufficient evidence to establish a definite relationship, the possibility exists that the Kinsey Ranch species of *Tanupolama* is ancestral to *T. stevensi*. A new species may be represented here but the present limited material and the existing confusion in camelid taxonomy would seemingly make the naming of a new species unwise.

cf. *Megatylopus* Matthew and Cook

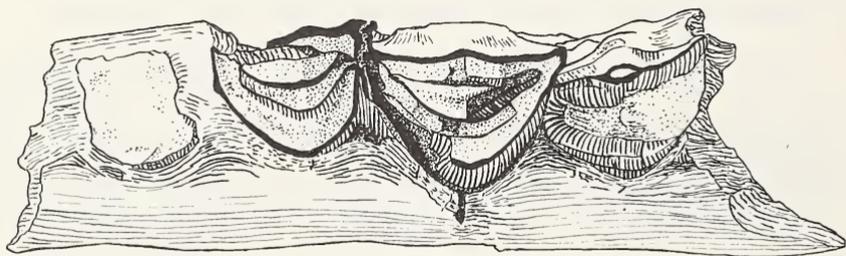
Figure 6

*Material*—A jaw fragment, LACM 28348; and a median phalanx, LACM (CIT) 2959.

The jaw fragment (Fig. 6) contains an  $M_2$  (noticeable wear is indicated) and the anterior lobe of  $M_3$  (erupted but not in occlusion). This camel is significantly larger than any described species of *Tanupolama*, *Protolabis*, or *Procamelus*. The  $M_2$  has an anteroposterior basal length of



A



B

  
10mm

FIGURE 6. cf. *Megatylopus*, fragment of left dentary showing  $M_2$  and anterior lobe of  $M_3$ , LACM 28348; a. labial view, b. occlusal view.

35 mm (greatest anteroposterior length, 42.3 mm) and is 34.1 mm in greatest transverse width.

The present specimen fits more closely within the range of variation of *Megatylopus* than any other genus seen. In the  $M_2$  a relatively deep medio-lingual groove is evident which is partly enclosed superiorly by the metastylid. The anterior lobe of  $M_3$  is directed slightly labially so that the posterolingual margin of the tooth is not appressed. Later wear stages would alter this condition slightly, however.

The median phalanx is no longer than that of an adult *Tanupolama* but is noticeably broader. Since the proximal epiphysis is missing, a juvenile is indicated, and the ultimate possible length of the phalanx is unknown. Its distal configuration differs significantly from specimens of *Tanupolama*. The lateral sulci are much less distinct (this character may in part be due to the juvenile stage) and the articular surface is markedly different, especially in much greater width of its superior expanse.

Family Antilocapridae  
Subfamily Antilocaprinae

**Ottoceros peacevalleyensis** new genus and species

Figures 7-13

*Holotype*—LACM 1372, incomplete skull including left horn core and upper dentition,  $P^3$ - $M^3$ , of a mature male from the Kinsey Ranch local fauna, Peace Valley, Los Angeles County, California (LACM Loc. 1092, Fig. 7).

*Referred material*—All numbers refer to the Natural History Museum (LACM). An asterisk (\*) after numbers refers to specimens in addition to the holotype that were used in the composite skeletal restoration (Fig. 8). Cranial measurements are given in Table 1 and postcranial measurements in Table 2. The slabs of sandstone containing the mass of antilocaprid specimens were found on strike within 30 meters of each other. There were two major slabs which yielded the type and referred material (Figs. 9 and 10) and two lesser slabs. All slabs averaged 5 to 10 centimeters in thickness. Before the fossils were extracted from the matrix of the two larger pieces, casts were made in order to preserve the original association of deposition. William P. Otto meticulously prepared the remains with a small motor-driven grinding wheel and hard, pointed needles. On the basis of mandibles recovered, there were at least five individuals preserved.

Right orbital-maxillary region, 29722; occipital condyles, 29366\*; auditory bullae, 29367\*, 29702; palate with  $P^4$ ,  $M_1$ - $M_3$  (right and left side), 29041; right horn core with orbital area, 1374\*; left maxillary region with  $P_4$  (part),  $M_1$ - $M_3$ , 1375\*, right mandible with  $P_4$ ,  $M_1$ - $M_3$ , 29043\*; right mandible with  $P_3$ - $P_4$ ,  $M_1$  and partial  $M_2$ , 29045\*; right posterior mandible portion with ramus and alveolus for  $M_3$ , 29365\*; right mandibular condyle, 29550; right mandibular symphyseal fragment with  $I_3$ , 29734; right mandibular fragment with  $P_4$  and  $M_1$ , 29736; right mandibular fragment with part of  $P_4$ , 29737\*; left mandible with  $P_4$ ,  $M_1$ - $M_3$ , and alveolae for  $P_2$  and  $P_3$ , 29042\*; left mandible with  $P_4$ ,  $M_1$ - $M_3$ , 29044; left mandible with  $P_4$ ,  $M_1$ - $M_3$ , 29046; left mandibular condyle, 29551; left mandible with symphyseal fragment,  $P_3$  and  $P_4$ , 29735; left mandibular fragment with parts of  $P_4$  and an  $M_1$ , 29738; cheek tooth fragments, 29739-29743; incisors, 29744-29747.



FIGURE 7. *Otoceros peacevalleyensis*, new genus and species. Holotype, LACM 1372, incomplete skull (white on horn core represents plaster restoration); lateral view, left side.

*Axial skeleton*—atlas, 29233\* and 29234\*; atlas fragments, 29588-29589; axis fragment, 29235\*; cervical vertebrae (3rd), 29236\*; (4th), 29237\*, (5th), 29238\*; (6th), 29239\*; (7th), 29240\*; cervical fragments, 29552-29553; thoracic vertebrae (1st), 29241\*; (2nd), 29242\*; (3rd), 29243\*; (4th), 29244\*; (5th), 29245\*; (6th), 29246\*; (7th), 29247\*; (8th), 29248\*; (9th), 29249\*; (12th), 29250\*; (13th), 29251\*, thoracic vertebrae fragments, 29709-29718, 29554-29557; lumbar vertebrae (1st), 29252\*; (2nd), 29253\*; (3rd), 29254\*; (4th), 29255\*; (5th), 29256\*; (6th), 29257\*; lumbar fragments, 29558-29559 and 29703; lumbar fragments, 29560, 29561, 29594-29598, 29704-29708; sacrum, 29258\*; 29440; sacral fragments 29592-29593; caudal vertebrae (1st), 29296\*; (4th), 29297\*; vertebral fragments, 29719-29721; right ribs (1st-10th), 29271\*-29279\*; (12th), 29280\*; (13th), 29281\*; left ribs (1st-9th), 29259\*-29267\*; (11th-13th), 29268\*; 29270\*; rib fragments, 29539-29733; manubrium, 29282\* and 29723; sternebrae, 29283\*-29286\*, 29294\* and 29428-29431- xiphoid, 29295\*.



FIGURE 8. Composite skeletal mount of *Otoceros peacevalleyensis*, new genus and species. Darker areas represent original bone, lighter ones plaster restoration. This is a cast based on at least five individuals in the reference collection and stands approximately 56 cm at the shoulder.

*Appendicular skeleton*—right scapula, 29048\*, 29441, 29567; left scapula, 29364\*, 29422, 29565, 29566; right innominate, 29358\*, 29426, 29590, 29591; left innominate, 29359\*, 29427; right humerus, 29047\*, 29436; right humerus proximal fragment, 29579 and distal fragment, 29574; left humerus, 29363\*; left humerus proximal fragments, 29562, 29578, and distal fragment, 29580 and 29581; right femur, 29575; left femur proximal portion, 29053\*; right patella, 29357\*, 29724; left patella, 29356\*; right radius-ulna, 29049\*; right radius, 29573; right radius proximal fragment, 29584; left radius, 29361\*, 29571, 29572; left radius proximal fragment, 29583 and distal fragment, 29582; right ulna, 29435, 29568, 29576, 29577; left ulna, 29362\*, 29439, 29569; right tibia, 29054\*, and distal fragments, 29585, 29586; left tibia distal fragment, 29587; right fibula, 29312\*, 29530, 29534; right scaphoid, 29298\*, 29523, 29525, 29511; left scaphoid, 29304\*, 29510, 29524; right lunar 29299\*, 29516; left lunar, 29305\*.

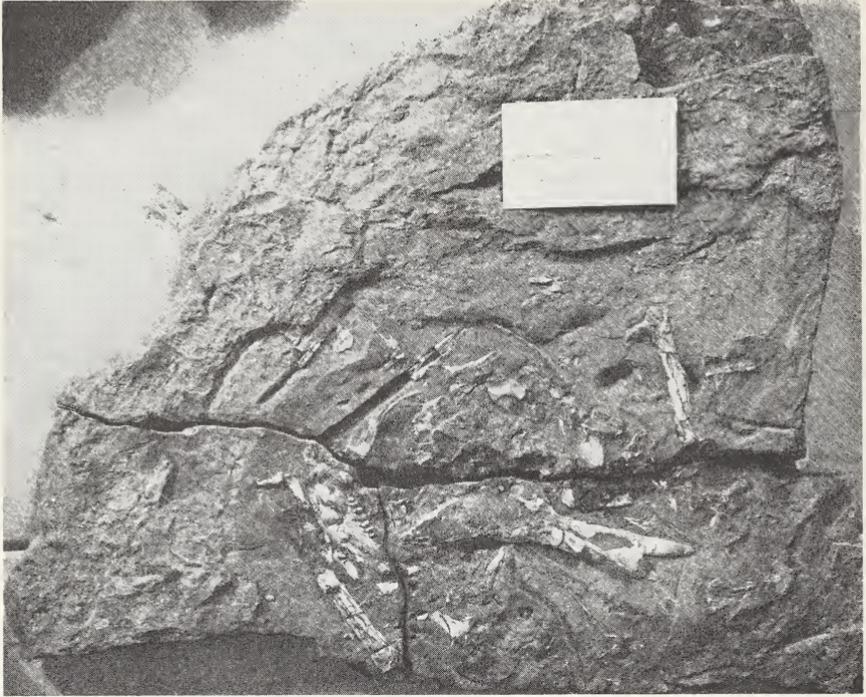


FIGURE 9. Photograph of sandstone block containing the type specimen of *Otoceros peacevalleyensis*, LACM 1372. Medial view of incomplete skull with horn core in lower center.

29515; right cuneiform, 29300\*, 29532, 29537; left cuneiform, 29306\*, 29531, 29533, 29535; right pisiform, 29301\*, 29514, 29529; left pisiform, 29307\*, 29538; right trapezoid-magnum, 29302\*, 29508, 29520, 29527; left trapezoid-magnum, 29308\*, 29513, 29519, 29522, 29526; right unciform, 29303\*, 29509; left unciform, 29507; right astragalus, 29058\*, 29060, 29728; left astragalus, 29059\*, 29521; right calcaneum, 29062, 29063\*; left calcaneum, 29061\*, and fragments, 29725, 29727; right navicular-cuboid, 29309\*, 29518; left navicular-cuboid, 29313\*, 29517; right entocuneiform, 29311\*; left entocuneiform, 29315\*, 29538; right meso-ectocuneiform, 29310\*; 29512; left meso-ectocuneiform, 29314\*; right metacarpal, 29051, 29360\*, 29438, 29570, 29729 (fragment); left metacarpal, 29050, 29052\*, 29432, 29437; right metatarsal, 29055, 29057\*, 29434; left metatarsal, 29056\*, 29433, sesamoid of manus, 29328\*-29335\*; sesamoid of pes, 29348\*-29355\*; sesamoid, 29748-29765; first phalanges of manus, 29316\*-29319\*; first phalanges of pes, 29336\*-29339\*; incomplete first phalanges, 29368-29385; second phalanges of manus, 29320\*-29323\*; second phalanges of pes, 29340\*-29343\*; incomplete second phalanges, 29386-29390, 29402-29412; ungual phalanges of manus, 29324\*-29327\*; ungual phalanges of pes, 29344\*-29347\*; incomplete ungual phalanges, 29413-29425.

*Age and formation*—Hemphillian (Middle Pliocene) Peace Valley beds.

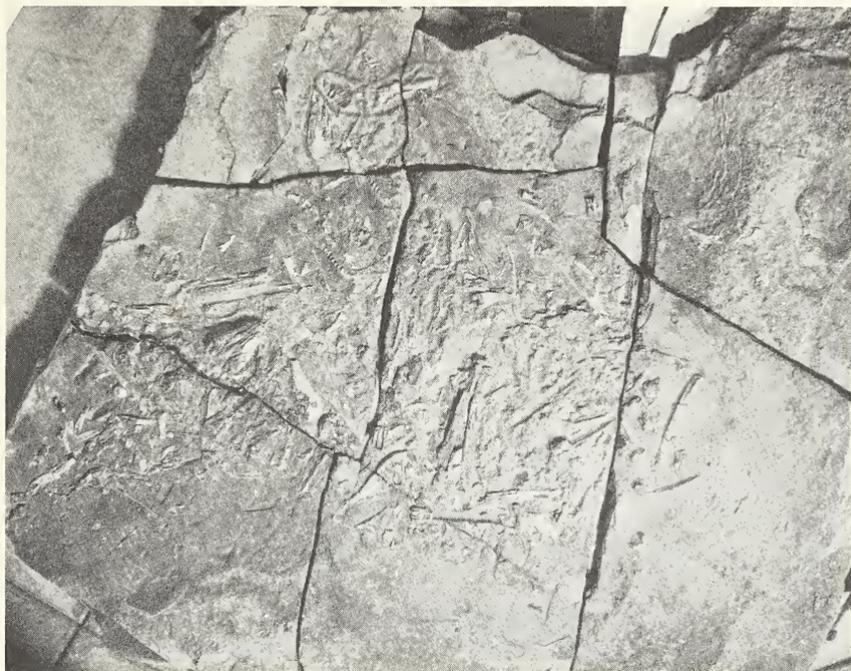


FIGURE 10. Photograph of sandstone block containing portion of skull, LACM 1374 (encircled area).

*Diagnosis of genus*—*Ottoceros* is distinguished from other *Antilocaprinae* as follows. It has a distinct lateral flange on the horn core which arises just above the orbit and terminates well below the bifurcation. The horn core slopes posteriorly approximately  $30^\circ$  from a line perpendicular to the palatal plane as determined by the restored skull (Fig. 11), and is situated on the posterior region of the orbit. There is a high horn core base with a bifurcation at the distal end which separates into two short prongs; the anterior one being slightly shorter. The height of the horn core base is three times the least anteroposterior diameter of the horn core. A slight constriction of the horn core base is present immediately above the orbit, with the maximum anteroposterior width being slightly below the point of bifurcation. *Ottoceros* has a less massive horn core than described species of *Sphenophalos* Merriam and it is relatively longer than the horn core in the extant genus, *Antilocapra* Ord. The horn core twists slightly counter clockwise and is slightly arcuate, presenting a shallow medial concavity and lateral convexity. The horn core is also flattened transversely and a section at the midpoint of the vertical height presents a roughly triangular outline, the apex at the lateral flange (Fig. 12). There is less protuberance of the orbit in *Ottoceros* than in *Antilocapra*.

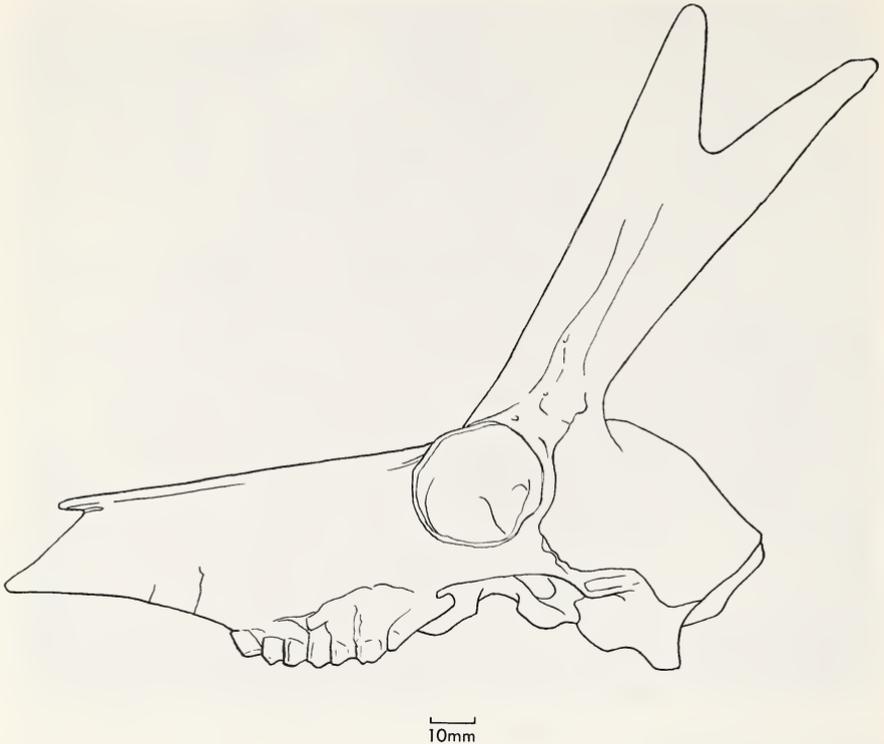


FIGURE 11. *Ottoceros peacevalleyensis*, new genus and species. Outline drawing of restoration (cast) of skull, based on LACM 1372, 29366, 29367, 29041, 1374, 1375, 29043, 29045, 29365 and 29042. Restoration by W. J. P. Otto.

*Diagnosis of species: peacevalleyensis*, is as for the genus.

*Etymology*—Otto, in honor of William J. P. Otto; *ceros*, Gr. *Keros*, horn; *peacevalleyensis* toponymic for the area of discovery, Peace Valley, California.

*Description and discussion*—Genera of antilocaprids have been erected primarily on differences in horn cores (e.g., see Stirton, 1932:46 and Webb, 1969:171 and Webb, 1973). However, the type specimen of *Ottoceros peacevalleyensis* contains both dentition and horn core. The relationship of *Ottoceros* to Antilocaprinae is indicated in: absence of burrs on the pedicel, non-deciduous horn cores, probable sheathed horn cores and horn cores straight compared to those in Merycodontinae (see Webb, 1973:203-204).

The type specimen, LACM 1372 (Figs. 7 and 12), represents an individual in early maturity as evidenced by the dentition ( $M^3$  shows a modest amount of wear). Most of the left side of the skull, somewhat lateral to the midline, is present. Some crushing and distortion are apparent, particularly along the medial side (Fig. 12). With the exception of most of the anterior

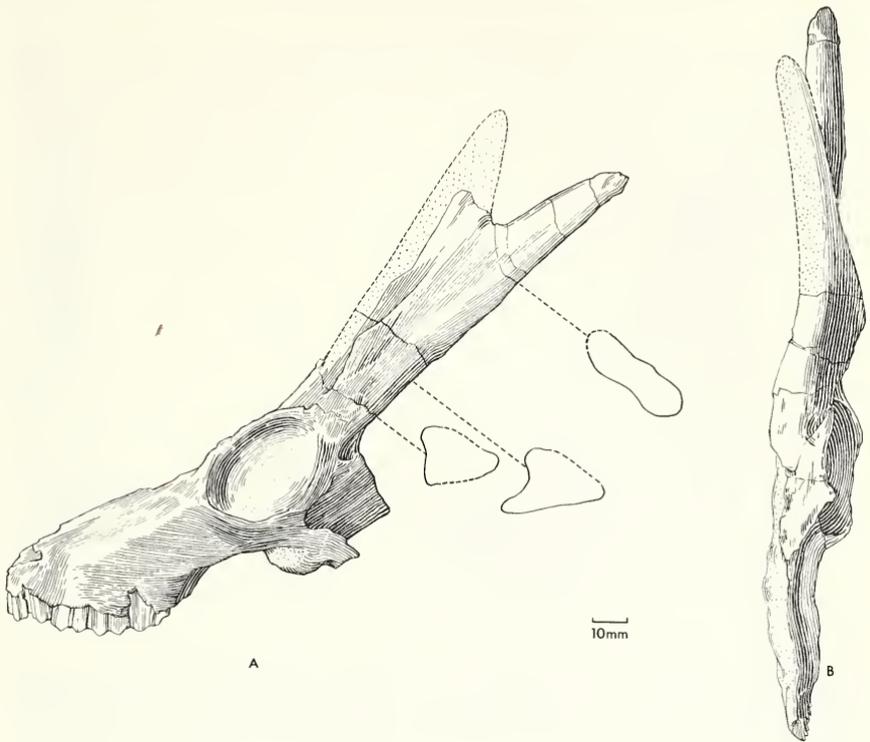


FIGURE 12. *Ottoceros peacevalleyensis*, new genus and species. Holotype, LACM 1372; a. lateral view of incomplete skull and outlines of horn core cross sections (stippling on horn core represents plaster restoration); b. anterior view of incomplete skull (stippling on horn core represents plaster restoration).

tine and some of the anterior edge, the horn core is complete. The posterior portion of the skull, just anterior to the auditory region, as well as the anterior part, from P<sup>2</sup> forward, are missing. From P<sup>3</sup>-M<sup>3</sup> the dentition is complete and in good condition.

Comparison with another specimen (LACM 1374) from the same fauna indicates that the holotype is probably a male. This second specimen (Fig. 13) is a skull fragment which includes the orbit, horn core (minus the anterior tine and a small portion of the base beneath it), and the posterior part of the maxilla including fragments of M<sup>2</sup> and M<sup>3</sup>. The horn core is markedly smaller than that of the type specimen and the lateral flange is only slightly evident. A mature animal is indicated, however. This can be shown by the presence of M<sup>3</sup> and an orbit that is slightly larger than the restored one of the type specimen. Significant disparity exists in the horn core size of the two specimens as well as in development of the lateral flange. Therefore, the holotype reasonably represents a male and LACM 1374 a female.

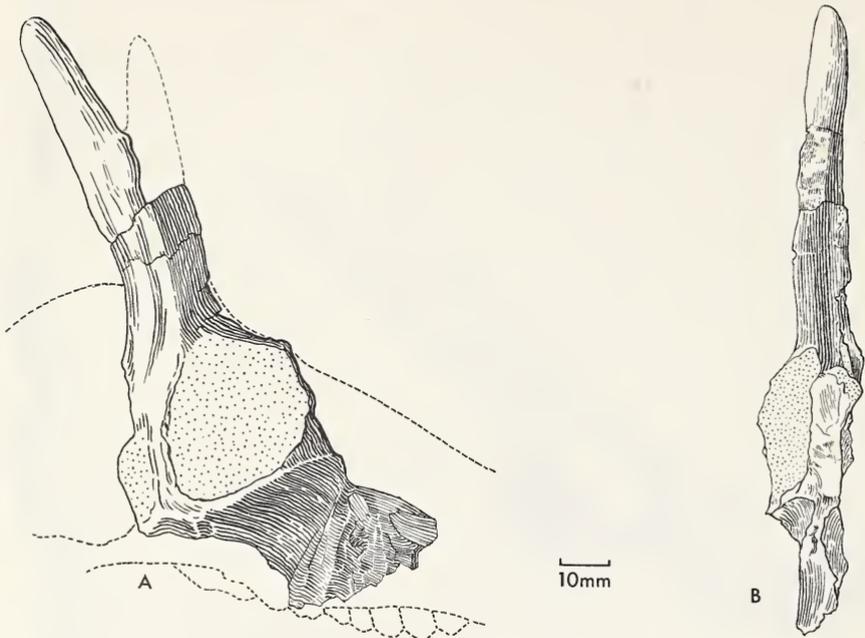


FIGURE 13. *Ottoceros peacevalleyensis*, new genus and species. Referred specimen, LACM 1374. Skull fragment from the right side showing horn core, orbital area and posterior portion of the maxilla; a. lateral view (dashed line represents outline of anterior horn core fragment as taken from natural mold), b. anterior view.

As indicated by the above two-specimens, female *Ottoceros* horn cores are decidedly smaller than those of the male but the sexual dimorphism is not as extreme in this respect as is true for the modern pronghorn, *Antilocapra*. The smaller horn core of *Ottoceros* is estimated to be nearly vertical in orientation, being only slightly posteriorly directed; whereas the type specimen displays a pronounced sloping posteriorly. However, the more noticeable distortion (due to postmortem conditions) in the type may account for some of the difference. Significant variation, though, has been recorded for this character in males of the extant antilocaprid (Skinner, 1942:199) and in some extinct forms (Furlong, 1941:27).

A distinct lateral flange (Fig. 12) is noted in the type specimen which is directed outwardly at almost a right angle from the horn core. It originates immediately above the orbit, peaks about 25 mm distally and terminates approximately 20 mm below the bifurcation. Although the anterior tine is largely missing from the type specimen, it is presumed to be slightly smaller than the posterior one. This conclusion is based on LACM 1374 in which a mold was preserved in the sandstone matrix (Fig. 10). In this specimen the anterior tine is slightly smaller than its posterior counterpart. The two

specimens indicate some degree of porosity of bone, especially on the external surface of the tines. Also there is suggestion of the presence of a horn core sulcus on the type, running parallel and posterior to the lateral flange. The sulcus appears to begin about 14 mm above the orbit and continues as a slightly undulating groove bifurcating near the distal-extent of the lateral spine, each branch continuing toward the anterior and posterior tines. There do not appear to be any nutrient foramina at the base of the cores, however, the nature of the preservation of the bone may prevent accurate interpretation. The presence of a sulcus and the porosity do suggest there was a sheath on cores of *Ottoceros*.

A significant quantity of additional antilocaprid material, mostly in juxtaposition (Figs. 9 and 10), was recovered from the Kinsey Ranch, LACM locality 1092. Only antilocaprid specimens are known from this site, and based on the numerous skeletal elements, at least five individuals were buried (particularly as shown by the number of mandibles). Possibly some type of minor catastrophe occurred such as being stampeded over a cliff or into quicksand, which collectively killed a small herd or partial herd of these animals. Judging from the condition of the bones, their skeletal remains were probably transported only a very short distance.

In addition to the holotype of *Ottoceros*, two other specimens, LACM 1374 and LACM 1375, have incomplete upper dentitions. Of the three M<sup>1</sup>s represented by these two specimens, none shows any parastyle or anterior rib, thus differing from the type. Also, the ribs in M<sup>2</sup> and M<sup>3</sup> of the type are more distinct than their counterparts in these two specimens. With these exceptions the configuration and size of all specimens are nearly identical.

The mandible of *Ottoceros* is a slender structure particularly so in depth beneath the diastema, even when compared to the other genera of antilocaprids. Although the jaws of *Ottoceros* are slightly larger than compared specimens of *Capromeryx* Matthew their thickness beneath the diastema is relatively (and in some instances absolutely) less. Current study shows antilocaprid teeth apparently are not very diagnostic in distinguishing closely related genera, let alone species. This conclusion has been reached previously by several workers (e.g., Stirton, 1932:46; Barbour and Schultz, 1934:3; Colbert and Chaffee, 1939:8; Savage, 1851:273 and others). Nevertheless, it seems desirable to list dental characters in the event future work should disclose means of differentiation. M<sup>3</sup> has a third lobe that is a little smaller than the anterior two. No evidence exists for a fourth lobe. P<sub>4</sub> shows no tendency toward molarization as can be seen in *Antilocapra* and some Pleistocene forms such as *Tetrameryx* Lull. In the six *Ottoceros* P<sub>4</sub>'s a strong anterior lingual fold separates the paraconid from the metaconid, and shows no tendency toward closure. An incomplete jaw, presumably of *Sphenophalos*, from Rome, Oregon (LACM 6659), also shows an open anterior lingual fold in its P<sub>4</sub>.

X-ray radiographs were taken of several *Ottoceros* mandibles. They

showed that  $M_2$  and  $M_3$  were very hypsodont, extending to the base of the jaw.  $M_2$  in two specimens shows a slight bifurcation of the root; the other  $M_2$ s and  $M_3$ s show no root separation. All  $M_1$ s appear subhypsodont and have a pronounced bifurcation of the root. The  $M_1$  root base extends down only about half the depth of the jaw. The degree of hypsodonty decreases anteriorly through the premolar series which all show definite root separation, with roots extending down to half or less the jaw depth. The degree of hypsodonty in the cheek teeth is greater in the Pleistocene *Tetrameryx* where  $M_1$  shows little or no root separation. This trend is carried still further in the Pleistocene and recent *Antilocapra*, where all premolars show little or no root separation and are decidedly more hypsodont than *Tetrameryx* (see Skinner, 1942:203).

Sufficient antilocaprid material was collected to allow restoration of a composite skeleton by William J. P. Otto (Fig. 8). The mounted skeleton is a cast and modeled from original specimens. The latter are available for study in the LACM reference collection. *Ottoceros* was apparently a small, delicate creature, standing about 56 cm (22 in) at the shoulders, and as noted above, was probably similar to *Capromeryx* in size except that the horn cores seems to be relatively larger in *Ottoceros*. It should be noted that while measuring and comparing portions of the skeleton of *Capromeryx* (LACM No 1126, referred to as a plesiotype of *Breameryx* by Furlong, 1946), it was determined that the cranium, scapula, ulnae, carpals, tarsals (excluding calcaneum), phalanges (of manus and pes), ribs, vertebrae, femora and tibiae consist of plaster. This does not necessarily invalidate the interpretation of the skeleton and restoration (the latter was also done by William Otto, and figured in Furlong, 1946); but it does serve to caution workers in deriving too detailed comparisons of original material with LACM No 1126.

Future studies of the details of the postcranial material of *Ottoceros* should be useful in determining functional behavior of this unique antilocaprid. Preliminary observations concerning selected postcranial material indicate that the radius-ulna is moderately fused and the metacarpals are slightly shorter in proportions as compared with *Antilocapra*, with the longitudinal groove faintly discernible on the anterior surfaces and more distinct on the posterior surface in *Ottoceros*. There is no apparent evidence of the presence of side toes; the metatarsals are slightly longer in proportions as compared with *Antilocapra*.

*Comparisons*—The horn core of *Ottoceros* (Fig. 8) is quite distinct from any known genus of antilocaprid. It differs from the only existing genus, *Antilocapra*, by the forked core with a distinct lateral flange. Although both genera have subtriangular cross sections near the horn core base, they differ greatly in that the apex points laterally in *Ottoceros* and the side opposite the apex is the widest. In *Antilocapra* the apex is anteriorly directed and the side opposite is the narrowest.

TABLE 1

Cranial measurements (in millimeters) of *Ottoceiros peacevalleyensis*, new genus and species  
(Measurements in ( ) are estimates)

Element	LACM specimen nos.									
	1372	1374	1375	29041	29042	29044	29043	29735	29045	29046
(Holotype)										
Horn core:										
length, from tip of orbital rim to posterior tip	115.5	73.4								
length, from tip of orbital rim to bifurcation	80.2	43.5								
anteroposterior diameter at base	24.5	19.8								
anteroposterior diameter at point of bifurcation	36.7 <sup>a</sup>									
transverse diameter at base	17.0 <sup>b</sup>	9.8 <sup>b</sup>								
transverse diameter at point of extreme extension of lateral flange	20.5 <sup>b</sup>	10.4								
transverse diameter at point of bifurcation	11.2									
transverse diameter of posterior prong (greatest)	11.6	7.7								

TABLE 1 (Continued)

Cranial measurements (in millimeters) of *Otoceros peacevalleyensis*, new genus and species  
(Measurements in ( ) are estimates)

Element	LACM specimen nos.									
	1372	1374	1375	29041	29042	29044	29043	29735	29045	29046
(Holotype)										
Cranium:										
anteroposterior diameter of orbit	30.9 <sup>c</sup>	32.1								
transverse diameter of palate at base of anterior crest M <sup>2</sup>				29.8						
Upper dentition:										
left side anteroposterior diameter P <sup>3</sup>	11.2									
transverse-diameter P <sup>3</sup>	4.6									
anteroposterior diameter P <sup>4</sup>	5.1			5.5						
transverse diameter P <sup>4</sup>	4.5			5.3						
anteroposterior diameter M <sup>1</sup>	10.8		10.1	9.5						
transverse diameter M <sup>1</sup>	7.6		8.0	7.7						
anteroposterior diameter M <sup>2</sup>	12.8		12.1	11.7						

TABLE 1 (Continued)

Cranial measurements (in millimeters) of *Otoceros peacevalleyensis*, new genus and species  
(Measurements in ( ) are estimates)

Element	LACM specimen nos.									
	1372	1374	1375	29041	29042	29044	29043	29735	29045	29046
(Holotype)										
transverse diameter M <sup>2</sup>	7.7		8.3		7.6					
anteroposterior diameter M <sup>3</sup>	11.8		12.5 <sup>f</sup>		11.5 <sup>e</sup>					
transverse diameter M <sup>3</sup>	6.0		7.1		6.4					
Mandible:										
greatest length, posterior edge of symphysis to angle					120.6	124.2 <sup>g</sup>	110.5			
length of diastema I <sub>3</sub> -P <sub>2</sub> post-ant. alveoli					45.1					
height, ventral surface of angle to dorsal edge of coronoid					59.3					
least depth below the I <sub>3</sub> -P <sub>2</sub> diastema					7.6	7.4		9.1		
depth below P <sub>4</sub> (labial)					17.8	14.1	17.3		17.3	16.7
depth below posterior crescent of M <sub>2</sub>					23.5	17.5	25.3			22.4

TABLE 1 (Continued)  
 Cranial measurements (in millimeters) of *Otioceros peacesvalleyensis*, new genus and species  
 (Measurements in ( ) are estimates)

Element	LACM specimen nos.									
	1372	1374	1375	29041	29042	29044	29043	29735	29045	29046
(Holotype)										
depth below third crescent of M <sub>3</sub>					28.2	22.5	27.3			26.3
transverse diameter M <sub>2</sub>					7.4	8.7	8.7			7.6
Lower dentition:										
anteroposterior diameter P <sub>2</sub> (alveolus)					4.8	4.8				
transverse diameter P <sub>2</sub> (alveolus)					2.3	2.5				
anteroposterior diameter P <sub>3</sub> (alveolus)					5.8	6.3		6.4	6.8	
transverse diameter P <sub>3</sub> (alveolus)					3.2	3.2		3.0		
anteroposterior diameter P <sub>4</sub>					7.7	8.1	8.0	8.6	7.8	7.7
transverse diameter P <sub>4</sub>					2.8	3.4	2.9			
anteroposterior diameter M <sub>1</sub>					9.7	8.6	(9.7)		9.3	9.7

TABLE 1 (Continued)

Cranial measurements (in millimeters) of *Othoceros peacevalleyensis*, new genus and species  
(Measurements in ( ) are estimates)

Element	LACM specimen nos.									
	1372	1374	1375	29041	29042	29044	29043	29735	29045	29046
(Holotype)										
transverse diameter M <sub>1</sub>					5.0	4.7	5.5			
anteroposterior diameter M <sub>2</sub>					(10.2)	1.8	11.4			(11.8)
transverse diameter M <sub>2</sub>					(3.6)	5.4	5.7			
anteroposterior diameter M <sub>3</sub>					16.4	15.9	(15.6)			15.0
transverse diameter M <sub>3</sub>					5.1	5.0	4.5			

<sup>a</sup>Estimate, assuming restoration as shown in figure 7.

<sup>b</sup>Slightly crushed internally.

<sup>c</sup>From restoration, see figure 7.

<sup>d</sup>Greatest diameters at occlusal surface; measurements in ( ) are estimates: Wear on dentition; *Uppers* no. 1372 slight; no. 1375 slight; no. 29041, slight to moderate. *Lowers*; no. 29735, 29045, 29046, slight; no. 29042, no. 29043, slight to moderate; no. 29044 moderate.

<sup>e</sup>From right side.

<sup>f</sup>Not completely erupted.

<sup>g</sup>Estimate, angle broken.

TABLE 2

Postcranial measurements (in millimeters) of *Ottoceros peacevalleyensis*,  
 new genus and species  
 Measurements in ( ) are estimates

Part a. — axial skeleton

Element	LACM specimen no.	Length of centrum at mid-point
Cervical vertebrae		
atlas	29233	22.1
axis (incl. dens)	29235	(45.0)
3rd	29236	38.2
4th	29237	33.0
5th	29238	33.8
6th	29239	27.3
7th	29240	18.6
Thoracic vertebrae		
1st	29241	15.4
2nd	29242	15.4
3rd	29243	16.6
4th	29244	17.2
5th	29245	16.4
6th	29246	17.2
7th	29247	17.8
8th	29248	18.3
9th	29249	18.2
10th	(unnumbered)	(18.4)
11th	(unnumbered)	(19.7)
12th	29250	21.4
13th	29251	23.2
Lumbar vertebrae		
1st	29252	22.3
2nd	29253	23.7
3rd	29254	23.7
4th	29255	24.4
5th	29256	25.6
6th	29257	23.9
Sacrum	29258	62.5
Caudal vertebrae		
1st	29296	15.5
2nd	(unnumbered)	(14.7)
3rd	(unnumbered)	(13.4)
4th	29297	16.4
5th	(unnumbered)	(13.5)
6th	(unnumbered)	(12.0)
7th	(unnumbered)	(11.3)
8th	(unnumbered)	(10.6)
9th	(unnumbered)	(12.2)

## Part b. — appendicular skeleton

Element	LACM specimen no.	Length of centrum at mid-point
Scapula	29048	121.7
(greatest distance, tip of coracoid process to posterior edge)		
Humerus	29047	118.5
(greatest length)		
Radius-ulna	29049	186.4
(greatest length)		
Metacarpals	29050	131.5
(greatest length)	29051	135.8
	29052	141.1
Femur	29053	(148.7)
(greatest length including restored distal half)		
Tibia	29054	(180.0)
(greatest length)		
Metatarsals	29055	149.8
(greatest length)	29056	159.2
	29057	154.5
Astragalus	29058	25.5
(greatest length)	29059	25.7
	29060	22.9
Calcaneum	29061	47.2
(greatest length)	29062	55.8
	29063	51.0
Innomimates	29358	154.4
(greatest length, tip of ilium to tip of ischium)	29359	(151.3)
(anteroposterior distance across acetabulum)	29358	16.4
	29359	(14.5)
	29426	18.5
	29427	15.2
(greatest length across obturator foramen)	29358	33.2
	29359	33.2
	29427	39.3
	Observed range	Mean
Proximal phalanges	28.3-32.8	30.0
(greatest length, involving 10 specimens)		
Median phalanges	15.7-19.3	17.5
(greatest length, involving 13 specimens)		14.6
Distal phalanges	14.1-15.2	
(greatest length, involving 5 specimens)		

Estimated length, right forelimb, 473.2; estimated length right hindlimb, 555.6.

Many Pliocene and Pleistocene genera of antilocaprids have been recognized. One distinguishing feature that has been used to separate them into two groups is the height of the horn core base before bifurcation ("high core-based and low core-based" forms of Skinner, 1943:176). Probably only adult males should be used in this dichotomy with present knowledge. Since *Ottoceros* has a most definite high core base, genera with a pronounced low core base such as *Ceratometryx* Gazin, 1935, (type specimen probably a female); *Tetrameryx* Lull, 1921 (= *Stockoceros* Frick, 1937, *Hayoceros* ? *Texoceros* Frick, 1937); *Capromeryx* Matthew, 1902 (= *Breameryx* Furlong, 1946) or those without bifurcation such as *Osbornoceros* Frick, 1937 and *Proantilocapra* Barbour and Schultz, 1934; (type specimen possibly a female) will be excluded from serious consideration. Frick (1937) designated *Stockoceros* and *Hayoceros* as subgenera of *Tetrameryx*, but treated them as separate genera. Several authors have continued to regard them as distinct genera, including Furlong (1941:28) and Skinner (1942:177).

Of the remaining antilocaprinae, *Ilingoceros* (Merriam, 1909) and *Hexobelometryx* (Furlong, 1941) show unique horn core development which separate them from *Ottoceros*. *Ilingoceros* shows a pronounced twisting to its nearly circular (disregarding sulci) shaft and *Hexobelometryx* is peculiar by its distinct three prongs of the horn core. The remaining described genus with a high core base is *Sphenophalos* Merriam, 1909. This antilocaprid compares most closely to the present genus, however, significant differences do exist. *Sphenophalos* is a decidedly larger form; *Ottoceros* being a very small antilocaprid, about the size of *Capromeryx*. *Sphenophalos* has a decidedly stockier horn core whose greatest antero-posterior width is greater just a short distance above the orbit (the point of greatest width was seen to vary in the type species, *S. nevadanus*, but it is most always along the proximal half). In *Ottoceros* the horn core is a relatively slender structure and its greatest anteroposterior width is just below the bifurcation. A distinct lateral flange directed externally is present in *Ottoceros*, whereas in *Sphenophalos* no such flange exists. One specimen described by Furlong (1931, plate 1, no. 16) of *S. nevadanus* does indicate a small anterior flange. However, most specimens known do not show this development.

One species of *Sphenophalos*, from Nebraska, *S. middleswarti* Barbour and Schultz, 1941, exhibits a greater similarity to *Ottoceros* than the other described species, *S. nevadanus*, *S. blicki* (Frick, 1937) and *S. floblairi* (Frick, 1937). *S. middleswarti* has longer, more pointed tines, which are more nearly equal in size, and possesses a distinct anterior flange. *S. middleswarti*, although smaller than the type of *S. nevadanus*, is decidedly larger than *Ottoceros*. Two measurements given by Barbour and Schultz (1941:61) are, length of horn core from top of orbit to crotch, 109.5 mm and length of horn from top of orbit to posterior tip, 177.0 mm. Similar measurements in *Ottoceros* holotype are, 79 and 116 mm respectively. The

purpose of the lateral flange in *Ottoceros* is unknown. Species of *Sphenophalos* have the maximum anteroposterior width nearer the orbit than the point of bifurcation of tines, in distinct contrast with *Ottoceros*. In a personal communication, S. David Webb (1973) has given us a very plausible explanation: "The purpose of the lateral flange may be related to the mode of shedding the horn sheath. In *Ottoceros* much of the widest part of the horn core is near the base of the tines, contrary to most *Sphenophalos* species in which the base of the pedicel is usually wider. In low-based taxa, where the prongs are more divergent, each prong was probably sheathed separately (Webb, 1973). But *Ottoceros* would have had special difficulty shedding a sheath, if indeed it had a deciduous horny sheath. The prominent flange on the outer convex horn wall might have helped crack the shedding sheath open in the narrowest (stickiest) part of the base."

Webb (1969:174) has tentatively divided *Sphenophalos* into two subgenera. The western forms from Nevada, Oregon, and California were placed in one group, *S. (Sphenophalos)* and those described from Nebraska and New Mexico were placed in the other, *S. (Plioceros)*. The only species mentioned belonging to the first group was *S. (Sphenophalos) nevadanus* while the more eastern group included *S. (Plioceros) blicki* and *S. (P.) floblairi*. Subgeneric distinctions given were, "Horn cores of the western *Sphenophalos (Sphenophalos)* have relatively wider bases (greater than half of their lengths), tend to be subtriangular rather than dumbbell-shaped in cross section, are more strongly twisted, and have relatively larger more flaring tines in mature individuals than in *Sphenophalos (Plioceros)*." *S. middleswarti* from Nebraska was not mentioned by Webb. It does not seem to fit this classification as it shows greater similarity to the western group on all the above listed criteria. However, *S. middleswarti* is significantly distinct from *S. nevadanus* and possibly should be classed as a separate genus.

Teeth are rarely definitely associated with horn cores of *Sphenophalos* but at least one instance has been recorded (Stirton, 1932). No significant differences in teeth other than the smaller size of the present type, were found in comparison of the two genera.

A small portion of a horn core, LACM 28348, and an incomplete upper molar, LACM 27970, are the only antilocaprid specimens that were found at a site other than LACM locality 1092. The horn core fragment is from LACM (CIT) locality 486, which might be either in the Peace Valley beds or Hungry Valley Formation, and the incomplete molar is from LACM (CIT) locality 471, which is in the Hungry Valley Formation. The horn core fragment represents a portion of the core just ventral to the bifurcation and extends about 30 mm below that point. Both tines are missing and there is not an adequate portion of the shaft to indicate presence or absence of the lateral flange which is known in *Ottoceros*. The molar fragment represents the broken posterior selene and partial anterior selene of an upper molar. These fragments are within the size

range of known *Ottoceros* specimens but they are not sufficiently diagnostic for generic identification.

#### KINSEY RANCH LOCAL FAUNA

The first reference to vertebrate fossils from the Kinsey Ranch area was a brief statement by Chester Stock in Crowell (1950:1638). This primarily concerned the equid material known at that time from the Hungry Valley Formation but reference was also made to the presence of camel, mastodon, and turtle. This fossil material, included with all later recovered specimens from both the Hungry Valley Formation and the Peace Valley beds, is herein named the Kinsey Ranch local fauna.

Tedford (1970) has convincingly demonstrated the need for clarity in the application of such terms as fauna and local fauna. Following the apparent common practice of vertebrate paleontologists, the Kinsey Ranch fossil collection might be referred to as the Kinsey Ranch fauna. However, as stated by Tedford (1970:683) "The local fauna may be represented by samples from a single site or a series of closely associated sites having a limited geographic and stratigraphic distribution." In contrast, Tedford (1970:684) states that, "The concept implied by the term fauna in vertebrate paleontology involves a higher level of inference than that of local faunas. It represents the maximum geographic and temporal limits of group of organisms sharing a suite of common species." It would seem logical to designate the Kinsey Ranch as a local fauna. However, previously described collections of fossils will be designated as faunas if they were originally established as such (e.g., Mt Eden fauna).

The Kinsey Ranch local fauna has been collected from an area approximately three and one-half miles long by three-quarters of a mile wide. Recovered specimens are from section 32, T8N, R18W and sections, 5, 6, 8, 16, 17, 19 and 21, T7N, R18W, located on the Black Mtn quadrangle, California, 1958. With the possible exception of the site yielding the bulk of antilocaprid material, LACM 1092, nothing resembling a massed accumulation or a fossil quarry is known. Rather, the vertebrate fossils have been found in a disseminated condition with at least bone chips being present over most of the area. All fossils constituting the Kinsey Ranch local fauna have been recovered from the uppermost Peace Valley beds and the lowermost part of the conformably overlying Hungry Valley Formation (Miller and Downs, 1971). These fossils are tentatively being treated as a single local fauna until such time as a more detailed stratigraphic study might suggest otherwise. Fossil localities included in the Peace Valley beds and Hungry Valley Formation are shown in Table 3. The locality information is based on data from LACM records, current field observations, and the geologic map in Crowell (1950), and the localities are marked on the Black Mtn quadrangle on permanent file in the section of Vertebrate Paleontology, LACM.

TABLE 3

Kinsey Ranch local faunal list with distribution of localities in lithologic units

Kinsey Ranch local fauna	Lithologic unit (with CIT and LACM locality assignments)		
	Peace Valley beds	Peace Valley beds or Hungry Valley Fm.	Hungry Valley Formation
Chelonia			
Testudinidae			
<i>Clemmys</i> cf.	CIT 435, 459	CIT 486, LACM 7248	LACM 7050
<i>C. marmorata</i>			
cf. <i>Geochelone</i>		CIT 486, LACM 7248	LACM 7049
Carnivora			
?Felidae	CIT 453		
Proboscidea			
Family indet.	CIT 453		CIT 444, LACM 7049
Perissodactyla			
Equidae			
<i>Pliohippus</i> sp.	CIT 452, 453, 459	CIT 486, 487, 488, LACM 4248	CIT 444, 466, 468, 469, 471, LACM 7049, 7050
Tapiridae			
<i>Tapirus</i> sp.			CIT 471
Rhinocerotidae			
? <i>Aphelops</i>		?locality	
Artiodactyla			
Camelidae			
cf. <i>Tanupolama</i>	CIT 452, 453, 459	CIT 486	
cf. <i>Megatylopus</i>			CIT 444
Antilocapridae			
<i>Ottoceros</i>			
<i>peacevalleyensis</i>	LACM 1092		
? <i>Ottoceros</i>		CIT 486	CIT 471

The long axis of the fossiliferous area noted above approximates the strikes of the Peace Valley beds and Hungry Valley Formation, which is essentially north-south. The highly scattered and fragmented vertebrate fossils as well as noted abrasion on many specimens supports the interpretation of a fluvial depositional environment.

Only one vertebrate, the pond turtle, *Clemmys* cf. *C. marmorata*, requires an aquatic habitat. Two genera of fresh water molluscs, *Anodonta* and *Lymnaea*, and some smooth-shelled ostracods have been recovered from the Peace Valley beds according to Crowell (1950:1638). These invertebrates are known from present streams and lakes. The requirement of an aquatic habitat would be met by the presumed fluvial conditions that existed in the studied area. The western pond turtle is capable of living in

open streams and is not restricted to ponds or marshes. Neither of these latter habitats are indicated by the sedimentological record. While it is often thought that the tapir is only associated with tropical or subtropical conditions where there are excessive amounts of water, fossils are known from areas where the bulk of faunal and floral evidence indicate temperate to even semiarid climates (eg., various Pleistocene sites in western North America). Perennial streams and sufficient cover are all that many living tapirs require. A permanent stream would also satisfy all the water requirements of the remainder of the Kinsey Ranch local fauna.

A majority of the taxa from the present local fauna is indicative of grassland conditions. *Ottoceros* and *Pliohippus*, the two genera making up the bulk of known fossil specimens, have hypsodont dentition. *Pliohippus* is regarded as a grazer as are the antilocaprids in general. The camels and *Aphelops* are also compatible with grassy areas. The tapir and mastodont, both primarily browsers, possibly indulged in some grazing. This is true of modern tapirs. A significant grassland area with some woody or thicketed regions is suggested by the known local fauna. Lack of abrasion on the tapir elements as well as on the cuboid of the mastodont indicates these bones were not washed in from a more distant locale.

#### AGE AND CORRELATION

Crowell (1950) assigned a Middle Pliocene age to the Peace Valley beds and a Late Pliocene age to the conformably overlying Hungry Valley Formation. However, the present study area shows no faunal distinction between fossils found in the two rock units (uppermost Peace Valley beds and lowermost Hungry Valley Formation). The structural grade of the *Pliohippus* and the rhinocerotid (this family is unknown in North America after the Hemphillian which is traditionally equated with the Middle Pliocene) coupled with *cf. Tanupolama*, are indicative of a Hemphillian age. Every other taxon in the fauna has a fossil record that is in part Hemphillian in age. The evolutionary stage of *Ottoceros* also seems compatible with this age assignment.

A flora (Piru Gorge flora) from a rock unit conformably underlying the Peace Valley beds, and three to four miles south of the present area, was described by Axelrod (1950). Although he stated that it is not entirely safe to use the Piru Gorge flora for a specific age indicator, Axelrod did assign it a "middle Pliocene" (= Hemphillian) age as based on, "its cliseral relations, its climatic implications, and its floristic composition." It is his opinion that a "middle Pliocene" age applies to the Peace Valley beds also.

The limited collection representing the Kinsey Ranch local fauna, in which the best represented taxon, *Ottoceros*, is unknown elsewhere, makes correlation difficult. Greatest similarities, however, do exist between the present fauna and those recognized as Hemphillian. As mentioned previously, the Kinsey Ranch species of *Pliohippus* most resembles the form

from Mt Eden, California, recognized as Hemphillian (Wood, et al., 1941). No other taxon precludes the Kinsey Ranch local fauna being the same age as the Mt Eden fauna. A new species of camel in the Mt Eden fauna identified by Frick (1921) as *Procamelus* (?) *edensis* shows great similarity to the smaller camel from Kinsey Ranch referred to as cf. *Tanupolama*. The size and configuration of teeth of the small camelid from Eden closely compares with *Tanupolama* and the Eden specimens possess llama buttresses similar in development to those of the Kinsey Ranch form.

The apparently more advanced stage of the Kinsey Ranch *Pliohippus* as compared with the one from the Kern River fauna of California, *Pliohippus* cf. *spectans*, suggests a later Hemphillian age for the former fauna than the latter.

Several Hemphillian vertebrate faunas have been described from the panhandle region of Texas by Johnston and Savage (1955). Among them are the Axtel, Christian Ranch, Currie Ranch, and Smart Ranch faunas. Each of these faunas is relatively small in numbers of taxa and specimens but the taxa of each were considered sufficiently diagnostic for a late Hemphillian age assignment. The Kinsey Ranch local fauna appears to approximate these in age based on the limited material available from both areas.

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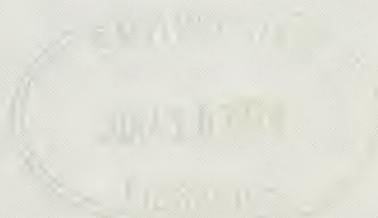
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NOTES ON THE DISTRIBUTION AND TAXONOMY  
OF SOME NORTH AMERICAN *CENTRIS*  
(HYMENOPTERA: ANTHOPHORIDAE)

By ROY R. SNELLING

CONTRIBUTIONS IN SCIENCE



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NOTES ON THE DISTRIBUTION AND TAXONOMY OF SOME  
NORTH AMERICAN *CENTRIS*  
(Hymenoptera: Anthophoridae)<sup>1</sup>

By ROY R. SNELLING<sup>2</sup>

ABSTRACT: A key to the recognized subgenera is given. Characters by which females of the subgenera *Paracentris* and *Wagenknechtia* may be separated are discussed. Three new species of *Paracentris* (*C. ectypha*, *C. fisheri* and *C. harbisoni*) are described from Baja California, Mexico; the taxonomy and distribution of several North American species are discussed. A new species, *C. heithausi*, is described in subg. *Trachina* from Costa Rica. In the nominate subgenus the new species, *C. aethytera* from Costa Rica, and *C. erubescens* from Mexico, are described. Observations on taxonomy and distribution of other species are given. Within the newly described subgenus *Acritocentris* (type species: *C. ruthannae* Snelling), *C. agameta* is described from Mexico. Other new subgenera are: *Xerocentris* (type species: *C. californica* Timberlake) and *Exallocentris* (type species: *C. anomala* Snelling). Keys are provided for species in the subgenera *Xerocentris*, *Paracentris*, *Exallocentris* and *Acritocentris*. The following new synonymies are proposed: subg. *Trichocentris* = *Paracentris*; *C. marginata* = *morsei* = *caesalpiniae*; *C. birkmanii* = *subhyalina* = *lanosa*; *C. rhodoleuca* = *rhodopus*; *C. inermis gualanensis* = *inermis*.

INTRODUCTION

Since publication of my two earlier papers (1956, 1966), I have been able to study much additional material of this genus. With this added information I am now able to correct some errors in those papers and to clarify the status of a number of names. I take the opportunity also to describe a number of new taxa so that the names may be available to other researchers.

In an effort to emphasize group relationships within the North American species, I feel it expedient to propose several new subgenera and to slightly modify the characteristics of the subgenus *Paracentris*. The result is that two previously named subgenera, *Paracentris* and *Melanocentris*, from each of which extraneous elements are here removed, are now more homogeneous. A new key to the subgenera of *Centris* is presented below, based on that of Michener (1951), and reflecting the taxonomic rearrangements here proposed.

<sup>1</sup>REVIEW COMMITTEE FOR THIS CONTRIBUTION

CHARLES L. HOGUE  
ROBBIN THORP  
THOMAS J. ZAVORTINK

<sup>2</sup>Section of Entomology, Natural History Museum of Los Angeles County, Los Angeles, California 90007

Abbreviations used below in the keys and descriptions are explained in my earlier paper (Snelling, 1966)

### KEY TO SUBGENERA OF *CENTRIS*

1. Maxillary palpus three-segmented; hind leg of male swollen, basitarsus usually with spine or elevated carina on posterior margin ..... 2  
 Maxillary palpus four or five-segmented; hind leg of male usually not swollen, basitarsus without spine on posterior margin ..... 4
2. Male with large apical processes on eighth and ninth sternites; female without distinct secondary basitibial plate; clypeus without median yellow line ..... 3  
 Male eighth sternite with apical process greatly reduced, segment essentially a transverse band; female with secondary basitibial plate separated from primary plate by transverse line; both sexes with longitudinal yellow line on clypeus, sometimes incorporated into yellow of rest of clypeus ..... *Trachina*
3. Male with second mandibular tooth larger than inner and closer to inner than apical; female with inner upper mandibular carina elevated basally and labrum variously modified ..... *Heterocentris*  
 Male with second mandibular tooth smaller than inner and closer to apical than inner; female with inner upper mandibular carina simple or elevated at apex, labrum simple ..... *Hemisiella*
4. Females ..... 5  
 Males ..... 13
5. Secondary basitibial plate with distinct overhanging margin ..... 6  
 Secondary basitibial plate without distinct overhanging margin ..... 9
6. Maxillary palpus five-segmented; mandible quadridentate ..... 7  
 Maxillary palpus four-segmented; mandible tridentate (scutellum not bilobed) ..... *Acritocentris*
7. Fore and mid basitarsi with an anterior row of short, flattened setae, fore basitarsus in addition with about four very long spatulate setae on posterior margin ..... 8  
 Fore and mid basitarsi without modified setae on either anterior or posterior margins (scutellum not bilobed) ..... *Exallocentris*
8. Large forms, abdomen nonmetallic; scutellum usually bilobed; upper inner mandibular carina ending near base of next to innermost tooth; mandible subapically broadened ..... *Melanocentris*  
 Usually smaller forms, scutellum simple; abdomen usually at least faintly metallic; upper inner mandibular carina ending near base of innermost tooth; mandible slender subapically ..... *Centris*, s. str.
9. Scutellum not bilobed, without bare areas; smaller species ..... 10  
 Scutellum bilobed and with well defined bare areas; very large species ..... *Ptilotopus*
10. Mandible without tooth on under surface ..... 11  
 Mandible with distinct tooth on under surface near base of first apical tooth ..... *Xanthemisia*
11. Fore basitarsus, on at least apical half, with anterior row of flattened setae and several elongate, apically spatulate setae on posterior margin of inner face; mid basitarsus with row of short, stout setae (except *C. cineraria* F. Sm.) ..... 12  
 Fore and mid basitarsi without setae which are differentiated from dense pubescence ..... *Xerocentris*

12. Basitibial plate with secondary plate; pygidium with raised, triangular, secondary plate basally; clypeus usually maculate, rarely wholly black ..... *Paracentris*  
 Basitibial plate without secondary plate; pygidium without raised, basal secondary plate (with raised longitudinal area in *C. muralis* Burmeister); clypeus wholly black ..... *Wagenknechtia*
13. Genitalia with giant branched setae arising from gonocoxite near base of gonostylus ..... 14  
 Genitalia without giant branched setae ..... 17
14. Giant branched setae restricted to region near base of gonostylus; gonocoxite without apical projection; abdomen usually not metallic and without extensive maculae ..... 15  
 Giant branched setae scattered along inner margin of apical styliiform projection of gonocoxite; abdomen usually at least feebly metallic, often extensively maculate ..... *Centris*, s. str.
15. Gonostylus not broadened on a vertical plane; maxillary palpus usually five-segmented ..... 16  
 Gonostylus much broadened in a vertical plane; maxillary palpus four-segmented ..... *Xanthemisia*
16. Lateral ocellus separated from eye by less than its own diameter; terga I-IV with abundant fully erect pale pubescence on disc ..... *Xerocentris*  
 Lateral ocellus separated from eye by its own diameter or more; terga II-IV usually with sparse dark pubescence, pubescence rarely erect . . *Paracentris*
17. Hypoepimeral area without tubercle; scutellum bilobed or not; maxillary palpus four or five-segmented ..... 18  
 Hypoepimeral area with tubercle; scutellum bilobed; maxillary palpus four-segmented ..... *Ptilotopus*
18. Scutellum without lateral tubercles or swellings; upper inner mandibular carina ending near base of innermost tooth; abdomen at least feebly metallic (if not, terga with dense, erect pale pubescence) ..... 19  
 Scutellum with lateral tubercles or swellings; upper inner mandibular carina ending near base of next to innermost tooth; abdomen not metallic ..... *Melanocentris*
19. Lateral ocellus separated from eye by about its own diameter; gonocoxite not apically drawn out, gonostylus elongate; clypeus usually maculate; maxillary palpus four or five-segmented ..... 20  
 Lateral ocellus separated from eye by more than its own diameter; gonocoxite apically drawn out and bearing at its tip the short gonostylus; clypeus immaculate; maxillary palpus five-segmented . . *Wagenknechtia*
20. Maxillary palpus five-segmented; innermost mandibular tooth truncate; clypeus black or with a pair of pre-apical maculae ..... *Exallocentris*  
 Maxillary palpus four-segmented; innermost mandibular tooth acute; clypeus largely pale ..... *Acritocentris*

### **XEROCENTRIS**, new subgenus

*Diagnosis.* Female: fore basitarsus without row of flattened setae on inner anterior margin or elongate spatulate setae on inner posterior margin; fore tarsal segments each with several coarse, flattened setae on each corner; mid basitarsus without row of flattened setae on inner anterior margin; pygidial plate not flattened on apical half, with median area longitudinally convex. Male: without exposed pygidial plate; gonocoxite without apical processes

but with giant branched setae basally; terga I-VI with dense pale discal pubescence; lateral ocellus separated from eye by less than an ocellar diameter.

*Description.* Mandible tri- or quadridentate, upper inner carina ending at base of innermost tooth, neither subapically broadened nor bent; maxillary palpus four or five-segmented, apical segment shorter than basal; ocelli anterior to narrowest part of vertex, lateral ocellus of male separated from eye margin by less than an ocellar diameter; first flagellar segment of male shorter than, equal to, or longer than scape or following three segments combined; mesonotum without defined bare areas; fore basitarsus of female without elongate spatulate setae or a row of coarse, flattened setae ventrally, but each tarsal segment with a few coarse, conspicuous, flattened setae on each apical angle; hind basitibial plate of female variable, but secondary plate not clearly delimited, either longitudinal or oblique; first recurrent vein entering second submarginal cell in basal third; discs of abdominal terga with abundant appressed or erect pubescence, often sufficiently dense to obscure surface; male without defined pygidial plate; pygidial plate of female distinctly elevated along midline, usually merely convex, sometimes subcarinate, never plane; male terminalia much as in *Paracentris*.

*Type species.* *Centris californica* Timberlake, 1940.

*Included species.* *C. hoffmanseggiae* Cockerell, 1897; *C. mixta* Friese, 1904; *C. pallida* Fox, 1899; *C. rhodomelas* Timberlake, 1940; *C. tiburonensis* Cockerell, 1923; *C. vanduzeei* Cockerell, 1923.

*Etymology.* Gr., *xeros*, dry, plus generic name *Centris*, in allusion to the arid and semiarid habitats of the included species.

This subgenus is proposed for the reception of several related aberrant species which had previously been placed in *Paracentris*. These species all agree in the structure of the female pygidium and in the lack of modified setae on the fore and mid basitarsi of the females and in the placement of the male ocelli. The males of all species of *Xerocentris* have abundant erect discal pubescence and the females have more discal pubescence than in species assigned to *Paracentris*.

All the species occur in arid or semiarid habitats. The group is North American with the exception of *C. mixta* which is found in arid regions of Chile and Peru.

## KEY TO NORTH AMERICAN *XEROCENTRIS*

### Females

1. Maxillary palpus four-segmented; abdominal terga with dense, appressed, pale pubescence obscuring surface; thoracic pubescence pale, fulvous tinged above; pygidium truncate, median ridge broad to apex . . . . . 2
- Maxillary palpus five-segmented; abdominal terga usually with dark suberect to erect pubescence; if pale beyond second segment, pygidium is narrow at apex and median ridge is carinalike on apical one-fourth; pubescence often dark on lower half of mesopleura . . . . . 3

- 2. Mandible tridentate; abdominal sterna II-IV with pale, pubescent fasciae on margins; clypeus often maculate . . . . . *pallida* Fox  
Mandible quadridentate; abdominal sterna II-IV without pale, pubescent fasciae; clypeus immaculate . . . . . *tiburonensis* Cockerell
- 3. Scopa blackish; abdominal terga beyond second with long and short, simple, dark pubescence; pygidial apex broadly truncate, median ridge broad, evenly rounded . . . . . 4  
Scopa yellowish ferruginous; terga I-V with abundant pale, erect, plumose discal pubescence; pygidial apex narrowly truncate, median ridge carinalike toward apex . . . . . *vanduzeei* Cockerell
- 4. Pubescence of upper half of mesopleuron pale, of mesoscutum tinged with fulvous; second tergum with at least some short pale pubescence on disc and along margin; terga finely, densely piligerously punctate . . . . . 5  
Pubescence of mesopleuron entirely dark brownish, of mesoscutum dark ferruginous; terga beyond first wholly dark pubescent; terga shiny, with sparse piligerous punctures . . . . . *rhodomelas* Timberlake
- 5. Eye, viewed from side, wider than gena; clypeus distinctly bulging basally; pubescence of second tergum entirely pale; sterna III-V with pale apical fringes; vernal to early summer . . . . . *hoffmanseggiae* Cockerell  
Eye, viewed from side, no wider than gena; clypeus weakly bulging basally; at least some discal pubescence on second tergum dark; sterna III-V without pale fringes; late summer to autumnal . . . . . *californica* Timberlake

Males

- 1. Maxillary palpus four-segmented; scape immaculate beneath and pubescence of terga entirely pale; clypeus pale . . . . . 2  
Maxillary palpus five-segmented; scape usually maculate, but if immaculate, some fuscous pubescence on terga IV-VI or clypeus wholly dark . . . . . 3
- 2. Lateral ocellus separated from eye margin by slightly less than its diameter; basal sterna with some discal pubescence brownish; clypeus uniformly lightly tessellate, shiny . . . . . *tiburonensis* Cockerell  
Lateral ocellus separated from eye margin by half its diameter; sterna with brownish pubescence restricted to two apical segments; clypeus densely tessellate, slightly shiny, sometimes with shinier midline . . . . . *pallida* Fox
- 3. Clypeus pale; margin of apical tergum truncate or convex; lateral ocellus separated from eye margin by one-half or more its diameter . . . . . 4  
Clypeus black; margin of apical tergum weakly emarginate in middle; lateral ocellus about one-fourth its diameter from eye margin . . . . . *vanduzeei* Cockerell
- 4. Pubescence of legs, two apical terga and all sterna pale; apex of last tergum broadly rounded . . . . . 5  
Pubescence of legs, last two terga and most sterna largely or entirely brownish; apex of last tergum narrowly truncate; scape maculate . . . . . *rhodomelas* Timberlake
- 5. TFD 1.35-1.38 x OCD; scape maculate beneath; terga IV-VI with pale pubescence only; late summer to autumnal . . . . . *californica* Timberlake  
TFD 1.49-1.53 x OCD; scape immaculate; terga IV-VI with some fuscous pubescence; vernal to early summer . . . . . *hoffmanseggiae* Cockerell

Subgenus *PARACENTRIS* Cameron

*Paracentris* Cameron, 1903. Amer. Entomol. Soc., Trans. 29:235-236. Type species: *Paracentris fulvohirta* Cameron, 1903.

*Penthemisia* Moure, 1950. Dusenia 1:390. Type species: *Centris chilensis* Spinola, 1851.

*Centris* subg. *Penthemisia*, Michener, 1951. Kans. Entomol. Soc., Jour. 24:3-4.  
*Centris* subg. *Trichocentris* Snelling, 1956. Pan-Pacific Entomol. 32:4-5.  
Type species: *Centris rhodoleuca* Cockerell, 1923. NEW SYNONYMY.

The subgenus *Trichocentris* was proposed for two species: *C. rhodoleuca* and *C. morsei* Cockerell. A third species, *C. vanduzeei* Cockerell was tentatively included. The first two species were known only from males and female characteristics were derived from *C. vanduzeei*. In 1966 I removed *C. morsei* to *Paracentris* and reaffirmed the distinctness of *Trichocentris*, largely on the unusual characteristics of *C. vanduzeei*.

More thorough consideration of the type species of *Trichocentris* has convinced me that this subgenus, as exemplified by *C. rhodoleuca*, should not be separated from *Paracentris*. Although superficially different in appearance, *C. (Paracentris) rhodopus* is a senior synonym of *C. rhodoleuca*. The second species of *Trichocentris*, *C. morsei*, is placed in synonymy with *C. (Paracentris) caesalpiniae*. On the other hand, *C. vanduzeei*, in both sexes, shares a number of characteristics with several unusual species here removed from *Paracentris*. These comprise the new subgenus *Xerocentris* described above.

Removal of these species results in a more uniform series of species in *Paracentris*. Contrary to the statements of Moure (1950) and Michener (1951) species of *Paracentris* do possess modified setae on the fore and mid basitarsi of the females. An additional characteristic of *Paracentris* females is the flat apical portion of the pygidial plate. The male characteristics of *Paracentris* remain as defined by Michener (1951).

Moure (1950) and Michener (1951) also are in error in their characterization of *Wagenknechtia*, for the females of this subgenus also possess modified setae on the fore and mid basitarsi of most included species. The usual row of short, flattened setae on the anterior inner margin of the fore basitarsus is present in *C. cineraria* F. Smith (apical half only), *C. muralis* Burmeister, *C. orellanai* (Ruiz) (apical half only) and *C. rhodophthalma* (Perez), the four described species of *Wagenknechtia*. In addition, each of these possesses on the inner posterior margin three or four elongate, apically spatulate setae, such as occur in *Paracentris*, *Centris*, s. str., and other subgenera. The mid basitarsi of *C. muralis* and *C. rhodophthalma* possess a compact row of short, broad, apically curved setae on the inner anterior margin as in *Paracentris*; this row is completely lacking in *C. cineraria*. In *C. orellanai* there is a row of stout flattened setae in this position, but these are separated by about their own width, are apically acuminate and are not curved. The structure of *Wagenknechtia* females is thus very similar to *Paracentris*.

The removal of several species, previously placed in *Paracentris* (as *Penthemisia*) by Michener (1951), to *Xerocentris* will now permit separation of females of *Paracentris* and *Wagenknechtia*. The basitibial plate of *Paracentris* females possesses a secondary plate. The secondary plate is situated at the base of the segment and is elevated above the level of the primary plate;

its anterior and lower margins are usually abruptly declivitous, although the anterior margin may slope less precipitously. The surface of the secondary plate is flattened in most species and there is usually an abundance of very short, fine appressed hairs. In the species of *Wagenknechtia* the basal portion of the basitibial plate is convex, usually polished and slopes gradually onto the lower, apical portion of the segment. A median depression may be present. In *C. muralis* the plate is elevated along the midline, with a small depression on either side.

The pygidial plate of *Paracentris* females always has a triangular, raised secondary plate basally; such a secondary plate is lacking in *Wagenknechtia*. The entire midlength of the pygidial plate is convexly raised in *C. muralis*, but in the other species of *Wagenknechtia* the pygidium is flat.

In *Wagenknechtia* species the hind tarsal claws are without a basal tooth, except *C. muralis*, in which a very low tooth is present. A sharp, distinct tooth is present on the hind tarsal claws of *Paracentris* species.

#### KEY TO NORTH AMERICAN *PARACENTRIS*

##### Females

1. Pubescence of head, thorax and legs entirely or predominantly black, that of mesopleuron entirely black . . . . . 2  
 Pubescence of head, thorax and legs entirely or predominantly pale, that of mesopleuron pale, at least in part. . . . . 6
2. Pubescence of thoracic dorsum entirely black . . . . . 3  
 Pubescence of thoracic dorsum pale, at least in part . . . . . 5
3. First flagellar segment 3.5 x length of second (median impunctate area of clypeus extending about 2/3 of distance toward apex; TFD 1.87-2.02 x OCD) . . . . . *laevibullata* Snelling  
 First flagellar segment at least 5.0 x second . . . . . 4
4. First flagellar segment 6.0 x second; TFD 1.12-1.23 x OCD; median impunctate line of clypeus extending toward apex as a very narrow, slightly raised line ending about 1/2 an ocellar diameter from apical margin . . . . . *aterrima* F. Smith  
 First flagellar segment 5.1-5.3 x second; TFD 2.26 x OCD; median impunctate line of clypeus broad over entire length . . . . . *anthracina* Snelling
5. Large species, TL 14.5-18.5 mm; pubescence of vertex and pronotal lobes black; clypeal punctures sparse, obscure apicad, without distinct median impunctate line . . . . . *mexicana* F. Smith  
 Small species, TL 12.5-14.5 mm; pubescence of vertex and pronotal lobes whitish; clypeus with punctures sharply defined and with distinct, median, impunctate line, wider above . . . . . *zacateca* Snelling
6. Clypeal integument entirely blackish . . . . . 7  
 Clypeal integument at least partially yellowish, orange or red . . . . . 9
7. Clypeus coarsely, closely punctate, with narrow, median, impunctate line which may be obscured by roughened integument; facial quadrangle broader than long . . . . . 8  
 Clypeus sparsely, finely punctate, with broad, poorly defined median impunctate band; facial quadrangle longer than broad . . . . . *angustifrons* Snelling

8. Clypeus with median impunctate line obscured by roughened integument, line not raised; first recurrent vein entering second submarginal cell at basal one-third; punctures of scutum and scutellum less than a puncture diameter apart ..... *harbisoni* new species  
 Clypeus with median impunctate line very narrow, distinctly raised; first recurrent vein entering second submarginal cell at middle; punctures of scutal center and of scutellum separated by more than a puncture diameter ..... *lanosa* Cresson
9. Small species, TL 8.5-13.5 mm; clypeal punctures separated by less than twice a puncture diameter ..... 10  
 Large species, TL 15.5-18.5 mm; clypeal punctures fine, separated by 2-4 times a puncture diameter ..... *caesalpiniae* Cockerell
10. Inner orbits distinctly convergent above; TFD 1.71-1.74 x OCD; integument of legs fuscous, never red ..... 11  
 Inner orbits parallel or slightly convergent above; TFD at least 1.9 x OCD; integument of legs either fuscous or ferruginous ..... 12
11. Clypeal maculation pale yellow ..... *cockerelli cockerelli* Fox  
 Clypeal maculation yellow-orange ..... *cockerelli resoluta* Cockerell
12. TFD 1.90-1.95 x OCD; face black, clypeus with variable sized pale to bright yellowish macula; legs fuscous ..... *atripes* Mocsary  
 TFD 2.0-2.1 x OCD; face blackish, clypeus, labrum and scape bright ferruginous; legs bright ferruginous ..... *rhodopus* Cockerell

#### Males

1. Clypeus wholly black; pubescence of mesopleuron wholly blackish ..... 2  
 Clypeus entirely or largely yellowish, whitish or orange-yellow; pubescence of mesopleuron variable ..... 4
2. Pubescence of thoracic dorsum pale ..... 3  
 Pubescence of thoracic dorsum blackish ..... *aterrima* F. Smith
3. Pubescence of pronotal lobe, and usually entire lateral pronotal area, pale; first flagellar segment 2.6-3.1 x second ..... *zacateca* Snelling  
 Pubescence of entire lateral pronotal area, including lobe, blackish; first flagellar segment 3.8-3.9 x second ..... *mexicana* F. Smith
4. Pubescence of head and thorax at least partially pale ..... 5  
 Pubescence of head and thorax blackish ..... *anthracina* Snelling
5. Hind basitarsus much broadened toward apex, about twice longer than greatest width; hind femur swollen, about twice longer than wide ..... 6  
 Hind basitarsus parallel-sided, elongate, at least 3.5 x longer than wide; hind femur usually about three times longer than wide, but may be swollen ..... 7
6. Punctures of mesoscutum much sparser than those of scutellum; mesopleuron with scattered obscure fine punctures; clypeus orange-ferruginous ..... *ectypha* new species  
 Punctures equally dense on mesoscutum and scutellum; mesopleuron closely, finely punctate; clypeus pale yellow ..... *harbisoni* new species
7. Face narrow, inner orbits strongly convergent above; TFD no more than 1.72 x OCD; terga closely punctate ..... 8  
 Face broad, inner orbits not or scarcely convergent above; TFD at least 1.8 x OCD, or less, then terga polished, virtually impunctate ..... 9
8. Paraocular area and underside of scape (usually) yellow; clypeus coarsely, closely punctate, with narrow impunctate median line. *lanosa* Cresson  
 Paraocular area and underside of scape immaculate; clypeus sparsely punctate, with broad median impunctate area ..... *cockerelli* Fox

9. Terga slightly shiny, with abundant coarse, simple black hairs arising from fine punctures separated by twice or less a puncture diameter; TFD at least 1.80 x OCD ..... 10  
 Terga polished, with very sparse, inconspicuous black hairs arising from obscure punctures separated by more than three diameters; TFD 1.54-1.59 x OCD (clypeus coarsely, closely punctate, interspaces dull, roughened) ..... *fisheri* new species
10. Posterior femur and tibia black or darkly rufescent; pubescence of hind tibia at least partially black; terga thinly pubescent, without pale apical fasciae, pubescence largely or wholly dark ..... 11  
 Posterior femur and tibia ferruginous; pubescence of hind tibia wholly pale; terga either with thin apical fasciae of pale pubescence or with abundant, long, erect, pale discal pubescence ..... *rhodopus* Cockerell
11. Clypeus polished, finely and very sparsely punctate; EL about 1.3 x length of mandible; TFD 1.91-2.00 x OCD ..... *caesalpiniae* Cockerell  
 Clypeus slightly to moderately shiny, coarsely and closely punctate, but often with more sparsely punctate median line, interspaces usually roughened; EL about 1.6 x length of mandible; TFD 1.82-1.88 x OCD ..... *atripes* Mocsary

*Centris (Paracentris) atripes* Mocsary

*Centris atripes* Mocsary, 1899. Termész. Füzetek 22:254. ♂; Friese, 1900. Ann. K. K. Naturh. Hofm. Wein 15:296.

*Centris atriventris* Fox, 1899. Acad. Nat. Sci. Phila., Proc. 51:68. ♀ ♂. PRE-OCCUPIED.

*Centris Foxi* Friese, 1900. Acad. Nat. Sci. Phila., Proc. 51:350. New name for *C. atriventris* Fox.

*Centris (Penthemisia) atripes*, Snelling, 1956. Pan-Pacific Entomol. 32:7.

*Centris (Paracentris) atripes*, Snelling, 1966. L. A. Co. Mus., Contrib. Sci. 112:20,21.

The type locality of *C. atripes* is "Praesidio, Mexico." This species appears to be common and widespread in Mexico; I have seen many specimens from the States of Sonora, Chihuahua, Nuevo León, Tamaulipas, Puebla, Guerrero, Oaxaca and Durango. A single male extends the range to COSTA RICA: Hacienda Comelco, elev 50 m, 24 km NW Cañas, Guanacaste Prov, 17 Nov 1971 (E. R. Heithaus, #13655; LACM), on *Hyptis* sp., 0730-0800 hrs.

A single male collected 2.5 mi SE La Huerta, 2200 ft. elev, Territorio Sur de Baja California, MEXICO, 8-9 Oct 1968 (E. L. Sleeper & F. J. Moore; LACM) is tentatively assigned to this species. It is similar to males from Arizona, but the mandibles are mostly yellow (black in all other males studied) and considerable pale pubescence is present on the fore and mid tibiae, usually entirely blackish pubescent in males of *C. atripes*. Although the genital structures are very similar to those of *C. atripes*, the shape of the gonostylus differs.

A similar male was taken in the foothills of the eastern slopes of the Sierra de los Cocopah, approximately 35 km S Mexicali, Baja California, MEXICO, 6 July 1953 (R. R. Snelling; LACM), on *Koerberlinia spinosa*. In this specimen pale pubescence on the legs is restricted to the fore femur and tibia and the clypeal punctures are distinctly separated with moderately shiny

interspaces. The clypeus of the La Huerta male is very closely punctate, the interspaces roughened and barely shiny.

These two males, if properly assigned to *C. atripes* are the first records of this species in Lower California. The male which I recorded (1956) from Brawley, Imperial Co., California, is a typical specimen of *C. atripes*. More material from Lower California is necessary in order to establish the identity of the population there.

*Centris (Paracentris) caesalpiniae* Cockerell

*Centris caesalpiniae* Cockerell, 1897. Ann. Mag. Nat. Hist. (6)19:394. ♀ ♂.

*Centris morsei* Cockerell, 1897. Acad. Nat. Sci. Phila., Proc. 49:355. ♂. NEW SYNONYMY.

*Centris marginata* Fox, 1899. Acad. Nat. Sci. Phila., Proc. 51:67. ♂. NEW SYNONYMY.

*Centris (Trichocentris) morsei*, Snelling, 1956. Pan-Pacific Entomol. 32:4.

*Centris (Paracentris) morsei*, Snelling, 1966. L. A. Co. Mus., Contrib. Sci., 112:2.

This species ranges from western Texas to southeastern Arizona and adjacent areas of northern Mexico. *Centris morsei*, and its long-standing synonym *C. marginata*, occupies the same area and is usually taken along with collections of typical *C. caesalpiniae*. Although superficially very different in appearance from typical males of *C. caesalpiniae*, it is now evident that *C. morsei*, known only from males, is not to be separated. In morphological characters the two forms are inseparable; the apparent differences are now known to be the result of allometry, disappearing with large series available.

The primary morphological features separating these two supposed species have been the larger overall size, proportionately broader head and thicker hind femur of *C. morsei*. Measurements of long series of specimens demonstrate that all these characters form continuous clines. The dramatic differences in color between the largest specimens (*C. morsei*) and more typical *C. caesalpiniae* males intergrade to the extent that the above synonymy is unavoidable.

*Centris (Paracentris) cockerelli cockerelli* Fox

*Centris Hoffmenseggiae* Cockerell, 1897. Ann. Mag. Nat. Hist. (6)19:395. ♀ (not ♂).

*Centris lanosa*, Cockerell, 1897. Ann. Mag. Nat. Hist. (6)19:397. ♂ (not ♀); Fox, 1899. Acad. Nat. Sci. Phila., Proc. 51:69. ♂ (in part); Cockerell, 1906. Amer. Entomol. Soc., Trans. 32:97 (in part); Lutz and Cockerell, 1920. Amer. Mus. Nat. Hist., Bull. 42:556 (in part); Timberlake, 1940. Pan-Pacific Entomol. 16:138 (in part); Snelling, 1956. Pan-Pacific Entomol. 32:7 (in part).

*Centris Cockerelli* Fox, 1899. Acad. Nat. Sci. Phila., Proc. 51:68. ♀.

*Centris cockerelli*, Cockerell, 1906. Amer. Entomol. Soc., Trans. 32:97 (in part); Lutz and Cockerell, 1920. Amer. Mus. Nat. Hist., Bull. 42:552 (in part); Timberlake, 1940. Pan-Pacific Entomol. 16:138 (in part).

*Centris lanosa lanosa*, Michener, 1951, In Muesebeck, Krombein and Townes, U. S. D. A. Monogr. 2:1241 (in part); Snelling, 1966. L. A. Co. Mus., Contrib. Sci. 112:6 (in part).

This is the form most often referred to as *C. lanosa*, but that species is known to be very different (see discussion under *C. lanosa*). The nominate form is found in Texas, New Mexico, Tamaulipas, Nuevo Leon and Chihuahua. In New Mexico and Chihuahua it intergrades with the following subspecies. Females of *C. cockerelli cockerelli* possess a pale yellowish clypeal maculation, ferruginous in *C. cockerelli resoluta*; the males of the two forms are inseparable.

*Centris (Paracentris) cockerelli resoluta* Cockerell

*Centris lanosa*, Fox, 1893. Calif. Acad. Sci., Proc. (2)4:22 (misident.).

*Centris cockerelli*, Cockerell, 1904. So. Calif. Acad. Sci., Bull. 3:160 (misident.); Lutz and Cockerell, 1920. Amer. Mus. Nat. Hist., Bull. 42:552 (in part); Timberlake, 1940. Pan-Pacific Entomol. 16:138 (in part).

*Centris cockerelli resoluta* Cockerell, 1923. Calif. Acad. Sci., Proc. (4)12:76-77. ♀ ♂.

*Centris lanosa resoluta*, Michener, 1951. In Muesebeck, et al., U. S. D. A. Monogr. 2:1241.

*Centris lanosa*, Snelling, 1956. Pan-Pacific Entomol. 32:7 (in part).

*Centris (Paracentris) lanosa resoluta*, Snelling, 1966. L. A. Co. Mus., Contrib. Sci. 112:6.

*Distribution.* Arizona, Nevada, California, Sonora, Baja California and Territorio Sur de Baja California.

***Centris (Paracentris) ectypha*, new species**

Figures 1-4

*Diagnosis.* Male: Labrum and clypeus yellowish ferruginous; hind femur swollen, about 1.75 x longer than wide; hind basitarsus more than half as wide as long, apical margin deeply emarginate; mesopleura nearly impunctate. Female: unknown.

*Description.* MALE (holotype). *Measurements.* HW 4.65; EL 3.25; UFW 1.90; LFW 2.30; TFD 2.05; SL 2.90; WL 12; TL 16 mm.

*Head.* Mandible slender, tridentate, inner tooth triangular. Clypeus moderately broad, CW 1.53 x CL; in profile, strongly bulging and convex, more sharply sloping basad; shiny, with scattered coarse and fine punctures, without defined median impunctate line. Face broad, inner orbits slightly convergent above, UFW 0.83 x LFW; TFD 0.63 x EL; TFD 1.64 x OCD. Scape elongate, about 2.3 longer than wide, SL 1.14 x 1F; 1F:2F:3F:4F = 51:13:19:20. OD:OOD:IOD = 8:6:13.

*Thorax.* Mesoscutum, between parapsides, finely punctate and shiny, interspaces twice or more a puncture diameter; scutellar punctures equal to scutal, separated by a diameter or less. Mesopleura shiny, very sparsely punctate. Propodeum shiny, sparsely and finely punctate. First recurrent entering second submarginal at basal third. Hind femur swollen, about 1.75 x longer than wide. Hind basitarsus (fig. 1) triangular, about 1.75 x longer than wide, apex deeply emarginate.

*Abdomen.* Terga shiny, finely, closely piligerously punctate; margin of apical segment convex; apical process of eighth sternum about 1.3 x longer than wide, apex truncate (fig. 3); process of ninth sternum about 1.75 x longer than wide, broadest subbasally (fig. 4).

*Color.* Black. Labrum, clypeus and transverse supraclypeal bar dull orange-ferruginous. Mandibles and legs brownish ferruginous, apical tarsal segments lighter. Pubescence pale ochreous; brownish on underside of thorax, on legs and on abdomen beyond first segment. Wings transparent, slightly brownish, veins and stigma brown.

FEMALE. Unknown.

*Type material.* Holotype male: Bahía San Francisquito, Baja California, MEXICO, 3 April 1947 (C. F. Harbison). Paratype male: 7 mi W Bahía San Francisquito, Baja California, MEXICO, 14 April 1947 (C. F. Harbison). Type material in LACM.

*Etymology.* Gr., *ektyphos*, puffed up or swollen, because of the enlarged hind femora.

*Distribution.* Known only from the area cited above.

*Discussion.* Both specimens, especially the paratype, are badly rubbed and some characters of the pubescence are uncertain. In general, the bee looks superficially like an unusually robust specimen of *C. cockerelli resoluta*. It differs from this and other known *Paracentris* by the very sparse, fine mesopleural punctation, the swollen hind femur and short, broad hind basitarsus.

This could possibly be the previously unknown male of *C. angustifrons* Snelling, described and known only from a single female from the Huachuca Mts, Arizona, but the thoracic punctation is quite different. Since the two sexes of *Paracentris* tend to be similar in thoracic punctation, I do not think it likely the two are conspecific.

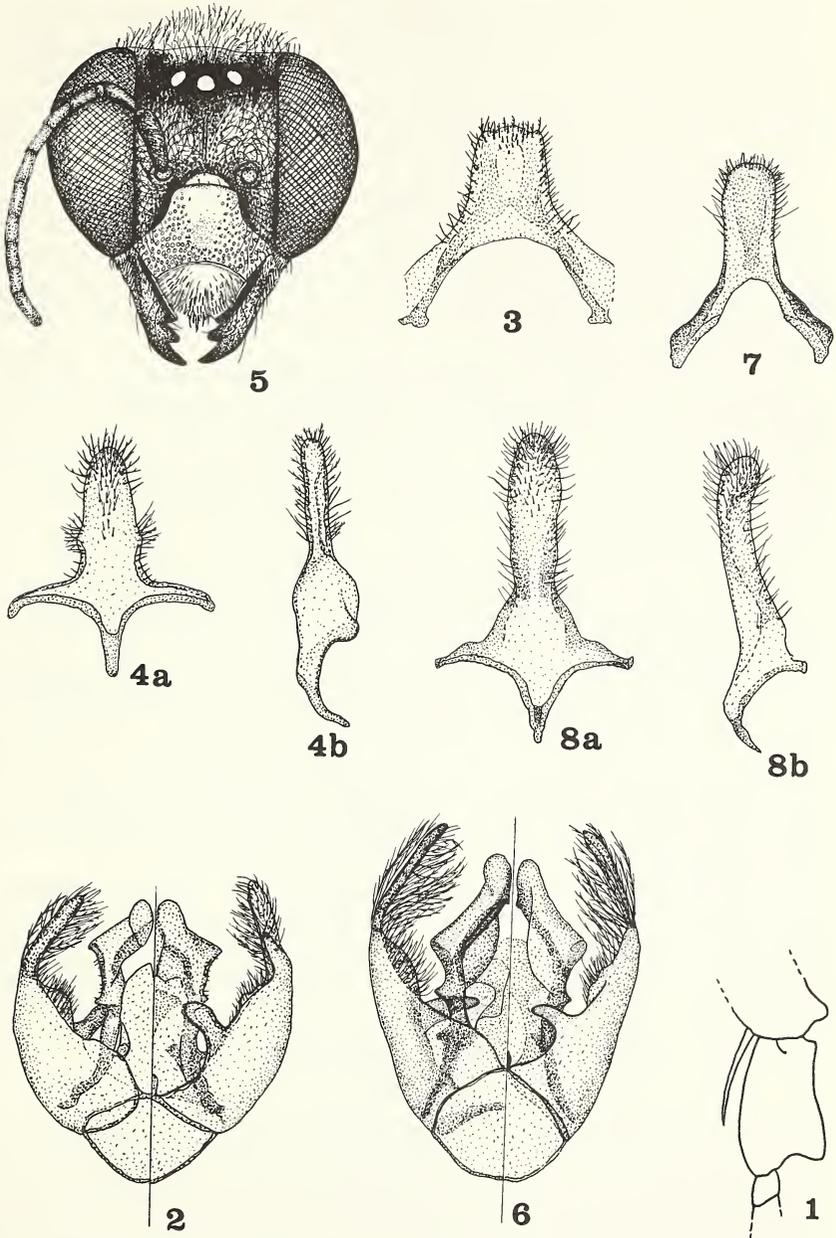
### ***Centris (Paracentris) fisheri*, new species**

Figures 5-8

*Diagnosis.* Male: Inner orbits parallel; labrum and clypeus pale yellow; clypeus dull, without polished median line; tergites polished, with widely scattered fine, piligerous punctures; pubescence on lower third of mesopleuron dark brownish. Female: Unknown.

*Description.* MALE (Holotype). *Measurements.* HW 4.50; EL 3.05; UFW 2.00; LFW 2.00; TFD 2.00; SL 2.50; WL 11.5; TL 17 mm.

*Head* (fig. 5). Mandible slender, tridentate, inner tooth triangular. Clypeus moderately broad, CW 1.50 x CL; in profile moderately bulging, most protuberant at midlength; disc dull, coarsely and closely punctate, interspaces closely tessellate, midline slightly raised, extreme base and sides polished. Face broad, inner orbits parallel; UFW = TFD = LFW; TFD 0.65 x EL; TFD 1.54 x OCD. Scape moderately long, about 2.3 x longer than wide, SL 1.43 x 1F; 1F:2F:3F:4F = 35:13:25:25. OD:OOD:IOD = 7:8:13.



FIGURES 1-8. 1-4, *Centris ectypha*, ♂: 1, hind basitarsus; 2, genitalia; 3, sternum VIII; 4, sternum IX (ventral and lateral views). 5-8, *C. fisheri*, ♂: 1, front of head; 2, genitalia; 3, sternum VIII; 4, sternum IX (ventral and lateral views).

*Thorax.* Mesoscutum closely punctate, except small, sparsely punctate median area, punctures finer than on clypeus; interspaces shiny; scutellum closely, finely punctate, punctures separated by a puncture diameter or more. Propodeum shiny, finely punctate, punctures separated by a puncture diameter or more. Hind femur stout, about 2.5 x longer than wide. Hind basitarsus slender, about 4 x longer than wide.

*Abdomen.* Terga I-V polished, with widely dispersed, fine punctures on disc from which arise short, fine hairs; tergum VI more closely punctate, especially at sides and toward apical margin; margin of apical segment convex; apical process of eighth sternum about 2.5 x longer than wide, apex slightly convex (fig. 7); process of ninth sternum about 2.8 x longer than wide, broadest beyond midpoint (fig. 8).

*Color.* Black. Labrum; clypeus, except laterobasal margin; transverse mark on supraclypeal area, pale yellowish. Mandibles, antennae and legs dark brownish, underside of flagellum lighter. Pubescence pale ochreous on head, thorax and first tergum. Lower third of mesopleuron, legs and all terga (beyond first) and sterna brown pubescent. Wings transparent light brown, veins and stigma dark brown.

FEMALE: Unknown.

*Type material.* Holotype and one paratype male: 5 mi NW San Ignacio, Territorio Sur de Baja California, MEXICO, 11 Oct 1972 (E. M. & J. L. Fisher), deposited in LACM.

*Etymology.* Named for Mr. Eric M. Fisher, collector of the two known specimens, who has presented many specimens from Lower California to the LACM.

*Discussion.* Superficially this most closely resembles *C. atripes* but is easily separated by the parallel inner orbits, dull clypeus and polished, virtually impunctate tergites. The proportions of the antennal segments and apical sternites are also different.

The paratype is similar to the holotype, but with the following measurements and proportions: HW 4.90; EL 3.25; UFW 2.10; LFW 2.15; TFD 2.15; SL 2.64; WL 12; TL 15 mm. CW 1.59 x CL. UFW 0.98 x LFW; TFD 0.66 x EL; TFD 1.59 x OCD. SL 1.46 x 1F; 1F:2F:3F:4F=37:14:20:27. OD:OOD:IOD=9:7:12.

### *Centris (Paracentris) harbisoni*, new species

Figures 9-13

*Diagnosis.* Male: Clypeus and labrum yellow, mandible and scape immaculate; hind femur about twice longer than wide; hind basitarsus almost half as wide as long; terga beyond first black pubescent. Female: Clypeus black; mesopleuron brown pubescent on lower half; clypeus coarsely, closely punctate, without raised impunctate line; first recurrent vein entering second submarginal cell well basad of middle; punctures of scutum and scutellum less than a puncture diameter apart.

*Description.* MALE (holotype). *Measurements.* HW 4.2; EL 3.0; UFW 1.7; LFW 1.9; TFD 1.7; SL 2.4; WL 10; TL 14 mm.

*Head.* Mandible slender, tridentate, inner tooth triangular, acute. Clypeus broad, CW 1.48 x CL, not abruptly sloping basad, evenly convex in profile, finely punctate, punctures separated by 1.5-2 diameters, interspaces shiny, without median impunctate line. Face broad, inner orbits slightly convergent above, UFW 0.87 x LFW; TFD 0.58 x EL; TFD 1.52 x OCD. Scape about 2.3 x longer than wide, about 1.06 x 1F; 1F:2F:3F:4F=45:15:18:18. OD:OOD:IOD=8:5:12.

*Thorax.* Mesoscutum and scutellum finely punctate, punctures about a diameter apart, more separated in middle, interspaces moderately shiny. Mesopleuron finely punctate, punctures about two diameters apart, interspaces moderately shiny. First recurrent entering second submarginal well basad of middle. Hind femur swollen, about twice longer than wide, sharply longitudinally angulate beneath; hind basitarsus (fig. 9) broad, almost half as wide as long.

*Abdomen.* Terga moderately shiny, finely, closely piligerously punctate; apex of last tergum broadly rounded; apical process of eighth sternum about as broad as long, apex truncate (fig. 11); apical process of ninth sternum a little over twice longer than wide, broadest subbasally (fig. 12).

*Color.* Blackish. Labrum; clypeus, except lateral margins; short paracocular stripe; triangular supraclypeal mark, all yellowish white. Tegulae light brownish yellow. Tarsal segments dark reddish. Wings hyaline, veins and stigma brown. Pubescence brown on legs, lower half of propodeal side, thoracic venter, abdominal segments beyond first; otherwise whitish, tinged with fulvous on thoracic dorsum.

FEMALE (Allotype). *Measurements.* HW 4.35; EL 2.80; UFW 2.25; LFW 2.20; TFD 2.35; SL 2.60; WL 10; TL 14 mm.

*Head.* Mandible slender, quadridentate. Clypeus broad, CW 1.60 x CL; evenly convex in profile; disc coarsely, contiguously punctate, midline roughened and irregular, not raised, smooth or shiny. Face broad, inner orbits slightly divergent above, UFW 1.02 x LFW; TFD 0.84 x EL; TFD 1.88 x OCD. Scape about 2.6 longer than wide, slightly longer than 1F; 1F:2F:3F:4F=51:13:15:15. OD:OOD:IOD=8:10:12.

*Thorax.* Similar to male, except usual sexual differences; basitibial plate as in fig. 13.

*Abdomen.* Similar to male, except usual sexual differences; pygidium narrowly truncate at apex, secondary plate broad, triangular, apex slightly prolonged.

*Color.* Very similar to male, but without pale face marks; lower half of mesopleura brownish pubescent; pubescence of scutum and scutellum more strongly tinged with fulvous.

*Type material.* Holotype male: Bahía San Francisquito, Baja California, MEXICO, 3 Apr 1947 (C. F. Harbison). Allotype female: 7 mi W Bahía San

Francisquito, Baja California, MEXICO, 14 Apr 1947 (C. F. Harbison). Paratypes: 1 ♂, same data as holotype; 1 ♀, 3 mi S Okie Landing, Baja California, MEXICO, 21 Mar 1970 (E. M. Fisher). All type material in LACM.

*Etymology.* Named for the collector of the primary type material, C. F. "Harbie" Harbison.

*Distribution.* Known only from the Gulf side of Baja California, Mexico.

*Discussion.* The combination of black clypeus and pale thoracic pubescence in the female occurs in but two other described North American species: *angustifrons* and *lanosa*. The former of these may be readily separated from *harbisoni* by the much narrower facial quadrangle, which is longer than wide, and by the finely, sparsely punctate clypeus with a broad, impunctate median line. In *lanosa* the median impunctate line is narrow, as in *harbisoni*, but is sharply defined and distinctly raised. The punctures of the scutum and scutellum are dense in *harbisoni*, separated by less than a puncture diameter; in *lanosa* the interspaces are greater than a puncture diameter, at least in the center of these segments.

The broadened hind femur and basitarsus will readily separate the male of *harbisoni* from those of all other species except *ectypha*. The mesopleuron of *ectypha* is finely and sparsely punctate, with the punctures shallow and ill-defined. In this species, also, the punctures of the center of the scutum are much more separated than are those of the scutellum. In *harbisoni* the scutum, scutellum and mesopleuron are all closely, finely punctate, the punctures well-defined.

#### *Centris (Paracentris) lanosa* Cresson

*Centris lanosa* Cresson, 1872. Amer. Entomol. Soc., Trans. 4:284. ♂.

*Centris subhyalina* Fox, 1899. Acad. Nat. Sci. Phila., Proc. 51:69. ♀. NEW SYNONYMY.

*Centris birkmanii* Friese, 1900. Termész. Füzetek 23:44. ♂ ♀. NEW SYNONYMY.

*Centris lanosa lanosa*, Mitchell, 1962. N. C. Exp. Sta. Tech. Bull. 152:334-355 ♀ ♂.

*Centris (Paracentris) subhyalina*, Snelling, 1966. L. A. Co. Mus., Contrib. Sci. 112:8-10. ♂ ♀.

*Centris lanosa* has been our most consistently misunderstood species. Cresson (1872) based this name on a series of males from Texas. Cockerell (1897) recorded males from Las Cruces, New Mexico, which he thought belonged to Cresson's species and associated females with them. Although not questioning the validity of Cockerell's identification of these males, Fox (1899) expressed the view that the females were actually those of *C. hoffmanseggiae* Cockerell; the females assigned by Cockerell to *C. hoffmanseggiae* were renamed *C. cockerelli* Fox. No female was assigned by Fox to *C. lanosa*, but he did remark that his *C. subhyalina* might be the female.

That *C. cockerelli* might be the true female of *C. lanosa*, as interpreted by Cockerell from the Las Cruces area, was ventured by Cockerell (1900).

Cockerell (1906) listed *C. lanosa* from "Texas, L. Cal., Sonora," but advanced no remarks concerning the sexes or the identity of the species; *C. cockerelli* was listed from New Mexico and California; *C. subhyalina* from Texas, questionably the female of *C. lanosa*.

Lutz and Cockerell (1920) proposed no changes in the status of any of these names but Cockerell (1923) described as new *C. cockerelli resoluta* from Baja California. The California species of *Centris* were enumerated by Timberlake (1940). He recorded the presence of *C. cockerelli*, noting that this was certainly the same as the bee recorded by Cockerell and Fox as *C. lanosa* from Nw Mexico and southern California and pointed out that the male did not quite agree with Cresson's original description of *C. lanosa*. He commented that the California form is probably not more than subspecifically distinct.

The first concrete arrangement of these names was made by Michener (1951 in Muesebeck, et al.) who listed the names as follows: *C. lanosa lanosa* (= *C. cockerelli*), *C. lanosa resoluta*, and *C. subhyalina* (possibly = *lanosa*). This arrangement was slightly modified by Snelling (1956) who proposed that *C. lanosa resoluta* be placed in synonymy. Mitchell (1962) recorded *C. lanosa lanosa* from Florida and redescribed the species, but Snelling (1966) pointed out that Mitchell's record was based on *C. subhyalina*, and that *C. birkmanii* was a synonym of *C. subhyalina*. The proposal that *C. subhyalina* was a synonym of *C. lanosa* (teste Timberlake, in Krombein, 1958) was rejected on what then seemed good evidence. In that same paper I resurrected *C. lanosa resoluta*.

Subsequently, I have examined type material of *C. lanosa* and found that Cresson's material is conspecific with males of *C. subhyalina* and *C. birkmanii* and these names are here synonymized with that. Material previously assigned to *C. lanosa* from New Mexico westward belongs to a separate species, for which the name *C. cockerelli* is available, with the western form separable as a subspecies, *C. cockerelli resoluta*. The true *C. lanosa*, as here understood, is known only from Kansas, central Texas and western Florida.

#### *Centris (Paracentris) mexicana* F. Smith

*Centris mexicana* F. Smith, 1854. Cat. Hymen. Brit. Mus. 2:378. "♀" = ♂.

*Centris (Melanocentris) mexicana*, Friese, 1900. Ann. K. K. Naturh. Hofmus. Wein, 15:289. ♀ ♂.

*Centris (Ptilotopus) mexicana*, Cockerell, 1906. Amer. Entomol. Soc., Trans. 32:73, 97.

*Centris (Penthemisia) mexicana*, Michener, 1951. Kans. Entomol. Soc., Jour. 24:4.

*Centris (Paracentris) mexicana*, Snelling, 1966. L. A. Co. Mus., Contrib. Sci. 112:10, 19, 21. ♀ ♂.

Dr. I. H. H. Yarrow has advised me (*in litt.*) that the type of this species, in the British Museum (Natural History) is a male, not a female as originally stated by Smith. Smith's description fails to mention the characteristic color of

the thoracic hairs, but Dr. Yarrow confirmed the usual interpretation of this species.

Friese (1900) described *C. albiceps* as a variety of *C. mexicana* based on males in which the labrum and clypeus are said to be whitish. If I correctly interpret the very brief sentence by which this form was characterized, the integument, and not the hair, is whitish. No *Paracentris* resembling *C. mexicana* is known to me which possesses a whitish labrum and clypeus in the male. I assume that *C. albiceps* belongs to another subgenus; it may be an earlier name for *strawi* Snelling, here placed in the subgenus *Acritocentris*, and described below. Until the type can be studied, *C. albiceps* must be considered unrecognizable.

This species was described from an unspecified locality in Mexico; Friese (1900) recorded it from Orizaba (Veracruz) and Cockerell (1906) from Cuernavaca (Morelos). The following records will considerably amplify the distribution of *C. mexicana*. MEXICO. *Durango*: 11 ♀♀, 12 ♂♂, Durango, 6200', 14 Aug 1947 (Cazier, Gertsch, Michener; D. Rockefeller Exped.; AMNH); 1 ♂, La Quebrada, 20 July 1947 (Michener; D. Rockefeller Exped.; AMNH); 1 ♂, Yerbanis, 6700', Cuencame Dist, 19 Aug 1947 (Michener; D. Rockefeller Exped.; AMNH); 3 ♂♂, San Juan del Rio, 5200', 30 July 1947 (Michener, Spieth; D. Rockefeller Exped.; AMNH). *Michoacan*: 6 ♀♀, 1 ♂, Apatzingan, 1200', 1-7 Aug 1940 (Hoogstraal and Knight; AMNH). *Nuevo Leon*: 2 ♀♀, 5 ♂♂, Galeana, 5-6000', 30 July and 3 Aug 1939 (R. Haag; MCZ). *Chihuahua*: 2 ♂♂, Agua Caliente, Santa Barbara Dist, 24 July 1947 (Michener; D. Rockefeller Exped.; AMNH); 1 ♀, 6 mi NE Meoqui, 2 Sept. 1950 (R. F. Smith; AMNH); 1 ♀, Delicias, 13 July 1947 (Michener; D. Rockefeller Exped.; AMNH); 1 ♀, 20 mi SW Camargo, 4500', 13 July 1947 (Michener; D. Rockefeller Exped.; AMNH), on *Cevallia sinuata*: 1 ♀, Salaices, 5200', 20 Aug 1947 (G. M. Bradt; AMNH). *Sonora*: 1 ♂, San Luis, Sept-Oct (Palmer; MCZ). *Distrito Federal*: 3 ♂♂, Chapultepec, 5 July 1897 (Koebele colln.; CAS). UNITED STATES. *Arizona*: 2 ♂♂, South West Research Station, 5400', 5 mi W Portal, Cochise Co, 18 July 1956 (C. & M. Cazier; AMNH), on *Melilotus alba*; 1 ♀, 6.0 mi SW Bisbee, 4800', Cochise Co, 29 July 1973 (T. J. Zavortink; TJZ), on *Menodora scabra*, 0630-0645 hrs; 1 ♀, same locality and collector, 30 July 1973, on *M. scabra*, 0630-0645 hrs. *New Mexico*: 1 ♀, McMillan Camp, 6800', 13 mi N Silver City, Grant Co, 19 July 1961 (F., P. & J. Rindge; AMNH); 1 ♂, Rock Hound State Park, 4600', 9 mi SE Deming, Luna Co, 14 Aug 1973 (T. J. Zavortink; TJZ), on *Hoffmanseggia densiflora*, 1330-1345 hrs. *Texas*: 2 ♂♂, Big Bend Natl Park, Brewster Co, 16 June 1948 (M. Cazier; AMNH); 1 ♀, 16 mi W Sanderson, Pecos Co, 23 June 1970 (E. M. Fisher; LACM).

*Centris (Paracentris) rhodopus* Cockerell

*Centris caesalpiniae* var. *rhodopus* Cockerell, 1897. Ann. Mag. Nat. Hist. (6)19: 394. ♀ ♂.

- Centris rhodopus*, Fox, 1899. Acad. Nat. Sci. Phila., Proc. 51:64, 65, 68. ♂ ♀; Lutz and Cockerell, 1920. Amer. Mus. Nat. Hist., Bull. 42:559; Timberlake, 1940. Pan-Pacific Entomol. 16:138.
- Centris (Melanocentris) rhodopus*, Friese, 1900. Ann. K. K. Naturh. Hofmus. Wein 15:297. ♀ ♂.
- Centris rhodopus* var. *pulchrior* Cockerell, 1900. Canad. Entomol. 32:363. ♂.
- Centris (Ptilotopus) rhodopus*, Cockerell, 1906. Amer. Entomol. Soc., Trans. 32:97.
- Centris rhodoleuca* Cockerell, 1923. Calif. Acad. Sci., Proc. (4)12:75. ♂; Timberlake, 1940. Pan-Pacific Entomol. 16:5. NEW SYNONYMY.
- Centris (Penthemisia) rhodopus*, Michener, 1950. Kans. Entomol. Soc., Jour. 24:4; Snelling, 1956. Pan-Pacific Entomol. 32:3, 4, 6. ♂ ♀.
- Centris (Trichocentris) rhodoleuca*, Snelling, 1956. Pan-Pacific Entomol. 32:4-5.
- Centris (Paracentris) rhodopus*, Snelling, 1966. L. A. Co. Mus., Contrib. Sci. 112:20, 21. ♀ ♂.

The form described by Cockerell as *C. rhodoleuca* differs from typical males of *C. rhodopus* primarily in the larger size, exceptionally stout femora and the abundance of long, shaggy white pubescence over the entire body, including the abdomen. This form, described from Lower California, has been known from a few specimens from southern California and Nevada. A male specimen from Rock Hound State Park, 4600', 9 mi SE Deming, Luna Co, NEW MEXICO, 26 Aug 1973 (T. J. Zavortink; TJZ), on *Cevallia sinuata*, 1600-1615 hrs, is intermediate between *C. rhodoleuca* and *C. rhodopus*. The femora, stouter than in *C. rhodopus*, are not as stout as in *C. rhodoleuca*. The terga are blackish, but with broad hyaline apical margins. The pubescence is shaggier than in *C. rhodopus*, but not as shaggy as in *C. rhodoleuca*. On the second and third terga it is appressed as in *C. rhodopus* but pale as in *C. rhodoleuca*; on the remaining segments it is erect and pale, as in *C. rhodoleuca*, but shorter than in that form. The hairs on the outer face of the hind basitarsus are pale, as in *C. rhodoleuca*. In size, the specimen is intermediate between the two forms.

Another male, also collected by Zavortink, 5 mi ESE Deming, 4200', Luna Co, NEW MEXICO, 15 Aug 1973, on *Hoffmanseggia densiflora*, 1015-1030 hrs, is similar, but more like typical *C. rhodopus*. In this specimen, the pubescence of the hind basitarsus is pale; that of the second and third terga is pale, with interspersed black hairs in the middle.

With these specimens at hand, it appears that *C. rhodopus* produces occasional aberrant individuals in a manner similar to those of *C. pallida* and *C. caesalpiniae*. Hence *C. rhodoleuca* must now be placed in the synonymy of *C. rhodopus*.

*Centris (Paracentris) zacateca* Snelling

- Centris (Paracentris) zacateca* Snelling, 1966. L. A. Co. Mus., Contrib. Sci. 112:11-12. ♀ ♂.

The following new records extend somewhat the range of this basically Mexican species.

NEW RECORDS. UNITED STATES. *Arizona*: 2 ♂♂, 0.7 mi W Portal, 4900', Cochise Co, 3 Aug 1972 (T. J. Zavortink; TJZ), 0850-0950 hrs, on *Hoffmanseggia densiflora*, 1 ♂, South West Research Station, 5400', 5 mi W Portal, Cochise Co, 10 Aug 1956 (C. & M. Cazier; AMNH), on *Melilotus alba*; 1 ♀, same locality as above, 8 Aug 1956 (E. Ordway; AMNH), on *M. alba*; 1 ♀, Carr Cyn, 5400', Huachuca Mts, Cochise Co, 21-23 Aug 1972 (R. R. Snelling; LACM); 1 ♀, Yaqui Spg, 5500', Huachuca Mts, Cochise Co, 28 Aug 1972 (R. R. Snelling; LACM). *New Mexico*: 1 ♀, Las Cruces, Doña Ana Co, 18 July 1963 (J. Lopez; Univ. New Mexico); 2 ♂♂, 1.4 mi E Animas, Hidalgo Co, 11 Aug 1972 (T. J. Zavortink; TJZ), on *Hoffmanseggia densiflora*, 0700-0730 hrs; 1 ♀, 1 ♂, same locality, 16 Aug 1972 (T. J. Zavortink; TJZ), on *H. densiflora*, 1000-1030 hrs.

Subgenus *TRACHINA* Klug

***Centris (Trachina) heithausi*, new species**

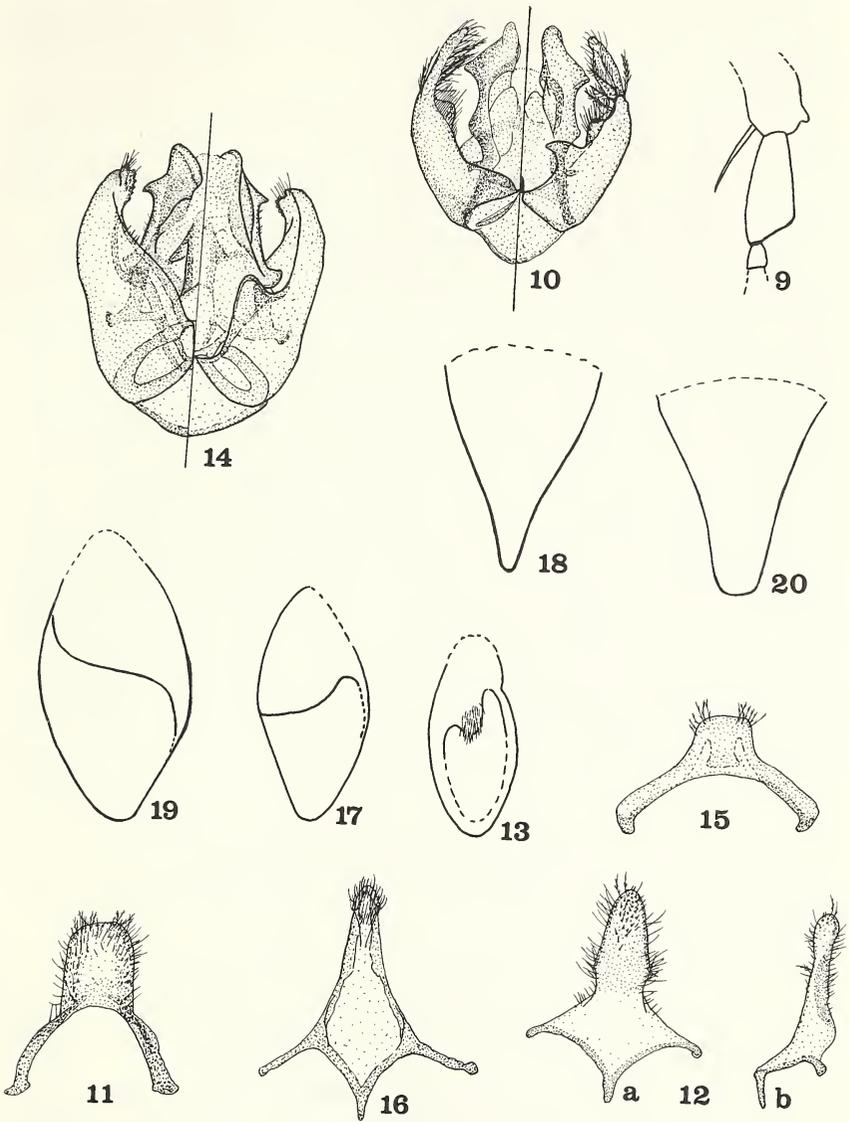
Figures 14-18

*Diagnosis.* Thoracic pubescence whitish, costal margin of fore wing blackish; abdomen bright, clear ferruginous. Female: basitibial plate as in fig. 17; pygidial plate with margins evenly convergent apicad, not reflexed; inner mandibular tooth subacute; scape dark beneath. Male: inner mandibular tooth broad, obliquely truncate, weakly emarginate; hind femoral process broader than high; hind tibia bicarinate, process elongate, straight; hind basitarsal carina produced distad as a broad tooth, ending beyond midlength of segment; ninth sternum slender.

*Description.* MALE (Holotype). *Measurements.* HW 5.20; EL 3.50; UFW 1.75; LFW 2.45; TFD 2.15; SL 0.68; WL 13; TL 15 mm.

*Head.* Mandible moderately stout, tridentate, inner tooth broad, obliquely truncate, the truncation slightly concave. Clypeus broad, CW 1.58 x CL, abruptly sloping basally; disc nearly flat in profile; median line not defined, punctures of black areas fine, separated by about half a puncture diameter, interspaces dull, densely tessellate; punctures coarser on maculate areas, separated by less than half a puncture diameter, interspaces shinier, especially below. Face broad, inner orbits moderately convergent above, UFW 0.71 x LFW; TFD 0.61 x EL; TFD 1.87 x OCD. Scape about 1.7 longer than wide, 0.61 x 1F; 1F:2F:3F:4F=67:16:20:20. OD:OOD:IOD=8:5:13.

*Thorax.* Mesoscutum finely, closely punctate, punctures separated by 1/4-1/2 puncture diameter, interspaces shiny; with narrow impunctate median line. Scutellum shiny, very finely punctate, punctures separated by 1-3 puncture diameters. Mesopleural punctures about equal to those of scutum, separated by 1/2-1 puncture diameter. Propodeal sides shiny, punctures fine, irregularly spaced, some punctures elongate. Ventral process of hind femur stout, thicker than high; hind tibia with anterior and posterior carinae complete on inner face, anterior tooth oblique, moderately long; posterior carina



FIGURES 9-20. 9-12, *Centris harbisoni*, ♂: 9, hind basitarsus; 10, genitalia; 11, sternum VIII; 12, sternum IX (ventral and lateral views). 13, *C. harbisoni*, ♀: basitibial plate. 14-16, *C. heithausi*, ♂: 14, genitalia; 15, sternum VIII, 16, sternum IX. 17-18, *C. heithausi*, ♀: 17, basitibial plate; 18, pygidial plate. 19-20, *C. fuscata*, ♀: 19, basitibial plate; 20, pygidial plate.

of hind basitarsus extending about  $3/4$  length of segment, terminating in a moderately elongate process. First recurrent vein entering second submarginal cell in basal one-fourth; accessory veinlet of first submarginal cell heavily pigmented.

*Abdomen.* Terga finely, closely piligerously punctate; seventh tergum apically bilobate; seventh sternum not cleft at apex; apical process of eighth sternum broader than long, posterior margin simple (fig. 15); apical process of ninth sternum elongate, slender, slightly broadened preapically (fig. 16); cusps at apex of gonocoxite stout, acute (fig. 14).

*Color.* Head blackish, following bright yellow: basal three-fourths of mandible externally; labrum, except margins; transverse apical band on clypeus (much broadened laterad) conjoined with narrow median line; paracocular area to level of antennal socket; underside of scape. Underside of flagellum dark rufescent. Thorax black. Tegulae transparent ferruginous. Fore and mid legs blackish; yellow basal spot on tibia; underside of tibia, all tarsi light rufescent; hind leg mostly dull ferruginous, femur with irregular median infuscation. Abdomen bright, clear ferruginous, more yellowish on first tergum and apical three segments and ventrally. Pubescence mostly whitish, but with abundant brownish hairs around antennal sockets, across vertex and on pronotal lobes. Mesopleuron above with hairs slightly tinged with brownish. Pubescence of legs mostly whitish to light ferruginous, brownish on underside of mid and hind femora, tibiae and anteriorly on basitarsi; brighter on hind leg. Discal hairs of terga 2-4 fuscous, longer at sides; ferruginous apically and ventrally, especially long and dense on sterna 4-6. Wings transparent brownish, veins and stigma black; costal margin conspicuously darker to about middle of marginal cell.

*FEMALE (Allotype). Measurements.* HW 5.50; EL 3.75; UFW 2.55; LFW 2.95; TFD 3.05; SL 0.88; WL 13.0; TL 18.0 mm.

*Head.* Mandible moderately stout, tridentate, inner tooth broadly triangular, acute. Clypeus broad, CW 1.68 x CL, similar to that of male. Face broad, UFW 0.86 x LFW; TFD 0.81 x EL; TFD 2.04 x OCD. Scape about twice longer than wide, SL 0.71 x 1F; 1F:2F:3F:4F = 75:15:20:20. OD:OOD:IOD = 8:9:17.

*Thorax.* Similar to that of male; basitibial plate as in fig. 17.

*Abdomen.* Similar to that of male, except usual sexual differences; pygidial plate (fig. 18) with margins evenly convergent toward narrowly truncate apex, margins not reflexed.

*Color.* Much as in male, but scape dark beneath. Without conspicuously brownish hairs around antennal sockets; hairs across vertex light brownish; hairs of pronotal lobe pale; scopa yellowish white; costal margin of forewing infuscated beyond apex of marginal cell.

*Type material.* Holotype male and allotype female: COSTA RICA, Guanacaste Prov: Hacienda Comelco, elev 50 m, 24 km NW Cañas, 16 Feb 1972 (E. R. Heithaus; #18329 ( $\delta$ ), #18215), on *Caesalpinia*, at 1000 ( $\delta$ ).

and 0730 hrs (♀). Paratypes, same locality and collector: 5 ♂♂, 2 ♀♀, 12 Feb 1972, on *C. eriostachys*, 0830-0945 hrs; 10 ♂♂, 13 ♀♀, same date, on *Gliricidia* sp., 0920 hrs; 8 ♂♂, 17 ♀♀, 14 Feb 1972, on *C. eriostachys*, 0730-1015 hrs; 5 ♂♂, 32 ♀♀, 16 Feb 1972, on *Caesalpinia*, 0730-1000 hrs; 1 ♀, 22 Feb 1971, on *Byrsonema crassifolia*, 0800 hrs; 1 ♂, 6 Mar 1972, on legume, 0800; 1 ♀, 7 Feb 1972, on *B. crassifolia*, 0730-0830 hrs. One paratype pair to the following: AMNH, UK, USNM and E. R. Heithaus. Holotype, allotype and remaining paratypes in LACM.

*Etymology.* This species is named for the collector of the type series.

*Distribution.* Known at present only from Guanacaste Province, Costa Rica. Two additional specimens are from Hacienda La Pacifica, 5 km NW Cañas, a female, 7 Jan 1972, a male, 20 Jan 1972 on *Cassia* sp., both collected by Heithaus.

*Discussion.* This species most closely resembles *C. fuscata* Lepelletier, with which it is sympatric at the type locality, but both sexes lack the yellow to light ferruginous color of the thoracic pubescence and the basal area of the propodeum is densely tessellate. In the female of *C. fuscata* the median line of the clypeus is distinctly raised, the scape is maculate beneath, the fore tibia has an external stripe, the basitibial plate is different (fig. 19), and the pygidial plate is abruptly narrowed to a rounded apex (fig. 20). In the male of *C. fuscata* the process of the hind femur is higher, the carina of the hind basitarsus is much shorter, the clypeus yellow, except two subbasal lateral spots, the fore tibia with an external yellow stripe.

The color of the thoracic pubescence is much like that of *C. carrikeri* Cockerell of Trinidad, but in that species the wings are light basally, dark beyond the basal vein. In both sexes the scutellum is flattened in the middle, depressed in the middle at the summit of the declivity. The scape is yellow beneath in both sexes.

#### VARIATION IN CEPHALIC CHARACTERS

	<i>TFD</i> × <i>EL</i>	<i>UFW</i> × <i>LFW</i>	<i>TFD</i> × <i>OCD</i>	<i>CW</i> × <i>CL</i>	<i>SL</i> × <i>SW</i>	<i>SL</i> × <i>IF</i>
♀ ♀	0.76-0.81	0.83-0.91	1.87-2.14	1.50-1.71	1.77-2.18	0.64-0.74
♂ ♂	0.56-0.63	0.71-0.75	1.52-1.87	1.44-1.59	1.75-2.00	0.58-0.70

#### Subgenus *CENTRIS* Fabricius

#### *Centris (Centris) aethyctera*, new species

Figures 21-26

*Centris fasciatella* Friese, 1900. Hofmus. Naturh., Ann. K. K. Wien, 15:332 (part).  
*Centris fasciata*, Lutz and Cockerell, 1920. Amer. Mus. Nat. Hist., Bull. 42:553 (part).

*Diagnosis.* Pubescence mostly pale; terga beyond first with broad, uninterrupted transverse yellow fasciae, apical margins transparent; pubescence

of mesoscutum black-tipped. Female: external hairs on fore and mid tibiae and tarsi light; appressed discal hairs of second and third terga fuscous; scape yellow beneath; fore tibia with a complete stripe on outer face and an evanescent one anterior to it. Male: face broad, UFW 0.80 x LFW; discal hairs of second and third terga fuscous; fore tibial stripe complete; scape longer than 1F.

*Description.* MALE (Holotype). *Measurements.* HW 4.90; EL 3.35; UFW 1.80; LFW 2.25; TFD 1.90; SL 0.73; WL 9.5; TL 15 mm.

*Head* (fig. 21). Mandibles slender, tridentate, inner tooth acute. Clypeus wide, CW 1.4 x CL, apical margin nearly straight; in profile, sharply sloping toward base; disc flat, raised on either side slightly below summit of basal slope, with barely indicated raised median line. Face broad, TFD 0.56 x EL, UFW 0.80 x LFW; TFD 1.65 x OCD. Scape short, slightly longer than 1F (44:41); 1F:2F:3F:4F = 41:12:24:23. OD:OOD:IOD = 8:5:14. Sloping clypeal sides clearly punctate, punctures separated by a puncture diameter or more, finer and denser basad, disc irregularly, finely roughened and tessellate, with scattered punctures, shinier and less roughened along midline.

*Thorax.* Mesoscutum closely, finely punctate, interspaces shiny, median line less closely punctate; scutellum shiny, finely punctate, interspaces variable, but mostly one to two puncture diameters; pleura finely, closely punctate, interspaces densely tessellate and slightly shiny; propodeal side closely, finely punctate, lightly tessellate and slightly shiny, basal and posterior areas shinier, very lightly tessellate, with scattered fine punctures. Second recurrent vein entering first submarginal cell at basal third. Hind femur about 2.5 x longer than wide, sharply longitudinally angulate beneath but not carinate; hind basitarsus simple.

*Abdomen.* Terga closely, finely piliferously punctate, interspaces shiny; pygidium apically bilobate, with short, low median ridge basally. Eighth sternum with apical margin of process emarginate (fig. 24); apical process of ninth sternum gradually widened toward apex (fig. 25); ventral process of gonocoxite elongate, narrowly rounded apically; inner dorsal angle of gonocoxite nearly right angular (fig. 23).

*Color.* Head blackish, the following light yellow: basal three-fifths of mandible externally; labrum, clypeus (except elongate laterobasal mark), narrow transverse supraclypeal mark, narrow paraocular stripe to level of clypeal base, malar area, underside of scape. Underside of flagellum dark ferruginous. Thorax black, scutellum light reddish. Legs mostly ferruginous; fore tibia with complete longitudinal stripe externally; mid tibia with evanescent external stripe; all femora and hind tibiae with blackish blotches; hind tibia with basal yellow mark. Abdomen: first tergum ferruginous, with yellow macula on each side, apical margin broadly transparent; second tergum reddish before gradulus, narrowly blackish with greenish reflections behind gradulus, disc largely light yellow, with wide apical transparent band; remaining terga similar, but last wholly ferruginous; sterna ferruginous. Hairs

mostly pale, but with conspicuous fuscous hairs on frons and in transverse band on vertex; hairs of scutum and scutellum black-tipped; hairs of tarsi mostly reddish, some fuscous on inner side of hind basitarsi.

**FEMALE** (Allotype). *Measurements*. HW 5.70; EL 3.65; UFW 2.55; LFW 2.85; TFD 3.00; SL 0.83; WL 11.0; TL 15 mm.

*Head* (fig. 22). Mandibles slender, tridentate, inner tooth acute. Clypeus wide, CW 1.5 x CL, similar to that of male, but sides and base less sharply sloping, shinier, with distinct, slightly raised median impunctate line sub-basally. Face broad, TFD 0.82 x EL; UFW 0.89 x LFW; TFD 2.5 x OCD. Scape about twice longer than wide, SL 0.76 x 1F; 1F:2F:3F:4F = 65:13:19:20, OD:OOD:IOD = 9:9:17.

*Thorax*. Scutum and scutellum equally finely, closely punctate; shiny; pleural punctures slightly coarser, dense, interspaces moderately shiny. Fore basitarsus, on inner face, with usual anterior row of short flattened setae and about four elongate, apically spatulate setae on posterior margin; mid basitarsus with anterior row of short, flattened setae beneath.

*Abdomen*. Similar, except usual sexual differences, to that of male; pygidium narrowly rounded or subtruncate apically.

*Color*. Much as in male, but clypeus with median stripe not reaching base and with a narrow median spot at apex; fore tibia with evanescent yellow stripe anterior to usual one on outer face. Hairs much as in male, but with fuscous hairs much less numerous on frons below level of ocelli; scopal hairs whitish.

*Type material*. Holotype male: COSTA RICA, Guanacaste Prov: Hacienda Comelco, elev 50 m, 24 km NW Cañas, 16 Feb 1972 (E. R. Heithaus #18355), collected 1000 hrs, on *Caesalpinia eriostachys*. Allotype female: same locality and date (E. R. Heithaus #18163), collected 0730 hrs, on *C. eriostachys*. Paratypes, all from type locality: (E. R. Heithaus): 2 ♂♂, 2 ♀♀, 12 Feb 1972, on *Gliricidia* sp.; 44 ♂♂, 2 ♀♀, 12 Feb 1972, on *C. eriostachys*; 60 ♂♂, 7 ♀♀, 14 Feb 1972, on *C. eriostachys*; 2 ♂♂, 16 Feb 1972, on *Andira inermis*; 42 ♂♂, 15 ♀♀, 16 Feb 1972, on *C. eriostachys*; 5 ♂♂, 13 Mar 1971, on *Securidacea tenuifolia*; 1 ♂, 15 Mar 1971, on *S. tenuifolia*; 1 ♂, 16 Mar 1971, on *S. tenuifolia*; 2 ♀♀, 16 Mar 1971, on *Byrsonema crassifolia*; 1 ♀, 21 Mar 1971, on *B. crassifolia*; 1 ♂, 21 Apr 1971, on *Arrabidaea corallina*. One paratype pair to each of the following: AMNH, BMNH, TAMU, UK, USNM, E. R. Heithaus; Holotype, Allotype and remaining paratypes in LACM.

*Etymology*. Gr., *aithykte*, darter, because of the swift, elusive manner of flight.

*Distribution*. Northwestern Mexico to Costa Rica. **ADDITIONAL MATERIAL**. MEXICO. 2 ♂♂, 7 ♀♀, Cocorit, Sonora, 11 June 1961 (A. Menke & L. Stange; LACM); 1 ♂, 10 mi S Alamos, Sonora, 13 June 1961 (F. D. Parker; LACM); 1 ♀, Rosario, Sinaloa, 24 June 1963 (J. Doyen; LACM). GUATEMALA. 1 ♂, 1 ♀, Los Amates, no date (Kellerman;

LACM); 5 ♂♂, no specific locality, 300 m elev, 28 Mar-3 Apr 1923 (AMNH). COSTA RICA, Guanacaste Prov.: 8 ♂♂, 2 ♀♀, 2 km S Liberia, 1 Mar 1972 (G. W. Frankie; LACM), on *Andira inermis*; 21 ♀♀, 25 ♂♂, Pan Amer. Hwy, 3 km SE Liberia, 26 Feb 1972 (G. W. Frankie; LACM, TAMU), on *A. inermis*, 1200-1300 hrs; 1 ♀, Palo Verde, 16 Feb 1972 (C. E. Jones; LACM).

*Discussion.* This species closely resembles *C. eisenii* W. Fox of Mexico and *C. fasciata* F. Smith of the West Indies. Central American records of the latter name probably all apply to *C. aethyctera*. From *C. eisenii*, females of the present species may be separated by smaller size, presence of dark appressed hairs on the second and third terga, presence of erect plumose white hairs on the fourth tergum and the presence of apical fasciae of plumose hairs on the second and third terga. The legs of the Mexican species are dark rufescent, with the pubescence of the middle pair dark brownish; the fore tibia is without an external yellow stripe. The antennal scape of *C. eisenii* is immaculate and is much shorter than 1F, the clypeus is wholly yellow, the legs are dark, the fore tibia lacks a yellow stripe and the fourth tergum is without plumose hairs. Also, the hairs of the thoracic dorsum lack blackish apices.

One male specimen possesses a scape which is slightly shorter than the first flagellar segment (0.96 x 1F). In all other males, SL is at least equal to 1F.

#### VARIATION IN CEPHALIC CHARACTERS

	TFD × EL	UFW × LFW	TFD × OCD	CW × CL	SL × SW	SL × 1F
♀♀	0.81-0.85	0.83-0.91	2.15-2.54	1.48-1.61	2.00-2.36	0.74-0.84
♂♂	0.56-0.68	0.76-0.86	1.59-1.82	1.41-1.54	1.75-2.04	0.96-1.09

The female of *C. aethyctera* differs from that of *C. fasciata* in possessing ferruginous legs, fore tibia with a yellow stripe from base to apex, hairs of pronotal lobe and upper mesopleura not black-tipped, second and third terga with apical fascia of appressed plumose hairs and the fourth tergum with sparse erect plumose white hairs. The legs of *C. fasciata* are dark rufescent and the stripe on the fore tibia extends only a little beyond the middle. The second and third terga lack apical fasciae of pubescent hairs and there are no erect plumose hairs on the disc of the fourth segment. The scutellum of the one *C. fasciata* female seen is black rather than ferruginous as in *C. aethyctera*, but this probably is of no significance.

The males of *C. fasciata* and *C. aethyctera* are similar, but the first flagellar segment is longer than the scape in *C. fasciata*. In this species, too, the hairs of the pronotal lobe are black-tipped, the legs are dark rufescent and the stripe on the fore tibia extends but half the length of the segment; the fourth tergum is without appressed plumose hairs along the apical margin. The eighth sternae are similar in the two species, but that of *C. fasciata* (fig.

27) is less deeply emarginate at the apex, hence does not appear bilobed as in *C. aethyctera* (fig. 24). The narrowest part of the apical process of the ninth sternum is beyond the middle in *C. fasciata* (fig. 28), basad of the middle in *C. aethyctera* (fig. 25).

***Centris (Centris) erubescens*, new species**

*Diagnosis.* Female: thorax, abdomen and legs ferruginous, pubescence pale, terga II-IV with distinct apical pubescent fasciae. Male: unknown.

*Description.* FEMALE (Holotype). *Measurements.* HW 5.45; EL 3.20; UFW 2.45; LFW 2.60; TFD 2.80; SL 0.70; WL 9.35; TL 15 mm.

*Head.* Mandibles slender, tridentate. Labrum about twice wider than long. Clypeus wide, CW 1.59 x CL, similar to that of *C. aethyctera*, but without distinct raised median line, slightly bulging basally; maculate areas shinier than nonmaculate, punctures fine, irregularly spaced, interspaces irregularly and obliquely raised. Frons closely and finely punctate; vertex shinier, punctures fine, sparse, irregularly spaced. Face broad, TFD 0.87 x EL; UFW 0.94 x LFW; TFD 2.2 x OCD. Scape about twice longer than wide, SL 0.76 x 1F; 1F:2F:3F:4F = 55:10:21:20. OD:OOD:IOD = 8:11:14.

*Thorax.* Scutum and scutellum similar, finely punctate, punctures separated by about a puncture diameter or less, interspaces shiny; mesopleuron more coarsely and closely punctate, interspaces closely tessellate and dull.

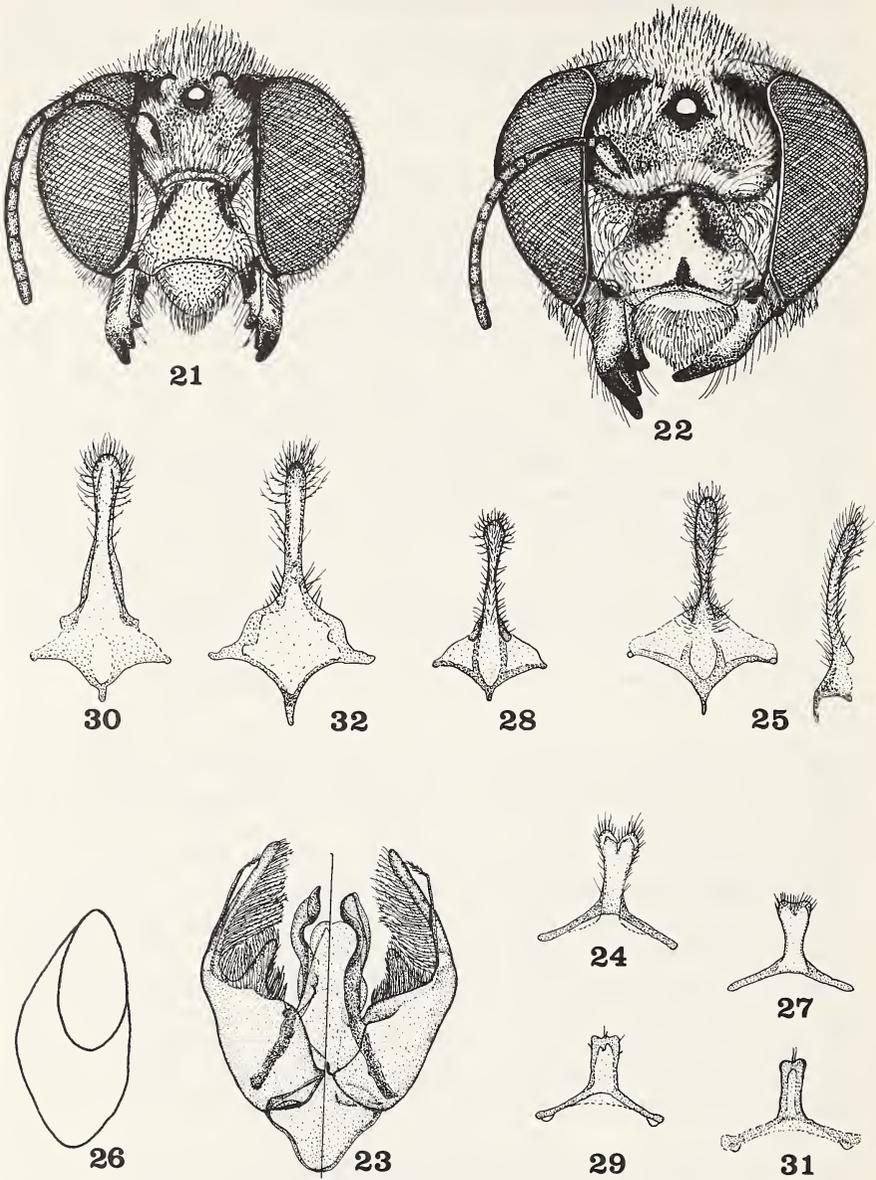
*Abdomen.* Similar to that of *C. aethyctera*, pygidial apex narrowly truncate.

*Color.* Head blackish, grading into rufescent on genae, following yellow: basal three-fifths of mandible; malar area; labrum, except dull rufescent margin and apical cloud; para-ocular area to level of antennal socket; median stripe on basal half of clypeus, then curved laterad to apicolateral corner; small supraclypeal spot; small preapical spot on scape. Thorax and legs dull reddish, with irregular blackish areas on pronotum, scutum, pleurae and propodeum; fore and mid tibiae with yellow basal spot, fore tibia with traces of yellow stripe basally. Abdomen wholly dull rufescent, without metallic tints. Pubescence mostly pale; frons and vertex with many black-tipped hairs; hairs of scutum and scutellum minutely fuscous-tipped; hairs on inner side of tibiae and tarsi ferruginous. First tergum with obscure preapical pubescent fascia (best viewed obliquely); terga II-IV with distinct, narrow, whitish apical pubescent fascia, obsolescent in middle on II; apical fimbria on V golden yellow.

*Type material.* Holotype and one paratype female: MEXICO: 67 km E Escarcega, Campeche, 3 May 1959 (T. C. Emmel), both in LACM.

*Etymology.* L., *erubescere*, blush or redden, because of the uniformly dull ferruginous abdomen.

*Distribution.* Known only from the States of Campeche and Yucatán, Mexico.



FIGURES 21-32. 21-22, *Centris aethyctera*, front of head, ♂ and ♀ respectively. 23-25, *C. aethyctera*, ♂: 23, genitalia; 24, sternum VIII; 25, sternum IX. 26, *C. aethyctera*, ♀: basitibial plate. 27-28, *C. fasciata*, ♂: 27, sternum VIII; 28, sternum IX. 29-30, *C. nigritula*, ♂: 29, sternum VIII; 30, sternum IX. 31-32, *C. flavifrons*, ♂: 31, sternum VIII; 32, sternum IX.

*Paratypic variation.* The paratype is very similar to the holotype, but is slightly larger; the wings are worn, hence not measured. Measurements and ratios for this specimen are: HW 5.55; EL 3.35; UFW 2.55; LFW 3.02; TFD 2.90; SL 0.78; TL 16 mm; CW 1.58 x CL; TFD 0.87 x EL; UFW 0.93 x LFW; TFD 2.23 x OCD; SL 0.79 x 1F; 1F:2F:3F:4F = 59:10:19:19; OD:OOD:IOD = 7:11:16.

*Discussion.* This distinctive species, presently known only from three specimens, is easily recognized by the dull, wholly ferruginous abdomen with narrow pubescent fasciae on terga II-IV. It apparently is not closely related to other species of *Centris*, s. str., with pubescent fasciae, for in these the fasciae are much broader, the fourth tergum is densely covered with erect plumose hairs and the first four terga are metallic greenish or blue-green.

A single specimen, not a paratype, is from Piste, Yucatán, 12 June 1967 (E. C. Welling; LACM). This female is in most respects like the two from Campeche and is certainly conspecific. It differs from these in lacking the ferruginous areas on the thorax and the first two terga possess irregular blue-green blotches basally. The legs are a little more brownish.

*Centris (Centris) fasciata* F. Smith

Figures 27-28

*Centris fasciata* F. Smith, 1854. Cat. Hymen. Brit. Mus. 2:377. ♀ ♂.

*Centris fasciatella* Friese, 1900. Hofmus. Naturh., Ann. K. K. Wien. 15:332. New name for *C. fasciata* F. Smith, nec *C. fasciata* Lepeletier, 1825.

When Friese (1900) monographed *Centris*, he included species now placed in the genus *Epicharis*. Consequently, *C. fasciata* F. Smith, 1854, was preoccupied by *C. fasciata* Lepeletier, 1825; Friese proposed *C. fasciatella* for Smith's species. Since *Epicharis* is now recognized as a separate genus, Smith's name is once more available.

Smith's *C. fasciata* was based on both sexes from Jamaica, West Indies. Friese (1900) reported the species present in Mexico and Brazil. I have seen no material from South America referable to this form, but find that specimens under this name from Central America are a different species, described above as *C. aethyctera*.

This species resembles *C. aethyctera* and *C. eisenii* in having the pubescence pale and the abdomen with broad yellow fasciae on segments II-V (♀ ♀) or II-VI (♂ ♂). The hairs of the vertex are black-tipped over the apical one-third to one-half in the female, the male with many hairs wholly dark. The hairs of the mesoscutum and scutellum are black-tipped, as are those of the pronotal lobes and the hypopimeral area. In both sexes the dorsal face of the first tergum is light metallic green (at least partially ferruginous in the other species); the fourth tergum is without erect plumose hairs on the disc (true also of *C. eisenii*).

*Centris (Centris) inermis* Friese

*Centris inermis* Friese, 1899. Termész. Füzetek 23:46. ♂ ♀; Ann. K. K. Naturh. Hofmus. Wein 15:314; Cockerell, 1928. Psyche 35:173; 1949, U. S. Natl. Mus., Proc. 98:479.

*Centris inermis gualanensis* Cockerell, 1912. Ann. Mag. Nat. Hist. (8)9:568. ♀ ♂; Schwartz, 1934. Amer. Mus. Nov. 722:12; Michener, 1954. Amer. Mus. Nat. Hist., Bull. 104:138-139; Snelling, 1966. L. A. Co. Mus., Contrib. Sci. 112:22. NEW SYNONYMY.

*Centris inermis pallidifrons* Cockerell, 1949. U. S. Natl. Mus., Proc. 98:479. ♂.

Long series of specimens from Costa Rica demonstrate that the dark legged form described by Cockerell from Guatemala (Gualan and Quirigua) as the subspecies *gualanensis* is not distinguishable from the nominate form. Friese recorded *C. inermis* from Brazil, Peru, Colombia and Panama. In the South American material, the legs of both sexes are largely ferruginous, with the fore tibiae a little darker. The Guatemalan material of Cockerell was characterized by darker legs, with little ferruginous. The Costa Rican samples exhibit a great deal of variation and, while the legs are, on the whole, somewhat more infuscated than in most South American material, the difference hardly seems significant.

*Centris (Centris) nigrifula* Friese

## Figures 29-30

*Centris flavifrons* var. *nigrifula* Friese, 1899. Termész. Füzetek 23:46. ♀.

*Centris nigrifula*, Cockerell, 1926. Ann. Mag. Nat. Hist. (9)17:518-519. ♀ ♂.

Friese's type female was erroneously labelled "Afrika," but Cockerell recognized specimens from Trinidad, British West Indies, as belonging to this form, which he felt should be accorded species status. A long series of both sexes (mainly males) from Trinidad (Manzanilla and Curepe) is in the AMNH. After examining these specimens, I tentatively agree with Cockerell.

Superficially, the females of the two species are obviously different. That of *C. flavifrons* has the thoracic pubescence largely whitish, with a broad band of blackish pubescence between the tegulae and blackish hairs are conspicuous in the scopa, especially on the basitarsus. The erect pubescence of the fourth and fifth terga is wholly pale. In the female of *C. nigrifula* the thoracic pubescence is largely blackish, white on the scutellum, axillae, at the base of the hind wing, pronotal dorsum and with a few pale hairs on either side of the midline at the anterior margin of the scutum. The scopa is pale externally, sometimes with a few brownish tinged hairs on the basitarsus. The pubescence of the fourth tergum is mostly blackish with a few white hairs basally and white patches laterally; on the fifth segment the pubescence is mostly white but with a strong admixture of blackish, especially in the middle.

The males reflect the similarities of their respective females. That of

*C. nigritula* is extensively dark pubescent on the thorax, the scutum entirely blackish or with a narrow band or median patch of whitish pubescence anteriorly. The fourth tergum has a narrow apical band of pale pubescence which is strongly tinged with brownish or fulvous; the fifth tergum is mostly pale pubescent, again strongly tinged with brownish or fulvous, with scattered blackish hairs. The genital structures of the males are very similar, but the eighth and ninth sterna of *C. nigritula* (figs. 29, 30) are more robust than those of *C. flavifrons* (figs. 31, 32).

The differences between these two species are slight, mostly in degree of melanism. While some differences in the eighth and ninth sterna have been noted, these also are not great and are possibly not significant. Until more material is available from Surinam and Guyana, where the two might be expected to intergrade if they are conspecific, it seems feasible to consider them specifically distinct.

*Centris (Centris) adani* Cockerell

Figures 33-35

*Centris (Cyanocentris) adani* Cockerell, 1949. U. S. Natl. Mus., Proc. 98:472-473. ♀.

This species was described from a single female collected at Zamorano, HONDURAS, and has not since been recognized. I have examined the type, now in the United States National Museum of Natural History, and found it at variance with the original description in several important aspects. Because Cockerell's eyesight was not as keen as formerly, I am sure that the faults lie with the description. Significant errors in the original description are as follows: first four terga blue-green, not dark blue; hair of face, occiput and thorax light ochreous, darker on dorsum of thorax, not light reddish; no dark hairs present on venter; middle tibia with fuscous, not gray, hair; scopal hairs yellowish white, not pale reddish; apical margin of fourth and entire fifth and sixth terga light ferruginous, not mentioned in original description; second tergum with medially interrupted apical fascia of pale pubescence; third tergum with complete marginal fascia; fourth tergum with dense, erect pale pubescence; scape with a narrowly interrupted stripe beneath; supra-clypeal mark present. Since this is a common Central American species I am redescribing it, including the previously unrecognized male.

*Diagnosis.* Female: scopa pale; first four tergites metallic blue-green, each with narrow apical pubescent fascia, evanescent on middle of second; terga V and VI ferruginous; legs dark. Male: pubescence of legs dark, but with apical fringes of mid and hind tibiae and basitarsi ferruginous or paler; first five terga metallic blue-green, second with basal yellow fascia, narrowly interrupted in middle, fifth with apical margin transparent ferruginous; second tergum with lateral apical pubescent fascia, third with fascia broadly evanescent in middle, fourth with complete fascia, obscured by dense erect discal pubescence.

*Description.* MALE. *Measurements.* HW 5.45; EL 3.55; UFW 2.10; LFW 2.80; TFD 2.30; SL 0.83; WL 12; TL 16 mm.

*Head.* Mandible slender, tridentate, inner tooth truncate. Clypeus broad, CW 1.47 x CL, apical margin nearly straight; in profile disc flat, obliquely sloping in basal one-fifth, not raised on either side of midline toward base, without defined raised median line. Face narrow, TFD 0.65 x EL, inner orbits strongly convergent above, UFW 0.75 x LFW; TFD 2.09 x OCD. Scape short, about twice longer than wide, about 0.8 x 1F; 1F:2F:3F:4F = 63:12:20:20. OD:OOD:IOD = 8:7:13. Clypeus moderately shiny, punctures fine, irregularly spaced, with broad median impunctate area.

*Thorax.* Mesoscutum and scutellum finely punctate, interspaces shiny, punctures separated by less than half a puncture diameter, a little more separated along midline. Mesopleuron finely punctate, punctures elongate, separated by more than a puncture diameter, interspaces dull, densely tessellate. Metapleura shinier, punctures round, coarser than those of mesopleura, separated by half a diameter or less. Propodeal sides more coarsely punctate, punctures variably spaced, separated by half a diameter or more, interspaces moderately shiny. First recurrent vein entering second submarginal cell at basal third. Hind femur about twice longer than wide, angular but not carinate beneath; hind basitarsus simple.

*Abdomen.* Terga moderately shiny, closely, finely piligerously punctate. Pygidium apically bilobate, with rather sharp median ridge.

*Color.* Head black, the following pale yellow: mandibles, except dark apices; labrum; malar area; clypeus, except elongate black bar along latero-basal margin; paraocular area to level of antennal socket; transverse supra-clypeal mark; underside of scape. Thorax blackish, tegulae light ferruginous, scutellum and pronotal lobes dull ferruginous. Legs dark rufescent to blackish; all tibiae with basal spot, fore tibia in addition with oblique yellow longitudinal stripe; mid tibia without external stripe. First five terga dark, with metallic blue-green reflections; second segment with broad, transverse basal yellow fascia, narrowly interrupted in middle; fourth and fifth with broad apical transparent ferruginous band; apical segments ferruginous. First four sterna dark basally, with transparent ferruginous margins, apical segments ferruginous. Pubescence mostly pale on head, with a few fuscous hairs on frons and in band across vertex. Thoracic hairs pale, ochreous-tipped on scutum and scutellum, uniformly grayish on pleurae; femora with progressively more fuscous pubescence from fore to hind; fore tibiae with external hairs ferruginous, lighter along hind margin; mid and hind tibiae with mostly fuscous hairs, but posterior fringe conspicuously light ferruginous; mid and hind basitarsi with fuscous hairs externally, except light ferruginous posterior fringe; mid and hind tibiae and basitarsi with fuscous hairs on inner faces. Wings transparent, moderately and uniformly infuscated, veins and stigma blackish.

FEMALE (Type). *Measurements*. HW 5.75; EL 3.55; UFW 2.50; LFW 3.00; TFD 3.00; SL 0.87; WL 12; TL 17 mm.

*Head*. Mandible slender, quadridentate, two inner teeth approximately equal, inner tooth acute. Labrum about twice wider than long. Clypeus wide, CW 1.56 x CL, similar to that of male, but base and margins less abruptly sloping; with narrow impunctate median line. Face broad, TFD 0.85 x EL; UFW 0.83 x LFW; TFD 2.50 x OCD. Scape 2.5 x longer than wide, SL 0.81 x 1F; 1F:2F:3F:4F = 64:14:18:20. OD:OOD:IOD = 8:10:15.

*Thorax*. As in male except usual sexual differences.

*Abdomen*. Similar, except usual sexual differences, to male; pygidial plate narrowly rounded.

*Color*. Head blackish, mandibles tricolored, yellowish basally, golden apically, narrowly piceous between; labrum cream-colored, margins and apicomedian spot piceous; clypeus with transverse preapical bar and conjoined median stripe which does not attain base; malar area cream-color; para-ocular area cream-color to level of antennal socket; underside of scape cream-color. Thoracic color as in male, but without external stripe on fore tibia. First four terga and extreme base of fifth dark, with metallic blue-green reflections; narrow apical margin of third and broad apical margin of fourth transparent amber; most of fifth and all of sixth terga ferruginous. Sterna mostly ferruginous, with variable infuscations basally and in middle. Pubescence much as in male, but that of fore and mid femora largely pale, of tibiae and tarsi fuscous; scopa yellowish white. Terga II-V with narrow apical fasciae of appressed whitish pubescence, evanescent in middle on II; IV with abundant short, erect plumose discal pubescence which does not wholly conceal surface.

This species ranges from southern Mexico to Costa Rica. I have studied the following material. MEXICO: 1 ♂, Lake Tequesquitengo, 2800', Morelos, 16 Mar 1959 (H. E. Evans; MCZ); 1 ♂, Tezcaltita, Los Tuxtlas, Veracruz, 2 May 1970 (V. Toledo; LACM); 1 ♀, 5 km E Zapata, Tabasco, 4 May 1970 (V. Toledo; LACM); 1 ♀, 10 mi SE Tehuitzingo, 3900', Puebla, 3 July 1953 (Univ. Kans. Mex. Exped.; LACM); 1 ♀, X-can, Quintana Roo, 28 Apr 1963 (E. C. Welling; LACM). HONDURAS: 1 ♀, Zamorano, 9 Feb 1900 (A. Rivera; USNM, type no. 58878). COSTA RICA: 1 ♂, Palo Verde, Guanacaste, 16 Feb 1972 (C. E. Jones; LACM); 7 ♂♂, 6 ♀♀, 2 km S Liberia. Guanacaste, 1 Mar 1972 (G. W. Frankie; LACM), on *Andira inermis*; 22 ♂♂, 20 ♀♀, 3 km SE Liberia, Guanacaste, 26 Feb 1972 (G. W. Frankie; LACM, TAMU), on *A. inermis*, 1200-1300 hrs; 5 ♂♂, 1 ♀, Hacienda Comelco, 50 m elev, 24 km NW Cañas, Guanacaste, 7 Feb 1972, on *Byrsonoma crassifolia*, 0730-0830 hrs; 2 ♂♂, 1 ♀, same locality, 14 Feb 1972, on *Caesalpinia eriostachys*, 0730-1015 hrs; 4 ♂♂, 3 ♀♀, same locality, 16 Feb 1972, on *C. eriostachys*, 0830-1000 hrs; 23 ♂♂, 6 ♀♀, same locality and date, on *A. inermis*, 1200-1215 hrs; 4 ♂♂, same locality, 22 Feb 1972, "perched on grass near ground, 0930-1000 hrs"; 1 ♂, same locality, 6 Mar

1972, on *A. inermis*, 1045-1120 hrs; 2 ♀♀, same locality, 12 Mar 1972, on *B. crassifolia*, 0700-0800 hrs (all E. R. Heithaus; LACM).

*Discussion.* Both sexes of this species are superficially similar to such species as *C. poecila* Lepeletier and *C. segregata* Crawford. Few specimens of the Cuban *C. poecila* are available. The one female studied has the erect hairs of the disc of tergum IV simple, and narrow apical fasciae are absent from terga II-IV, the scopa is dark, the mandibles have a small basal spot and the scape is immaculate beneath.

The female of *C. segregata* also has a black scopa and lacks pubescent fasciae on terga II-IV. Like the female of *C. adani*, that of *C. segregata* has erect plumose hairs on the disc of tergum IV; this segment, however, is largely bluish, with a narrow ferruginous margin, rather than mostly ferruginous. The fore tibia of *C. adani* females has a basal macula, but lacks the longitudinal stripe along the external surface present in *C. segregata*.

The male of *C. poecila* lacks maculae on the legs and tergum II, terga I-IV are dark metallic blue (margin of IV reddened), the legs are dark pubescent and the erect hairs of tergum IV are simple. The male of *C. segregata* is more similar to that of *C. adani*, but the basal macula of tergum II is smaller, the fore tibia has a complete external stripe, terga II-IV lack pubescent apical fasciae, on tergum IV plumose hairs are present only along the margin and the hind legs are mostly dark pubescent.

#### VARIATION IN CEPHALIC CHARACTERS

	<i>TFD</i> × <i>EL</i>	<i>UFW</i> × <i>LFW</i>	<i>TFD</i> × <i> OCD</i>	<i>CW</i> × <i>CL</i>	<i>SL</i> × <i>SW</i>	<i>SL</i> × <i>IF</i>
♀ ♀	0.82-0.87	0.82-0.90	2.00-2.50	1.50-1.59	2.27-2.60	0.78-0.84
♂ ♂	0.64-0.71	0.73-0.80	1.83-2.20	1.40-1.65	2.00-2.30	0.74-0.87

#### *Centris (Centris) segregata* Crawford

Figures 36-38

*Centris poecila* var. *segregatus* Crawford, 1906. Amer. Entomol. Soc., Trans. 32:159. ♀; Friese, 1916. Stett. Entomol. Zeit. 77:296; Lutz and Cockerell, 1920. Amer. Mus. Nat. Hist., Bull. 42:559.

This species was based on four females from San José, Costa Rica. Although described as a form of *C. poecila* Lepeletier, a Cuban species, I believe it must be elevated to species rank. In the female of *C. poecila* the midline of the clypeus is slightly raised, the fourth tergum is narrowly bluish at the base, otherwise ferruginous and the erect pubescence of the fourth tergum is simple and black. In *C. segregata* females the clypeus is slightly depressed along the midline, tergum IV is almost entirely bluish, with a narrow apical ferruginous band and the pubescence of the apical half of that segment is plumose and white in color.

The undescribed male of *C. segregata* is very similar to that of *C. poecila* but has conspicuous basal yellow fasciae on either side of the second tergum

and the fourth tergum is narrowly testaceous along the margin and has a few plumose white hairs. The genital structures are distinctly different. In *C. segregata* the apex of the lobe of the eighth sternum is expanded on either side of the midline (fig. 37); in *C. poecila* the apex is simply rounded (fig. 40). The ninth sternum of *C. segregata* has a much narrower apical process and the hairs are simple (fig. 38) (*C. poecila*, fig. 41). Finally, the ventral process of the gonocoxite of *C. segregata* is digitiform (fig. 36), rather than low and evenly convex as in *C. poecila* (fig. 39).

Specimens of *C. segregata* have been examined from Mexico, Guatemala, Honduras, Costa Rica, Venezuela and Trinidad.

### **EXALLOCENTRIS**, new subgenus

*Diagnosis.* Female without modified setae on fore and mid tibiae; male without giant branched setae on gonocoxites; scutellum neither bilobed nor tuberculate; maxillary palpus five-segmented; innermost mandibular tooth truncate, upper inner carina terminating near its base.

*Description.* Mandibles neither subapically broadened nor bent, quadridentate in female, tridentate in male, upper inner carina ending at base of innermost tooth in both sexes, inner tooth truncate in male; maxillary palpus five-segmented, apical segment shorter than basal; ocelli anterior to narrowest part of vertex, lateral ocelli of male about an ocellar diameter from eye margin; first flagellar segment slightly longer than scape, conspicuously shorter than following three combined; mesonotum without defined bare areas; scutellum neither bilobed nor bituberculate; hypopimeral area not tuberculate; inner face of fore basitarsus of female without row of flattened setae on anterior margin or long, apically spatulate setae on posterior margin; inner face of mid basitarsus of female without row of flattened setae on anterior margin; basitibial plate of female abruptly depressed and concave on apical two-thirds, without defined secondary plate; male with distinct pygidial plate; *male terminalia*: process of eighth sternum about twice longer than broad; apical process of ninth sternum long, narrowly rounded at apex; gonocoxites without apical processes or giant branched setae basally.

Medium-sized species, integument and pubescence dark, male sometimes with preapical maculae on clypeus.

*Type species:* *Centris (Melanocentris) anomala* Snelling, 1966.

*Etymology.* Gr., *exalles*, quite different, plus generic name *Centris*.

*Discussion.* This subgenus includes only the type species, known only from the State of Jalisco, Mexico. The lack of specialized setae on the fore and middle basitarsi of the female will separate this from the similar *Melanocentris* and *Acritocentris*. The male is less distinctive and is similar to those of *Acritocentris*, but has the inner mandibular tooth truncate and the maxillary palpi are five-segmented. The male may be separated from that of

*Melanocentris* by the termination of the upper inner mandibular carina which ends at the base of the innermost, rather than next to innermost tooth.

### **ACRITOCENTRIS**, new subgenus

*Diagnosis.* Female: secondary basitibial plate with overhanging margin; abdomen nonmetallic or with metallic reflections; scutellum flat, not bilobed; upper inner mandibular carina ending at base of inner tooth; mandible tridentate, not broadened or bent apically; maxillary palpus four-segmented. Male: gonocoxites without giant branched setae; scutellum flat, not bilobed, hypopimeral area non-tuberculate; mandible tridentate, upper inner carina ending at inner tooth, apex neither broadened nor abruptly bent.

*Description.* Mandibles no broader subapically than medially, not abruptly bent subapically, tridentate, upper inner carina ending at base of inner tooth, inner tooth triangular; maxillary palpus four-segmented in both sexes, apical segment about as long as basal and weakly subdivided; ocelli before narrowest part of vertex, lateral ocelli of male separated from eye by about an ocellar diameter; first flagellar segment of male longer than scape, shorter than following three segments combined; mesonotum without defined bare areas; scutellum without lateral tubercles or lobes; hypopimeral area non-tuberculate; fore basitarsus of females with elongate spatulate setae; secondary basitibial plate with overhanging margin; first recurrent vein entering second submarginal cell near basal one-third or two-fifth; male with exposed pygidial plate; *male terminalia*: process of eighth sternum about twice longer than broad; apical process of ninth sternum long, narrowly rounded apically; gonocoxites without apical processes or giant branched setae basally. Medium-sized species, black, with mostly black pubescence, males with labrum and clypeus maculate.

*Type species:* *Centris (Melanocentris) ruthannae* Snelling, 1966.

*Included species:* *C. agameta*, new species; *C. strawi* Snelling, 1966.

*Etymology.* Gr., *akritos*, confused or mixed, plus generic name *Centris*.

*Discussion.* *Acritocentris* is proposed to accommodate three species, two of which I had previously (1966) assigned to the subgenus *Melanocentris* as anomalous species. The three species here assigned to this new subgenus differ in several characteristics from *Melanocentris*: the mandibles are neither subapically broadened nor bent, they are tridentate and the upper inner mandibular carina ends at the base of the inner tooth; the inner tooth is triangular. In *Melanocentris* the mandibles are subapically broadened and bent, quadridentate in the females, tridentate in the males, with the upper inner mandibular carina ending near the base of the third tooth in the females, near the base of the second tooth in the males; the innermost tooth is often truncate or bidentate. The scutellum of *Melanocentris* is tuberculate or raised on either side of the midline in both sexes.

KEY TO SPECIES OF *ACRITOCENTRIS*

1. Pubescence of thoracic dorsum pale; female labrum pale pubescent . . . . . 2  
 Pubescence of thoracic dorsum black, concolorous with that of head,  
 sides of thorax and abdomen; female labrum black pubescent . . . . .  
 . . . . . *ruthannae* Snelling
2. Pubescence on sides of thorax mostly pale, concolorous with that of  
 dorsum . . . . . *agameta*, new species  
 Pubescence of sides of thorax dark, contrasting with that of dorsum . . . . .  
 . . . . . *strawi* Snelling

***Centris (Acritocentris) agameta*, new species**

Figures 42-44

*Diagnosis.* Male: pubescence of thoracic dorsum and most of pleurae pale; paraocular and supraclypeal areas maculate; clypeus coarsely punctate and rugulose. Female: unknown.

*Description.* MALE (Holotype). *Measurements.* HW 5.15; EL 3.55; UFW 2.00; LFW 2.46; TFD 2.25; SL 2.75; WL 14; TL 17 mm.

*Head.* Mandible slender, tridentate, inner tooth small, acute. Clypeus broad, CW 1.57 x CL, disc flat in profile, base and sides abruptly sloping; coarsely, closely punctate, interspaces irregularly rugulose, slightly shiny; without median impunctate line or area. Face narrow, inner orbits distinctly convergent above; UFW 0.82 x LFW; TFD 0.63 x EL; TFD 1.61 x OCD. Scape short, about 2.04 x longer than wide, 1.06 x 1F; 1F:2F:3F:4F = 52:16:25:25. OD:OOD:IOD = 8:7:13. Front of vertex at level of ocelli shiny, with very sparse, fine punctures.

*Thorax.* Mesoscutum dull, punctures coarser than on occiput, contiguous; scutellum a little shinier, punctures much as those of mesoscutum, a little separated medially. Mesopleura slightly shiny, punctures contiguous, finer and shallower than those of mesoscutum. Propodeum slightly shiny, minutely roughened, finely and sparsely punctate. Hind femur about three times longer than wide. First recurrent vein entering second submarginal cell at basal third.

*Abdomen.* Terga slightly shiny, finely, closely piligerously punctate. Sterna shinier, a little more coarsely, less closely punctate. Pygidium dull, margins distinct, concave. Eighth sternum similar to that of *C. strawi*, with apical process broader preapically than basally (fig. 43); ninth sternum (fig. 44) similar to that of *C. strawi*, but broadest beyond middle and distinctly narrowed in apical fourth.

*Color.* Black. Labrum, clypeus, triangular paraocular mark and transverse bar on supraclypeal area bright yellow. Tegulae testaceous. Antennae brownish, lighter beneath. Legs dark brownish. Wings transparent, moderately brown, veins and stigma dark brown. Cephalic pubescence light ochreous, fuscous on face between antennal sockets and occiput; a few long, fuscous hairs on sides of clypeus. Thoracic pubescence ochreous, paler on

pleurae; light brown on metapleuron and propodeal side. Pubescence of legs mostly fuscous, paler posteriorly on fore femur and tibia. Anterior face of first tergite with pale ochreous pubescence, abdomen otherwise fuscous pubescent. Eyes with very sparse, short, erect golden hairs.

FEMALE. Unknown.

*Type material.* Holotype male: Tequila, Jalisco, MEXICO, 18 July 1953 (C. & P. Vaurie, D. Rockefeller Mex. Exp. 1953; AMNH). Paratypes: 1 ♂, Cuautla, Morelos, MEXICO, July-Aug. 1903 (W. L. Tower coll; AMNH); 1 ♂, 10 mi W Colima, Colima, MEXICO, 1 Aug 1954 (M. Cazier, *et al.*; AMNH). Holotype and Cuautla paratype in the AMNH; Colima paratype in LACM.

*Etymology.* Greek prefix *a-* (without) plus *gamete* (wife or spouse), indicating current lack of females to be assigned to this species.

*Distribution.* Known only from the above cited localities in central Mexico.

*Discussion.* Aside from slight difference in measurements and proportions, the two paratypes are very similar to the holotype. *Statistical data:* Cuautla ♂: HW 5.30; EL 3.65; UFW 2.00; LFW 2.35; TFD 2.25; SL 2.80; WL 14; TL 17 mm; CW 1.53 x CL; UFW 0.85 x LFW; TFD 0.62 x EL; TFD 1.61 x OCD; SL 2.07 x SW; SL 1.04 x 1F; 1F:2F:3F:4F = 54:15:-23:22; OD:OOD:IOD=8:7:13. Colima ♂: HW 5.45; EL 3.80; UFW 2.05; LFW 2.60; TFD 2.35; SL 2.80; WL 14; TL 18 mm; CW 1.58 x CL; UFW 0.79 x LFW; TFD 0.62 x EL; TFD 1.62 x OCD; SL 2.00 x SW; SL 1.02 x 1F; 1F:2F:3F:4F = 55:17:24:25; OD:OOD:IOD = 8:7:14.

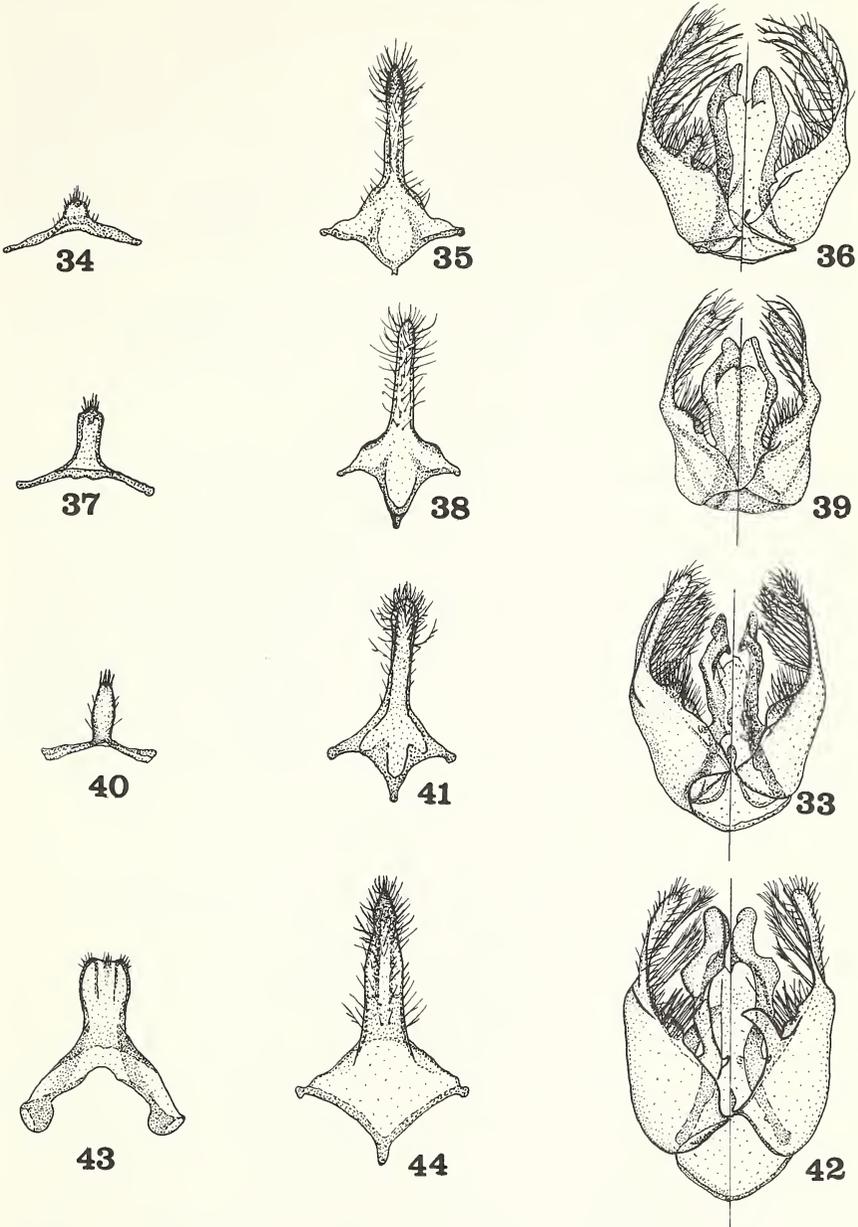
The unknown female of this species probably will be similar to the male except for the usual sexual differences, such as possessing a black clypeus. The distribution of pale pubescence should be as in the male.

### *Centris (Acritocentris) strawi* Snelling

*Centris (Melanocentris) strawi* Snelling, 1966. L. A. Co. Mus., Contrib. Sci. 112:27-27. ♂.

Described from a single male from the State of Guanajuato, MEXICO, a number of females certain to belong to this species are now available. Pubescence and color are as in the male, except for the complete lack of maculae. The mandibles are tridentate, the inner tooth triangular, the inner upper carina ending at its base. The clypeus is rugulose in the middle, laterally with coarse, elongate punctures. A prior name for this species may be *C. mexicana albiceps* Friese, 1899, but this cannot be determined until the type is examined.

*Distribution.* MEXICO. *Nayarit:* 3 ♀♀, Ixtlan del Río, 5 Aug 1963 (P. Fonda-Bonardi; LACM). *Jalisco:* 1 ♀, 20 mi N La Quemada, 27 July 1954 (M. Cazier, *et al.*; AMNH); 1 ♀, 27 mi N Barra de Navidad, 6 Sept 1966 (E. M. Fisher; LACM); 3 ♀♀, 6 mi NE El Rincón, Hwy 80, 3 Aug 1971 (E. M. Fisher; LACM).



FIGURES 33-44. 33-35, *Centris adani*, ♂: 33, genitalia; 34, sternum VIII; 35, sternum IX. 36-38, *C. segregata*, ♂: 36, genitalia; 37, sternum VIII; 38, sternum IX. 39-41, *C. poecila*, ♂: 39, genitalia; 40, sternum VIII; 41, sternum IX. 42-44, *C. agameta*, ♂: 42, genitalia; 43, sternum VIII; 44, sternum IX.

*Centris (Acritocentris) ruthannae* Snelling

*Centris (Melancentris) ruthannae* Snelling, 1966. L. A. Co. Mus., Contrib. Sci. 112:28-30. ♂ ♀.

NEW RECORDS. 7 ♂♂, 11 ♀♀, 1 mi E Douglas, Cochise Co, ARIZONA, 14 Aug 1969 (J. G. & K. C. Rozen; AMNH); 6 ♀♀, same locality, 24 Aug 1967 (J. G. Rozen; AMNH); 2 ♀♀, same locality, 29 Aug 1967 (J. G. Rozen & G. Krueger; AMNH); 7 ♀♀, 3 ♂♂, 30 mi N Nogales, Pima Co, July 1972 (T. J. Zavortink; TJZ), on *Kallstroemia grandiflora*, 0730-0930 hrs.

Previously recorded from Madera Cyn, Santa Rita Mts (type locality), Baboquivari Cyn, Baboquivari Mts and Continental, all ARIZONA.

## ACKNOWLEDGMENTS

The bulk of the material recorded above is in the collections of the Natural History Museum of Los Angeles County (LACM). The Costa Rican material was largely collected by E. R. Heithaus and deposited at LACM. An additional important Costa Rican collection was loaned by G. W. Frankie, Texas A & M University (TAMU) and miscellaneous material from Mexico and the United States was sent by M. Favreau, of the American Museum of Natural History (AMNH). Numerous specimens with valuable floral data were loaned from his private collection by T. J. Zavortink (TJZ). Invaluable data on type material in the British Museum (Natural History) was supplied by I. H. H. Yarrow. The figures were prepared by Ruth Ann DeNicola.

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THE ISTHMIAN LINK AND THE EVOLUTION  
OF NEOTROPICAL MAMMALS

By JAY M. SAVAGE

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# THE ISTHMIAN LINK AND THE EVOLUTION OF NEOTROPICAL MAMMALS<sup>1</sup>

By JAY M. SAVAGE<sup>2</sup>

**ABSTRACT:** The mammal fauna of the New World Tropics is comprised of four major historical source units. The most ancient of these units (the South American) is composed of marsupials, xenarthan edentates, condylarths, protonotoungulates, and some bats whose ancestors were in South America by Early Tertiary and evolved, diversified and in many instances became extinct, *in situ*. A second unit (the Young Southern) is comprised of primates, cavimorph rodents, manatees, some bats and sigmadontine mice, whose ancestors arrived from North America by waif overwater dispersal at various times from Paleocene to Pliocene. No strong evidence for an intercontinental connection between North and South America in Cretaceous or Early Tertiary can be adduced from the available mammal evidence.

During later times (Eocene-Miocene), a series of more modern mammal stocks evolved in Middle America (the North Tropical unit) which invaded South America when the Isthmian Link connection between the two continents was established in Early Pliocene. A final unit (the North American) are stocks only recently moving southward through the Middle American tropics into northern South America. Following establishment of the Isthmian Link 24 southern families of mammals have moved northward into Central America, 12 of these reach temperate North America; 19 northern families entered South America, 15 of these reach temperate areas of the continent. Today both southern and northern faunas have been significantly modified by these increments but the exchange has been balanced without a disproportionate effect in either direction. Tropical Middle America is essentially a complex transitional zone between northern and southern elements and is not now, nor was at anytime in Cenozoic a significant evolutionary center for mammals. The present mammal fauna of the West Indies is derived almost in its entirety from northern South America.

## INTRODUCTION

The origins and history of the land mammals of tropical America have long been a source of extreme interest to biogeographers and students of

<sup>1</sup>REVIEW COMMITTEE FOR THIS CONTRIBUTION

Malcolm McKenna  
Donald R. Patten  
Andrew Starrett

<sup>2</sup>Department of Biological Sciences, and Allan Hancock Foundation, University of Southern California, Los Angeles, California 90007; and Research Associate, Natural History Museum of Los Angeles County

evolution (Darlington, 1957). The general accepted classic story of long Tertiary isolation of South America from any land connection to the north, with a Quaternary invasion of southern groups moving northward (16 out of 26 families) and northern groups moving southward (16 out of 25 families) across an emergent land bridge established in Early Pleistocene has been developed by Simpson (1950) extended by Patterson and Pascual (1963, 1968), and accepted through repetition until it has permeated textbooks and even popular accounts (Barnett, 1960).

Recently Hershkovitz (1966, 1968) challenged this interpretation based on evaluation of the distribution of living mammals (Hershkovitz, 1958). He concluded that mammals crossed the water barriers between Nuclear Central America and South America throughout the Tertiary, in both directions, so that present patterns are not the result of dramatic major invasions in the Early Pleistocene.

The critical geographic region involved in the faunal exchanges is the lower Central American Isthmian Link that extends today as a narrow connection between Nicaragua and northwest Colombia. The geologic and ecologic history of this link provides the key to unraveling the apparent inconsistencies and differences in interpretation of mammalian distributional evidence. The geographic and ecologic relations of the Middle American region including the Isthmian Link are summarized (Wauchope and West, 1964) and evaluated with regard to vertebrate distributions (Stuart, 1964, 1966). The terminology for major geographic and ecologic patterns in this paper follows their usage:

North America—the continental mass from the Isthmus of Tehuantepec in southern Mexico, northward;

Central America—the land south and east of the Isthmus of Tehuantepec to the border between Panama and Colombia;

South America—the continent south of the border between Colombia and Panama;

Mesoamerica—Mexico and Central America;

Middle America—Mexico and Central America;

Nuclear Central America—the northern portion of Central America that has been land positive and continuously connected to North America throughout Cenozoic; essentially from the present day Isthmus of Tehuantepec to and including northern Nicaragua, but with its seaward margins variously modified at different times;

Isthmian Link—the unstable area of present day Nicaragua, Costa Rica and Panama that was covered by marine waters during much of Cenozoic;

Tropical North America—the portions of North and Central America under tropical climatic regimens; currently restricted on the north to the coastal and southern areas of Mexico but earlier in Cenozoic including the southern portions of what is the United States; the tropical limits have now been gradually forced southward by the cooling trend of Late Cenozoic;

Upper Central America—Mexico south of the Isthmus of Tehuantepec to the Honduras-Nicaragua border;

Lower Central America—Nicaragua, Costa Rica and Panama.

The present paper is an attempt to review the ideas and evidence advanced to explain current neotropical mammalian distribution, particularly in the light of the almost diametrically opposed views of the outstanding authorities on Latin American fossil mammals (Simpson, Patterson and Pascual) and a leading student of living forms (Hershkovitz). This paper developed out of my interests in the biogeography of tropical America. Although not a specialist in mammalogy, I thought that my recent experience in analyzing the history of the Central America herpetofauna (Savage, 1966) might bring a new point of view to the problem, especially because of my familiarity with, and study of, the influence of Isthmian Link history and ecology on vertebrate distributions. Hopefully, it will at least delineate the basic points at issue between the classic and Hershkovitz' interpretations.

#### ACKNOWLEDGMENTS

My interest in the problem was initiated by reading the recent papers by Hershkovitz (1966, 1969) and Patterson and Pascual (1968) in the pages of the *Quarterly Review of Biology*. These authors presented lucid and well-documented statements of their opposed theories of the origin and history of mammals in the New World tropics. The paper by Patterson and Pascual and the outstanding illustrations of extinct southern mammals brought the fossil record to life in my imagination. Hershkovitz likewise made the recent situation alive and engrossing through his text and figures of modern forms that reveal his own enthusiastic appreciation of, and intimacy with tropical New World mammals. Both papers contain beautiful coverage of many problems not related to the present discussion and should be read in entirety by those wishing a fuller understanding of the life of present and past mammals of Middle and South America. Although I disagree strongly with these authors on many points of biogeographic interpretation, I deeply appreciate the stimulation provided by them, and the evidence presented in their papers which provided substantial data for my analysis. Simpson's (1969) recent paper agrees with the Patterson and Pascual view in most particulars and is essentially an updating of Simpson's (1950) more popular account. Although not appearing until 1969, the paper clearly was written prior to the accounts of Hershkovitz (1969) and Patterson and Pascual (1968) and much delayed in publication. Reference is made to this latest Simpson paper only where his views conflict with Patterson and Pascual or his own earlier statements.

Several colleagues of diverse background have critically reviewed drafts of the manuscript and offered constructive advice. Although I have not always followed their suggestions I have profited from the ideas they provided and acknowledge the help with thanks to: John S. Garth and Edwin M. Perkins,

University of Southern California; Andrew Starrett, San Fernando Valley State College and Natural History Museum of Los Angeles County; and David B. Wake, University of California, Berkeley. Ronald T. Harris of the University of Southern California prepared the figures.

#### REVIEW OF HYPOTHESES

Simpson (1950, 1969) and Patterson and Pascual (1963, 1968) present the generally accepted view of mammalian history in the American tropics, based ultimately on the original data in Simpson (1940), together with less extensive but recent finds. According to this view three major historical units (strata) are present in South America:

I. *South American Oldtimers*; derived from Cretaceous-Paleocene ancestors and evolving in isolation in South America after the intercontinental land connection floundered in Late Paleocene.

II. *Old Island Hoppers (Waifs)*; derived from Middle American ancestors that crossed the water barrier into South America in post-Paleocene times and differentiated in isolation in South America.

III. *Northern Newcomers*; derived from Early Pleistocene invaders that crossed the land bridge into South America after its reconnection or connection to Middle America.

Mammals of units I and II also invaded Middle America (after the establishment of the intercontinental connection) and some (opossums,

TABLE 1

#### SOUTH AMERICAN MAMMAL GROUPS BY HISTORICAL UNITS OF SIMPSON

I	II	III	
SOUTH AMERICAN	WAIF	NORTHERN	
OLDTIMERS	DESCENDENTS	NEWCOMERS	
Marsupials	Primates	Insectivores	Perissodactyls
didelphoids	marmosets	shrews	*horses
caenolestoids	monkeys	Lagomorphs	tapirs
*borhyaenoids	Caviomorph rodents	rabbits	Artiodactyls
Edentates	porcupines	Rodents	peccaries
armadillos	cavies	squirrels	camels
*glyptodonts	capybara	mice	deer
*ground sloths	aguti	Carnivores	
tree sloths	paca	dogs	
anteaters	chinchilla	bears	
*Condylarths	vizcacha	raccoons	
*Lipterns	hutia	weasels	
*Notoungulates	tucotuco	and others	
*Astrapotheres	spiny rats	cats	
*Pyrotheres	Carnivores	Proboscidioids	
	procyonids	*mastodons	
	(coati, kinkajou,		
	olingo)		

\*groups now extinct in the New World

armadillos and porcupines) have extended their range into extratropical North America. The principal groups associated in these units are summarized (Table 1).

The essential features of Simpson's theory of New World tropical mammal origins are as follows:

1. The Isthmian Link connected Middle and South America for a considerable period in Paleocene; the link was flooded by seas between present day northern Nicaragua to western Colombia from Eocene through Late Pliocene; the link was re-established in Early Pleistocene (3 million years ago).

2. North America and Nuclear Central America were connected throughout the Cenozoic.

3. The ancestors of South American Oldtimers (I) invaded the continent in Paleocene across the link and were isolated and evolved independently from Middle America relatives from Eocene to Pleistocene.

4. The ancestral Old Island Hoppers (II) crossed into South America over the Panamanian Marine Portal in Eocene-Oligocene and underwent differential evolution in isolation there.

5. The ancestors of both stocks became extinct north of the portal.

6. Upon re-establishment of the Isthmian Link in Pleistocene a host of Northern Newcomers (III) invaded South America from Central America.

7. At the same time descendant forms of units I and II invaded Central America from the south.

8. Northern Newcomers generally were derived from tropical stocks already in Central America at the time of Isthmian Link re-emergence; a series of allied holarctic groups remained in more northern temperate areas and have recently invaded Middle America but fail to reach South America.

9. The invasion from north to south was the most effective.

10. The invasions in both directions were massive and dramatic and are often cited as the best example of major faunal interchange.

Patterson and Pascual (1968) substantiated this theory, except they believed that no Cretaceous or early Tertiary land connection existed; Stratum I groups are ancient overwater immigrants into South America in their opinion.

Herskovitz (1969) proposed a more elaborate scheme involving seven strata of mammals in tropical America. Essentially, he recognized only two principal units as contributing to the mammal fauna of South America. These two units are discussed below with the strata described by Herskovitz indicated by Roman numerals and small letter subscripts as in his discussion.

**A. SOUTH AMERICANS**—derivatives of groups isolated from Early Eocene to Pliocene in South America,

- II groups derived from ancestors isolated by submergence of the Isthmian Link in Late Paleocene and groups derived from overwater waifs from Middle America in mid-Tertiary

- III groups derived from stratum II as overwater south to north waifs to Middle America in mid-Tertiary
- IV groups derived from stratum II as post-Miocene overland invaders of Middle America
- Vb groups derived from stratum III as overland invaders of South America in Pliocene onwards.

B. *NORTHERNERS*—North American groups that developed in Middle America after its separation from South America,

Ib groups that developed in Central America during its separation from South America and Late Tertiary to Recent invaders from the north

Va derivatives of stratum Ib that have invaded South America since reconnection of the Isthmian Link.

Herskovitz' stratum Ia appears to be a composite of ancestors for both South Americans and Northerners. He recognized that no living or fossil assemblage corresponds to this stratum. For this reason I have not considered it further here. The composite nature of stratum Ib is also a conceptual difficulty since no mammal genera endemic to Middle America appear to be ancient relicts from early Tertiary. The compositions of the Herskovitz units are indicated in the accompanying summary (Table 2).

TABLE 2

TROPICAL AMERICAN MAMMALS BY HISTORICAL UNITS OF HERSHKOVITZ

SOUTH AMERICANS

A. BASIC STOCKS

1. Descendents of Groups Isolated in South America

(part of Stratum II)

- Marsupials
- Edentates
- Condylarths
- Litopterns
- Astrapotheres
- Pyrotheres

2. Descendents of Overwater Waifs from Central America

(part of Stratum II)

- Primates
- Rodents
  - Squirrels (*Sciurillus*, *Sciurus* 3 spp.)
  - Sigmodontine mice
  - Caviomorphs
- Lagomorphs
  - Tapeti (*Sylvilagus brasiliensis*)
- Carnivores
  - endemic dogs (*Speothos*, *Chrysocyon*, *Lycalopex*, *Atelocynus*, *Dusicyon*)
- Procyonids
  - endemic mustelids (*Lyncodon*, *Galictis*, *Eira*, *Pteronura*, *Mustela africana*)
  - endemic cats (*Felis colocolo*, *F. geoffroyi*, *F. guingna*, *F. jacobita*)

- Perissodactyls
  - tapirs (*Tapirus pinchague*, *T. terrestris*)
- Artiodactyls
  - peccary (*Tayassu*)
  - llamas and vicunas
  - endemic deer (*Mazama*, *Blastoceros*, *Blastoceros*, *Pudi*, *Hippocamelus*)

#### B. IMMIGRANTS TO MIDDLE AMERICA

3. Descendents of Overwater Waifs from South America to Central America: derived from 1 and 2 (Stratum III)
  - Genera and species with distribution centered on Central America including representatives of:
    - extinct edentates
    - Primates
    - Sigmodontine mice
    - some Caviomorphs
4. Overland invaders of Central America from South America: derived from 1 and 2 (Stratum IV)
  - Species common to lower Central America and northern South America, including as examples:
    - Central American edentates
    - tapeti
    - Some sigmodontine mice (13 sp.)
    - capybara
    - aguti
    - paca
    - crab-eating raccoon
    - brocket

#### C. REPATRIATES FROM CENTRAL AMERICA

5. Overland Invaders of South America: derived from 3 (Stratum Vb)
  - Species common to lower Central America and northern South America, including as examples:
    - bare-faced tamarin
    - black howler monkey

#### NORTHERNERS

6. Endemic Middle America Descendents of Northern Invaders (part of Stratum Ib)
  - a squirrel (*Syntheosciurus*)
  - gophers (*Orthogeomys*, *Heterogeomys*, *Macrogeomys*)
  - heteromyids (*Liomys*)
  - peromyscine mice (*Scotinomys*)
  - neotomine mice (*Nelsonia*, *Xenomys*, *Ototylomys*)
7. Invaders of Central America from the North, not reaching South America (part of Stratum Ib)
  - flying squirrel (*Glaucomys*)
  - peromyscine mice (*Baiomys*, *Neotomodon*, *Peromyscus*)
  - neotomine mice (*Neotoma*)
  - voles (*Microtus*)
  - coyote (*Canis latrans*)
  - weasel (*Mustela frenata*)
8. Overland Invaders of South America (Stratum Va)

a shrew (*Cryptotis*)  
 a rabbit (*Sylvilagus floridanus*)  
 some squirrels  
 heteromyids (*Heteromys*)  
 peromyscine mice (*Reithrodontomys*)  
 neotomine mice (*Tylomys*)  
 gray fox (*Urocyon*)  
 spectacled bear (*Tremarctos*)  
 river otter (*Lutra*)  
 hog-nosed skunk (*Conepatus*)  
 cats (*Smilodon* and *Felis concolor*, *F. onca*, *F. pardalis*, *F. wiedi*, *F. tigrina*,  
*F. yagouaroundi*)  
 mastodon\*  
 a tapir (*Tapirus bairdi*)  
 horse (*Equus*)\*  
 peccary (*Peccari*)  
 deer (*Odocoileus*)

The basic features of Hershkovitz' ideas on the origins of tropical American mammals (units and mammal groups are indicated in Table 2) are:

1. The Isthmian Link existed as a connection between Middle and South America in Paleocene; the link was submerged from Early Eocene through Miocene; the intercontinental connection was permanently re-established in Early Pliocene (12 million years ago).

2. North America and Nuclear Central America were connected throughout Cenozoic.

3. The ancestors of unit 1 were isolated in South America and evolved independently from Paleocene through Miocene.

4. The ancestors of unit 2 invaded South America from Central America overwater (across the Panamanian Portal) from Eocene onwards and each group as it arrived underwent independent evolution in South America.

5. Derivatives of units 1 and 2 re-invaded Middle America from Eocene to Pliocene overwater and became differentiated in Central America (unit 3).

6. Upon re-establishment of the Isthmian Link in Early Pliocene a great many mammals of northern affinities invaded South America (unit 8).

7. At the same time a large number of southern taxa invaded Central America (unit 4).

8. The Central American mammal fauna at the time of Pliocene reconnection was composed of a mixture of descendants of South American overwater waifs (unit 3) and northern groups endemic or adapted to tropical situations (units 6 and 8).

9. The general direction of invasion before and after the restoration of the Isthmian Link was primarily from south to north.

10. The faunal interchange between Central and South America quickened upon re-emergence of the bridge but overwater exchange from Eocene to Pliocene, a period of 30 million years, is principally responsible for present distribution patterns, rather than the land connection.

The essential differences between the theories developed by Simpson (S) and Hershkovitz (H) center around the following critical points:

A. Time of reconnection of Central and South America: Early Pleistocene (S), Early Pliocene (H).

B. Effectiveness of Panamanian Marine Portal as a barrier to mammal dispersal: extremely effective (S); of little significance (H).

C. Amount of independent faunal differentiation in Middle and South America during Eocene to Pliocene: extreme isolation and differentiation (S); substantial overwater faunal interchange (H).

D. Effect of reconnection of Isthmian Link: dramatic invasions with rapid postinvasion evolutionary radiation by northern groups in South America (S); minimal effects, principally through invasion of Central America by southern forms (H).

All other differences of interpretation by these authors center on these four key areas of controversy. Resolution of these points is the object of this paper as a basis for a revised view of the history of New World tropical mammals.

Keast (1969:133-134) has previously attempted to reconcile the opposing views of Patterson and Pascal (1968) and Hershkovitz (1969) with limited success, since he did not re-evaluate the situation or data in detail. He concluded that 1) the intercontinental land connection was established in Pliocene; 2) some groups including cricetids, otters and squirrels, reached South America from the north by overwater transport prior to Pliocene; 3) few if any large mammal stocks reached South America from the north by overwater transport; 4) many distinctive South American genera originated there; and 5) many groups including the cricetids attained their current diversity in South America.

#### THE HISTORY OF THE ISTHMIAN LINK REGION

Crucial to any attempt to place the conflicting views of Simpson and Hershkovitz in perspective is the necessity of a clear picture of the geologic history of Central and northern South America. I have previously reviewed the history of the link as it related to herpetofaunal distribution (Savage, 1966) based in large part on the ideas of Lloyd (1963) and Vinson and Brineman (1963). Since that time a revolution in geologic thought has occurred with the emergence of continental drift theory and the new tectonics (Dietz and Holden, 1970) as unifying themes in palaeogeography. Recent detailed studies of the areas of present and possible past intercontinental connections between North and South America from the view of new tectonic evidence (Freeland and Dietz, 1971; Malfait and Dinkelman, 1972) clarify significantly the palaeogeography of the region and seem much more congruent with the mammal evidence than my earlier (1966) interpretation. Where differences are apparent, I have relied heavily on the views of Freeland and Dietz (1971) and Malfait and Dinkelman (1972), together with

the work of Molnar and Sykes (1969) in developing the following section. I follow Hibbard, et al. (1965) in placing the lower limit of the Pleistocene as at the beginning of post-Pliocene Blancan times (Nebraskan onward), about 3 m.y. BP. This corresponds to the beginning of the Villafranchian of Europe and the Uquian in South America.

The significant structural units involved in the region are:

1. Nuclear Central America—including most of what is now southern Mexico, Guatemala, El Salvador, British Honduras, Honduras and extreme northern Nicaragua.

2. Guiana Shield—the major land mass of northern South America.

3. The Isthmian Link—the region from southern Nicaragua to northwestern Colombia, including Costa Rica and Panama.

4. The North Andean area and its western slope—continuous with the Guiana Shield through Cenozoic and uplift into the Andes during the latter part of the era.

There seems no question (Freeland and Dietz, 1971; Falfait and Dinkelman, 1972) that a substantial marine seaway existed between North America, including Nuclear Central America, and South America throughout the Cretaceous and until the Pliocene, between what is now northern Nicaragua and North Andean Colombia. The entire interoceanic connection may be called the Panamanian Portal. As the Isthmian Link became emergent in Late Tertiary, three main straits continued to connect the two seas: a) the Nicaragua Trough through southern Nicaragua, b) the Panama Trough east of the Talamanca—Chiriqui axis across central Panama, c) the Bolivar Trough running generally north to south across extreme northwestern Colombia.

In my herpetofaunal analysis of this area I accepted the views of Lloyd (1963), Simpson (1940, 1950) and others that North and South America were connected by land in the general region of the Isthmian Link during Paleocene (Nygren, 1950). Freeland and Dietz (1971) conclusively demonstrated that the last continuous broad contact between North and South America in the region under discussion, prior to the present one, was in mid-Jurassic (about 150 m.y. BP). Haffer (1970), Maldonado-Koerdell (1964), and Falfait and Dinkelman (1972) showed that the region from what is now Nicaragua to northern South America formed a broad seaway from Early Cretaceous to late Eocene, when a series of volcanic islands developed along the eastern margin of the Middle American Trench as the forerunners of the uplift that culminated in a land connection in earliest Pliocene. Because of sea-floor spreading the Panamanian Portal was about 400 km across in Middle Cretaceous and increased to a maximum of 1000 km in breadth in Early Tertiary.

Some of the biological evidence speaks strongly for a Paleocene-Eocene intercontinental land connection, Brame and Wake (1963), Olsson (1932), Parodiz (1969) and Savage (1966). If such a land connection existed in the Early Tertiary, the new tectonics and continental drift theory suggest that it

lay much further to the east than the present isthmus, somewhere in the proto-Antillean region. The evidence of Freeland and Dietz (1971) hints at a possible early land connection through the Nicaraguan Rise and proto-Antillean area (Jamaica-Porto Rico-Lesser Antilles), but Malfait and Dinkelman (1972) give this possibility little support.

The best available interpretations indicate that North and South America have been separated by a broad marine barrier connecting the East Pacific and Caribbean across the Panamanian region for all of the Cretaceous and the Early and Middle Cenozoic. In the Paleocene and Eocene the water gap was approximately 1000 kilometers in extent. Later in the epoch a series of volcanic islands developed to the southwest of the seaway (Fig. 1). From this time until Late Miocene (a span of around 25 million years) the marine barrier to overland intercontinental faunal exchange was relatively constant. Toward the middle of Miocene volcanic ridges and islands became more fully developed in the link region. Increasing and rapid uplift along the axis of present day lower Central America led to reduction of the seaway into three principal straits, the Nicaragua, Panama, and Bolivar Troughs. These portals closed along the Isthmian Link axis from northwest to southeast by the end of Miocene. The data of Whitmore and Stewart (1965) suggest that by Middle Miocene only the Bolivar Trough remained a marine barrier to overland dispersal. This latter area was uplifted and the connection completed in earliest Pliocene. It has persisted until today as a continuous intercontinental land connection.

No evidence supports the concept (Darlington, 1957:575) that Central America was an island or island chain separated from North America during any part of Cenozoic. Durham, Arellano and Peck (1952) laid the myth of a Cenozoic Tehuantepec seaway to rest years ago, although it continues to be invoked by biogeographers unfamiliar with the paleontological record. No question exists that Nuclear Central America has been land positive throughout Cenozoic and has been continuously connected with North America during that time.

Some confusion also persists regarding the role of the Bolivar Trough as a marine barrier to intercontinental exchange. Brame and Wake (1963: 65) presented an excellent summary of the data and ideas of Olsson (1932, 1942, 1956), Nygren (1950), and Durham and Allison (1960) relating to the Trough. These authors unequivocally regarded the Bolivar Trough area as uplifted and land positive from Late Cretaceous to Eocene. From Eocene to Late Miocene the trough was a marine seaway. According to Nygren (1950) the trough was bordered on the west by a land positive area that was submerged as the Andes and Bolivar Trough were uplifted during Miocene. This western borderland was never connected to Nuclear Central America and is not mentioned by other authors. Connections between the borderland across the Bolivar Trough to North Andean South America as mentioned by Nygren for several periods in Tertiary could not provide intercontinental migration

routes as suggested by Hershkovitz (1966:739, 745), since the principal Panamanian Portal was an open seaway throughout this time (Lloyd, 1963; Malfait and Dinkelman, 1972). Such connections, if they existed, did not effect mammal distribution between Nuclear Central America and South America.

Hershkovitz (1969:13) also implies that the Bolivar Trough was the principal marine barrier to overland distribution during Cenozoic and as such (1966:730, 732) was no major obstacle to faunal interchange. Again it must be emphasized that the Panamanian Portal formed an extensive seaway across all of lower Central America from early Cretaceous to at least Early Miocene. The Bolivar Trough was apparently the most persistent element of this seaway and finally closed in Late Miocene. To equate the relatively narrow Bolivar Trough with the Panamanian Portal as Hershkovitz has done ignores the vast marine barrier to land dispersal that restricted faunal exchanges between Central and South America during most of Tertiary. Patterson and Pascual (1968) also weaken their arguments by seeming to equate the Panamanian Portal with the Bolivar Trough.

## HISTORICAL MAMMALIAN FAUNAL COMPONENTS

### *The fossil record*

Patterson and Pascual (1968) and Simpson (1969) presented an excellent review of the mammal fossil record for Central and South America. The evidence is clear and uncompromising that South America had a long independent history as an island separated from North America influences until late in Cenozoic. The essential information from paleontology is:

1. Paleocene through Pliocene: predominance of marsupials, edentates, and the condylarths, litopterns, notoungulates, astrapotheres, pyrotheres, xenungulates and trigonostylopoids (the latter two only until Eocene).

2. Early Oligocene: appearance and increasing diversity throughout the rest of Cenozoic of caviomorph rodents.

3. Early Oligocene: appearance and increasing diversity of primates throughout rest of era.

4. Middle Pliocene: appearance of procyonids.

5. Late Pliocene: first appearance of North American groups.

6. Pleistocene: expansion of northern groups into South America.

7. Middle American Tertiary: sites with tropical North American groups.

8. Later Pliocene of Central and North America: first evidence of South American forms in fauna.

### *Recent distribution*

Hershkovitz (1958, 1969) presented a thoughtful and lucid summary of recent distribution patterns. The essence of his ideas is summarized (Table 2) and key points mentioned below:

1. The Neotropical fauna occurs from southern Mexico to extreme South America.
2. The Nearctic fauna is North American in distribution.
3. Early Tertiary Middle America was a center for mammal evolution and the early forms spread into South America.
4. Closure of the Panamanian Portal must have been Miocene-Pliocene.
5. The Panamanian Portal was not a major barrier to faunal exchange.
6. Distributional data do not support the idea of a major invasion of southerners northward or northerners southward in Pleistocene; most mammals had already reached the limits of their present distributions before Pleistocene.

#### *The faunal components*

A review of all available fossil and recent data convinced me that a re-interpretation of the components was required. This process led me to re-examine the units that comprise the recent tropical American mammal fauna, with respect to the Isthmian Link. It is clear that four major faunal units are involved, which do not correspond to those previously proposed:

#### I. SOUTHERNERS (Southern Element)

A. South American Complex—groups descended from ancestors isolated in South America in the Cretaceous; undergoing diversification from Early Tertiary onward.

B. Young Southern Complex—descendants of groups derived from Middle American ancestors in Tertiary by overwater invasion of South America; undergoing diversification from Eocene to present.

#### II. NORTHERNERS (Northern Element)

C. North Tropical Complex—groups of northern affinities associated with tropical situations, present in Central America in Late Tertiary; many invading South America after reconnection of Isthmian Link.

D. North American Complex—recent invaders of Central and South America from temperate North America.

The composition of these units is summarized (Table 3).

### HISTORY OF THE MAMMAL FAUNA

#### *Original colonization*

Of the major groups significant to our understanding of tropical American mammalian history, only the marsupials, condylarths and insectivores are known from Mesozoic fossils. In North America at the beginning of Paleocene, marsupials and insectivores are plentiful in the record together with primates, condylarths and other ungulates. By Late Paleocene, creodonts, pantodonts, uinatheres, tillodonts, and a primitive rodent are known. Most of the families represented are now extinct. Late Paleocene fossils in South

TABLE 3  
MAMMALIAN FAUNAL COMPONENTS

SOUTH AMERICAN	YOUNG SOUTHERN	NORTH TROPICAL	NORTH AMERICAN
Marsupials:	Bats:	1. Into South America	1. Into South America
Didelphidae	Natalidae	Bats (Molossidae)	a shrew ( <i>Cryptotis</i> )
**Borhyaenidae	Furiferidae	a squirrel ( <i>Sciurillus</i> )	man ( <i>Homo</i> )
**Necrolestidae	Thyropteridae	tropical dogs ( <i>Dusicyon</i> ,	rabbits
**Polydolopidae	Primates:	<i>Chrysocyon</i> , <i>Atelocynus</i> ,	Bats ( <i>Vespertilionidae</i> )
Caenolestidae	Callithricidae (marmosets)	<i>Speothos</i> , <i>Lycalopex</i> )	squirrels
**Argyrolagidae	Cebidae (monkeys)	Spectacled bear	heteromyids ( <i>Heteromys</i> )
Xenarthran Edentates:	Caviomorph Rodents:	( <i>Tremarctos</i> )	peromyscine mice ( <i>Aporodon</i> )
Dasypodidae (armadillos)	Octodontidae	procyonids (* <i>Cyonasua</i> ,	a neotomine mouse ( <i>Tylomys</i> )
**Palaeopeltidae	Abrocomidae	<i>Nasua</i> , <i>Potos</i> ,	gray Fox ( <i>Urocyon</i> )
**Glyptodontidae	Echimyidae (spiny-rats)	<i>Bassaricyon</i> )	racoons ( <i>Procyon</i> )
(glyptodonts)	Chinchillidae (chinchilla,	mustelids ( <i>Lyncodon</i> ,	weasels ( <i>Mustela</i> )
**Megalonychiidae	vizcachas)	<i>Galictis</i> , <i>Eira</i> , <i>Pteronura</i> )	otter ( <i>Lutra</i> )
(ground sloths)	Dasyproctidae (aguti)	cats (** <i>Smilodon</i> , some	skunk ( <i>Conepatus</i> )
**Megatheriidae	Cuniculidae (paca)	<i>Felis</i> )	cats (several <i>Felis</i> )
(ground sloths)	Caviidae (cavies)	**mastodons	deer ( <i>Odocoileus</i> )
Bradypodidae (tree sloths)	Dinomyidae (pacarana)	(Gomphotheriidae)	
**Myodontidae (mylodonts)	Hydrochoeridae (capybara)	**horses (Equidae)	2. In Central America
			a bat ( <i>Corynorhinus</i> )

**Entelopsidae	Erethizontidae (porcupines)	tapirs (Tapiridae)	flying squirrel ( <i>Glaucomys</i> )
Myrmecophagidae (ant-eaters)	Sigmondontine Mice (Cricetidae):	deer <i>Mazama</i> , <i>Pudu</i> , <i>Hippocamelus</i> , <i>Blastocerus</i> , <i>Blastoceros</i> )	peromyscine mice ( <i>Baiomys</i> , <i>Reithrodontomys</i> , <i>Peromyscus</i> )
**Condylarths	approximately 40 genera	camels ( <i>Lama</i> , <i>Vicugna</i> )	neotomine mice ( <i>Neotoma</i> )
**Liptoterns	Manatee		voles ( <i>Microtus</i> )
**Notoungulates		2. Endemic to Central America	coyote ( <i>Canis</i> )
**Astrapotheres		a bat ( <i>Idionycteris</i> )	cacomistle ( <i>Bassariscus</i> )
**Pyrotheres		a squirrel ( <i>Syntheosciurus</i> )	skunks ( <i>Mephitis</i> , <i>Spilogale</i> )
**Xenungulates		gophers ( <i>Orthogeomys</i> , <i>Heterogeomys</i> , <i>Macrogeomys</i> )	**mastodon (Mammutidae)
**Trigonostylopoids		a heteromyid ( <i>Liomys</i> )	**mammoth (Elephantidae)
Bats:		a peromyscine mouse ( <i>Scotinomys</i> )	**rhinoceros (Rhinocerotidae)
Emballonuridae		a neotomine mouse ( <i>Oryzomys</i> )	**Protoceratidae
Noctilionidae			**oreodonts (Merycoidodontidae)
Desmodidae			*bison (Bovidae)
Phyllostomatidae			

\*extinct in area

\*\*extinct in New World

America include marsupials, edentates, condylarths, litopterns and most of the other endemic ungulate lines.

It seemed to Simpson (1950) that the Early Paleocene mammal fauna of South America could best be considered an unbalanced assemblage of groups derived from stocks present in the Cretaceous of North America or from these stocks after they reached South America. Patterson and Pascual (1968) accept this view and argue for a definite relation between the South American fauna and that of North America since marsupials, edentates (the North American fossils are now known to be of a different stock, allied to pangolins; Emry, 1970), condylarths and other evolving ungulates are represented on both continents. McKenna (1969) accepts a northern origin for these groups and implies that they immigrated to South America in Cretaceous. He is influenced in part by the close relationship of Paleocene North American (Arctocyonidae) and South American (Didolodontidae) condylarths, and the similarity and probable origin of the most primitive member of this stock (*Protungulatum*, Cretaceous of North America) from northern insectivores. The recently described *Perutherium* (Thaler in Grambast, Mattauer, and Thaler, 1967), a somewhat advanced condylarth from the Cretaceous of Peru, confuses this issue. Nevertheless as suggested by Hoffstetter (1970 a, b), Reig (1968), and Fooden (1972), the North and South American Paleocene faunas may correspond to different stages of evolutionary development from Mesozoic world mammal faunas, with the South American stocks representing lines probably isolated on the continent by the fragmentation of Gondwanaland in Early Cretaceous. The Paleocene South American mammal fauna was a relict endemic fauna of metatherians (marsupials) and other primitive eutherians. The usual view has held (Simpson, 1950, 1969; Patterson and Pascual, 1963, 1968), that the peculiar and distinctive basic Paleocene mammal fauna was derived from North American ancestors respectively by overland or over-water invasion of the southern continent. The more recent view, based on continental drift theory and Cretaceous mammals, emphasizes that the Late Cretaceous and basic Tertiary mammal fauna of South America was principally an *in situ* development from a series of primitive Gondwanaland stocks (Fooden, 1972). McKenna (1973) seems to favor the northern origin hypothesis but implied that some of the similarities between Paleocene North and South America might be due to earlier connections or filter bridges that allowed limited faunal exchanges between South America — Africa — Eurasia — North America in Cretaceous.

Patterson and Pascual (1963, 1968) concur with Simpson (1950, 1969) that the basic lines of South American mammals (marsupials, edentates, and ungulates) arrived on the continent from the north in Late Cretaceous to Early Paleocene. They, however, propose that the composition of the fauna strongly argues for overwater invasion from Central America. Darlington (1957:592) expressed a similar view. The arguments for this position are essentially as follows:

- a. the Tertiary mammal faunas of South America are unbalanced as compared to contemporary continental faunas of the northern hemisphere
- b. only four overwater landfalls are required to establish the ancient mammal lines, marsupials, edentates, condylarths and notoungulates, since the remaining ungulate lines can be derived *in situ* from condylarth ancestors,
- c. the absence of insectivores, creodonts, multituberculates and prosimians from South American records, while abundant to the north, indicates lack of a land bridge.

I (1966) have elsewhere argued vigorously for a Paleocene land connection between Central and South America as essential for explaining the present distribution of amphibians and reptiles. Unlike the mammals these groups show evidence of a long-term independent evolution of major stocks in Central America from lines allied to South American units. The level of divergence led me to postulate an Early Tertiary separation of a Middle American Element and a South American Element derived from a formerly wide-ranging New World Tropical fauna that became fragmented and isolated in two centers (tropical North America and South America) by the separation of the two continents by a water barrier in Paleocene. The relationships and degree of difference between these two stocks are very real.

Of 31 families representing seven of the eight major stocks of living amphibians and reptiles in South America, 21 are wholly or in part (distinct subfamilies) of South American origin and development. Eight are New World tropical endemic families, all of South American origin. All of these stocks go back in time to Early Tertiary and many to Cretaceous. To establish these families in South America by overwater invasion would require a minimum of 13 landfalls, all in Late Cretaceous or Paleocene. Recently, Parodiz (1969), demonstrated that fossil South American freshwater mollusks, from virtually the same localities as the mammal fossils, indicate a Paleocene land-bridge; mid-Tertiary samples indicate isolation and differentiation between North and South America. Simpson (1969:895) re-affirmed his position that a Paleocene land-bridge connected North and South America. These differences in faunal relations cannot be explained in terms of a non-existent Paleocene land-bridge across the Panamanian region. They suggest some kind of Early Tertiary interchange between the North and South American continents, possibly across a filter-bridge or by island hopping through the proto-Antillean region. I cannot explore here the possible reasons for the apparent differences in mammal versus herpetofaunal and invertebrate data. Suffice it to say that the mammal fossil record and present distributions do not support or require the concept of a pre-Pliocene Tertiary land-bridge between North and South America.

Actually it seems possible that neither a land connection nor overwater invasions from the north were involved in establishing the ancient mammal lines, marsupials, edentates, condylarths and notoungulates in South America in Cretaceous and Paleocene. Some at least may be part of, or descended

from groups established on the southern continent prior to the Paleocene as derivatives of the west Gondwanaland mammal fauna (Fooden, 1972).

I have included four bat families as early South American faunal components. Unquestioned bats are known from the Eocene, but the order doubtlessly appeared earlier in Paleocene. Presumed ancestral groups of the modern families are well represented in Eocene in North America. Among the more primitive basal insectivorous stocks are the tropicopolitan family Emballonuriade, with 10 New World genera, all endemic; 7 of these also occur in Central America. The Noctilionidae (1 genus, 2 species) may be closely allied. The family Phyllostomatidae is a New World tropical endemic with 50 genera, only a few of which occur in temperate North America. Probably derived from phyllostomatids are the true vampires, family Desmodidae (3 genera), another New World tropical endemic. In my opinion, these four groups were derived from Early Tertiary ancestors in South America and underwent radiation and familial differentiation there.

#### *Later overwater invaders of South America*

The immediate ancestors of modern marsupials, edentates, ungulates, and bats evolved in South America from Cretaceous onward to at least Pliocene in essential isolation. All authors agree that several additional groups were added to the core mammal fauna by overwater transport presumably in Eocene-Oligocene, and underwent radiation in isolation in South America. These groups are an ancestor of the platyrrhine primates (Callithricidae and Cebidae) and the caviomorph rodents. Both appear as fossils in Early Oligocene in southern South America. Neither is known prior to these times elsewhere, but potential ancestral stocks of both groups occur in Late Paleocene and Eocene of North America. Whatever the ancestors, they became extinct north of the Panamanian Portal. Simpson (1950), Hershkovitz (1966, 1969) and Patterson and Pascual (1968), further agree that procyonid carnivores giving rise to *Cyonasua* and *Chapalmalania* of middle to Late Pliocene in west central Argentina were also pre-Pliocene overwater invaders from Central America. Hershkovitz (1966, 1969), in direct contradiction to the position of the paleontologists, proposed additional pre-Pliocene overwater transport into South America of the ancestors of mice of the sigmodontine group of the Cricetidae and a heterogeneous mixture of other mammals including some squirrels, a rabbit, several dogs, most mustelids, many cats, tapirs, peccaries, camels and many deer (see Table 2, Unit 3).

The rationale used by the several authors to explain these later invasions is essentially as follows: Simpson (1950, 1969) and Patterson and Pascual (1968) thought that the Isthmian Link was re-established in Early Pleistocene, thus any differentiated group represented in the South American fossil record prior to that time must have been a descendant of overwater waifs that invaded the continent prior to the emergence of the land bridge. Hershkovitz (1966, 1969) on the other hand believed that the Panamanian Portal was essentially

ineffective as a barrier to mammal distribution and that many groups (23 families) crossed it into South America prior to establishment of a land connection. To the possible overwater waifs already mentioned may be added the specialized bat families Natalidae (long-legged bats, 1 species), Furipteridae (smoky bats, 2 genera, 2 species) and Thyropteridae (disk-winged bats, 1 genus, 2 species), all apparently derived from insectivorous ancestors after isolation in tropical South America; and the manatee (*Sirenia*, Manatidae) with fossil genera from Late Miocene and Early Pliocene and a single living genus, all in South America.

Evaluation of the probability of fortuitous overwater invasions from north to south is closely tied to the history of the Isthmian Link. The following key points are reiterated from my description of its history above:

1. From Cretaceous into Miocene a major seaway extended across lower Central America and separated the Nuclear region from nearest South America by 400-1000 kilometers of water.

2. The closure of the seaway was progressive from north to south through Miocene.

3. By Early Pliocene the final water gap, the Bolivar Trough, was uplifted to complete the link and provide an overland route between North and South America.

Simpson (1950) and Patterson and Pascual (1968) take issue with the latter interpretation. They argue that the closure was in Early Pleistocene on the basis of mammal fossil data. Although the dating of the connection becomes a real issue for discussion later in this paper, for present purposes whether the bridge was completed in Early Pliocene or Early Pleistocene does not affect evaluation of overwater transport for most of the groups. The stocks (Young Southern Complex) that appear to have reached South America by waif overwater dispersal, after the initial establishment of mammals on the continent and prior to a later Cenozoic land connection, are considered below.

*Primates.*—Platyrrhine primates (usually placed in two families) are known today only from the New World tropics; fossils appear only in South America, the first in Early Oligocene, and on Jamaica. All living genera occur in South America, six range into Central America, two into tropical Mexico. One extinct marmoset (Oligocene) and several cebids (Oligocene-Miocene) are known from pre-Pleistocene deposits. These data support the view that the ancestor of the platyrrhines arrived in South America prior to mid-Tertiary. Although I have accepted the opinion of others that the ancestors of New World marmosets and monkeys reached South America by overwater transport in post-Paleocene times, it is with reservations. Basic prosimian lines occur in North America in Cretaceous and lemurs and tarsiers are relatively well known in Eocene. It is not out of the realm of possibility that an early tropical proto-platyrrhine may have crossed from Nuclear Central America or Africa to the South American continent in Cretaceous or Early

Tertiary. Nothing in the fossil record favors these alternatives and the morphology of African versus South American primates (fossil and living) seems to preclude any close relationship.

*Caviomorph Rodents.*—The first records of this important group are in the Early Oligocene of Argentina. An Eocene time of arrival is suggested because of the diversity of groups already present by upper Oligocene (6 families). Today 43 genera occur in tropical America, in 10 families; 6 genera, all common to South America, range into Central America and one (*Erethizon*) occurs far north into Canada. Three families are found in the West Indies, two (Capromyidae, with 6 genera, 3 living; Heptaxodontidae, with 7 genera, all extinct) are endemic, one (Echimyidae with 5 extinct insular genera, 4 of which are endemic) has a wide range in mainland tropical America. Rodents first appear in the fossil record in Late North American Paleocene and possible ancestors (Paramyidae) to the caviomorphs are of that age and area. A probable mid to Late Eocene overwater arrival of caviomorph ancestors from the north seems likely. Lavocat (1969) has argued that the caviomorph rodents of South America and the hystricomorph line of Africa are from a common origin. In this view the ancestors of the caviomorphs reached South America from Africa in late Mesozoic to early Tertiary, but this view is not followed here. Evolutionary radiation of the caviomorphs in isolation on the southern continent is verified by an extensive fossil record and recent distribution patterns for the group.

*Bats.*—Partially because of their relative vagility, bats usually have been ignored in dealing with problems of overwater invasion. The specialized families Natalidae, Furipteridae and Thyropteridae may best be explained as having undergone differentiation in isolation in South America. The time of invasion and isolation for these groups must have been prior to Pliocene.

*Manatee.*—Manatees are marine coastal and lowland river inhabitants. There is a single living genus with one species in tropical West Africa, and one or two forms in Florida, and around the Caribbean into the Amazon and Orinoco river systems. Two South American fossil genera *Potamosiren* (Late Miocene) and *Ribodon* (Middle Pliocene) suggest not overwater, but through water invasion of an ancestor in Eocene-Oligocene. They may be grouped without question as a Young Southern taxon.

*Procyonids.*—It is assumed by all previous authors that procyonids have invaded South America at least twice. The first time was prior to Middle Pliocene, where, in Argentina, two related fossil genera occur. The second invasion or invasions by essentially the Recent procyonid genera is assumed to have taken place after the connection of the two continents in post-Miocene times. If the connection occurred in Early Pliocene overwater dispersal is not needed to explain the Middle Pliocene fossils. If the bridge emerged in Early Pleistocene the ancestors of the fossil *Cyonasua* and *Chapalmalania* were doubtless overwater waifs from Central America. The earliest procyonids in

North America are from mid-Miocene so the entrance of this group into South America must have been no later than Early Pliocene.

*Cricetid Mice.*—Herskovitz (1966, 1969) has developed a convincing argument that most of the cricetid mice in South America must have differentiated there. Cricetids occur from Early Oligocene onward in North America. In the Americas two major stocks of the Cricetidae are known, one with all representatives having a complex penis and the second more advanced groups with a simple penial structure. The complex penis group contains around 40 genera, all but *Nyctomys* and *Otonyctomys* of Central America, one Galapagos Island, and one West Indian genus, are known from South America. This group is usually regarded as a distinct tribe Sigmodontini within the Cricetinae. Only two genera of the tribe range into temperate North America, the cotton rats, *Sigmodon* and rice rats, *Oryzomys*. The simple penis group includes peromyscine (7 genera), neotomine (5 genera) and microtine (9 genera) lines in the Americas. Only one peromyscine genus (*Aporodon*) and one neotomine genus (*Tylomys*) reach northern South America.

Herskovitz is convinced that the sigmodontines are derived from over-water invasion of South America by a complex penis ancestor in Oligocene-Miocene. Radiation and differentiation in South America led to the origin of the 40 or 50 genera. According to him, *Nyctomys* and *Otonyctomys* may be relicts north of the Panamanian Portal derived from the common ancestor that passed into South America. Any other allies of the sigmodontines in Central America have become extinct or replaced by the rather more recent intrusion of the simple penis lines. Herskovitz does not believe that the tremendous differentiation of sigmodontines in South America could have taken place in the last 3 million years (Pleistocene) as required by the Simpson (1950, 1969) and Patterson and Pascual (1968) theory of land connection. The latter two authors develop a counter argument that runs like this:

- a. there are no sigmodontine fossils from Miocene in South America, so there were no sigmodontines there,
- b. if sigmodontines were in South America in Miocene, many caviomorphs would have been replaced by competition,
- c. if sigmodontines were there in Miocene they should have differentiated beyond the generic group stage,
- d. the original sigmodontines evolved into multiple genera in Central America, since 17 cricetids live there today, and invaded South America; with little additional proliferation the 40 living genera evolved from the many invaders.

These views seem unacceptable to me. It is correct that no sigmodontines are known in Miocene fossil materials in South America but they are also unknown in the Miocene of North America. Given the predominance of southern Argentina fossil localities and the tendency of paleontologists to

collect larger animals, lack of cricetid remains in Miocene South America is not surprising. Contrary to the second point of Patterson and Pascual, there is no evidence that caviomorphs are currently suffering any ill effects from competition or replacement by cricetids. These authors make this point themselves (1968:443, 447). If a Pleistocene invasion of cricetids had no perceptible effect on the caviomorphs, why would a Miocene one affect caviomorphs adversely? Obviously a Miocene invasion of cricetids is not ruled out by caviomorph rodent history.

The third point is equally fallacious. The evolution of 40 genera since a presumed Miocene invasion and tribal differentiation are major events. They are of an equal or higher order of magnitude than the Miocene invasions and differentiations of murid mice in Australia or cricetid mice in Madagascar documented by Simpson (1961, 1940). In Australia two invaders of probable Miocene age evolved into 10 genera with five more on New Guinea. In Madagascar a group of seven endemic genera of cricetids (the endemic subfamily Nesomyinae of some authors) apparently have evolved from a single Miocene overwater waif.

The final argument is also difficult to accept. Today, 17 genera of cricetids are found in Central America, but only 3 sigmodontines occur north of extreme eastern Panama. It is unlikely that so many diverse genera as are now found in South America evolved post-Pliocene or if derived from a host of Central American ancestors left only three relicts behind. The data of Patterson and Pascual (1968:445-445, Tabs. 11-12) leave little question that sigmodontine mice have been in South America for a long period of time and differentiated there. Four genera of sigmodontines are known from Late Pliocene in Argentina, as compared to one in the Late Pliocene of North America.

The group must be regarded as overwater invaders of more recent origin than primates and caviomorphs, but clearly they arrived in South America prior to the uplift of the Isthmian connection.

*Other Invaders.*—The many additional groups proposed as overwater invaders by Hershkovitz (1969), appear to be relatively recent overland invaders. None of the genera is known as fossils in South America prior to Late Pliocene. Most do not appear in the record until Pleistocene. Hershkovitz' realization of the relatively early penetration by overwater transport of cricetids into South America and his misunderstanding regarding the extent of the Panamanian Portal and the effect of its reduced section, the Bolivar Trough, led him to overestimate the potential for overwater invasion.

#### *Overwater invasion from the south*

Because Hershkovitz regarded the Panamanian Portal as an ineffective barrier to mammal dispersion he proposed that a number of groups passed from the southern continent to Central America prior to re-establishment of the land connection (Table 2, Unit 3). Others including Patterson and Pascual

agree that Pliocene records of ground sloths and armadillos might result from overwater transport from south to north. In my opinion none of the other groups listed by Hershkovitz requires overwater transport prior to reconnection of the land bridge to explain their distributions. All seemed to have entered Central America fairly recently and certainly have had time to move northward since a Pliocene or even Pleistocene land bridge formation. Central and North American differentiation into a number of species as in *Sigmodon* and *Oryzomys* is most easily explained if reconnection occurred in Early Pliocene. If the connection were established in Pliocene no difficulty is encountered in explaining the presence of fossil edentates in North America as well; if it formed in Pleistocene overwater transport is required for these groups.

#### *The age of the Isthmian Link and faunal interchange*

The evidence previously discussed (p. 9) supports a concept of closure of the final link of the Panamanian Isthmus by uplift of the Bolivar Trough in Early Pliocene. Simpson (1950) and Patterson and Pascual (1963, 1968) take issue with the interpretation. They argue that the closure was in Early Pleistocene on the basis of mammal fossil data. A review of Pliocene faunas suggests that they have overstated their data. No mammals of the northern element appear in South America prior to Middle Pliocene (procyonids), but four cricetids, a skunk and two peccaries are known from Late Pliocene. Since most Pliocene fossil localities are from Argentina, it is not surprising that an invasion of northerners into northern South America might not affect the fossil record until later in the period several thousand kilometers to the south. Pleistocene localities, of course, abound with northern forms. Pleistocene fossil faunas in North America also show effects of invasion by southerners northward across the Isthmian Link, with about 20 genera represented. Unfortunately all Pliocene samples from North America lie in temperate climatic areas at least 4000 kilometers overland from South America. Generally, these localities are from regions that were semi-arid and affected by frost in Pliocene. They seem on ecologic grounds to be rather unsuitable sites for the ready establishment of the first tropical immigrants. Early Pliocene records of Southerners are to be expected in Middle American fossil faunas, but the only lowland finds of this age are strictly northern in composition (7-8 genera), all of relatively large animals (Olson and McGrew, 1941; McGrew, 1944; Mooser, 1959). Nevertheless, three southern genera, a ground sloth (*Megalonyx*), an armadillo (*Dasypus*) and a cotton rat (*Sigmodon*), are known from Late Pliocene in the United States.

The geologic and invertebrate paleontologic record, (Olsson, 1956; Nygren, 1950; Parodiz, 1969) tends to be in conflict with mammalian fossil data. Parodiz (1969:189) demonstrated that fossil freshwater mollusks in South America, from nearly the same sites as for fossil mammals, show immigration of northern families into South America for the first time in

Late Miocene-Early Pliocene. These data point unequivocally to an Early Pliocene connection between Central and South America. The mammal record demonstrates a full interchange of groups in Early Pleistocene, some group interchange in Middle to Late Pliocene but tends to discount an Early Pliocene land bridge. Whitmore and Stewart (1965) on the basis of mammal fossils from Panama indicate that by Middle Miocene only the Bolivar Trough remained as a marine barrier to intercontinental exchange with a water gap of no more than 100 kilometers. The view of Patterson and Pascual is that this barrier functioned for 10 to 12 million years to prevent fauna exchange, although a seaway of nearly 1000 kilometers in extent must have been crossed a minimum of six times during the previous 65 million years. If the Bolivar Trough remained a barrier through Pliocene some mammal groups probably crossed the narrow gap overwater. The procyonid, cricetid, skunk and peccary records from South America Pliocene might be accounted for in this manner. Similarly the earliest records for Southerners in North America might have been derived from early Pliocene overwater waifs from south to north.

Exact dating of the time of intercontinental connection (Pliocene versus Early Pleistocene) can only be finally resolved by discovery of additional Pliocene deposits in northern South America and lower Central America. Malfait and Dinkelman (1972) place the time of completion of the land bridge as mid-Pliocene. Nevertheless, my tendency is to accept Early Pliocene as the time of reconnection based upon geologic and invertebrate marine and freshwater paleontologic evidence, my review of the herpetofaunas (Savage, 1966) and Hershkovitz demonstration of significant differentiation in northern mammals that have crossed overland into South America. Among the components of the herpetofauna 37 genera found in Middle America appear to have invaded South America since the restoration of the Isthmian Link; 62 genera of South American origins have moved northward out of 159 genera found in Middle America. Out of the groups of mammals that unquestionably crossed the land bridge, whether in Pliocene or Pleistocene, 27 of the 138 genera in North and Central America passed from south to north, and 40 of the 160 in South America passed from north to south. These data suggest a relatively long history of connection, but do not preclude a Pleistocene date for reconnection of the continents.

The re-establishment of the Isthmian Link by Early Pliocene readily explains the presence of the Pliocene occurrence of procyonids, skunk, and peccaries in Pliocene South America and ground sloth, armadillo, and rice rats in North American Pliocene. It also allows enough time for differentiation of Northern groups in South America and Southern groups to the north, after crossing the land bridge, one of the weak links in any argument for a Pleistocene connection. The refusal of Patterson and Pascual (1968:436) to recognize the evidence from other groups and geology, and suggested by mammal fossils as well, seems to stem from a desire to make spectacularly recent what still is a dramatic, revolutionary meeting of two distinctive faunas

in Pliocene. Their statement "No better example of a geologically sudden meeting of two radically different faunas exists . . ." applies to the Pliocene encounter equally as well as to the presumed Pleistocene one.

Hershkovitz (1966, 1969) took a very original position regarding the role of the Panamanian Portal as a barrier to mammal dispersion. He argued that most genera of mammals crossed the portal with ease and that it had no major effect on regulating north-south or south-north movements into South or Central America, respectively. His interpretation is in marked disagreement with that of vertebrate paleontologists. A major weakness in Hershkovitz' discussion lies in his apparent misunderstanding of the nature of the Bolivar Trough. He seems to regard it as being equal to the Panamanian Portal. As emphasized above, until mid-Miocene, Nuclear Central America and South America were separated by a major seaway. The final portion of the marine portal to close was the Bolivar Trough, as nearly as can be determined in Early Pliocene. From Paleocene to Miocene, at least, any faunal exchange must have been across nearly 1000 kilometers of ocean or by island hopping. Hershkovitz (1969:65) regarded the matter of the timing of the bridge reconnection as academic, because he failed to appreciate the extent of the marine barrier during most of Tertiary. His own data require that the continental exchange begin at least by Pliocene, but by ignoring the history of the link region he is forced to propose a series of multiple, extensive overwater raftings of mammals to explain recent distribution patterns. Instead of being academic the dating of the connection is critical. Hershkovitz' proposed series of overwater waifs (Table 2: units 2, 3), except for those I call Young Southerners (Tab. 3), could all have moved north or south overland when the link was established in Early Pliocene. Since the major weight of evidence favors a Pliocene connection, Hershkovitz' principal objection to Simpson's views is negated. Surely the 10-12 million years since the emergence of the Isthmian Link allows enough time for the evolution of the levels of differentiation seen in both northern and southern immigrants in their new surroundings.

The efficacy of the marine portal as a barrier is fully attested by the fossil mammal record of South America from Cretaceous to Pliocene. Only late in the latter period do northern forms begin to appear. Even the reduced portal of mid-Miocene seems to have been an extremely effective barrier. Two fossil faunas, one just to the west of the Bolivar Trough (Whitmore and Stewart, 1965), another of slightly later age from its eastern border (Stirton, 1953), may be compared to illustrate this point. The faunal components are summarized (Table 4). Every animal in both samples is exclusively northern (Panama) or southern (Colombia). There can be no question but that even the reduced Bolivar Trough was a strong barrier to mammal dispersion. The Trough by Late Miocene was no more than 100 kilometers across. The two fossil sites are separated by a distance of about 350 kilometers and lie very close to the east and west margins of the trough zone. A facet of the effective-

TABLE 4

MID-MIOCENE	LATE MIOCENE
(Cucaracha)	(Friasian)
Central Panama	La Venta, Colombia
Horses	Opossum
<i>Anchitherium</i>	Borhyaenids:
<i>Archaeohippus</i>	<i>Lycopsis</i>
Rhinoceros	<i>Cladosictus</i>
<i>Diceratherium</i>	Bat (Phyllostomatidae)
Oreodont	<i>Notonycteris</i>
<i>Merycochoerus</i>	Monkeys:
Protoceratid	<i>Cebupithecia</i>
	<i>Hommunculus</i>
	<i>Neosaimiri</i>
	<i>Stirtonia</i>
	Condylarth
	Litopterns (2 families)
	Notoungulates (5 families)
	Astrapothere:
	<i>Astrapotherium</i>
	<i>Xenoastropotherium</i>
	Manatee:
	<i>Potamosiren</i>
	Megalanychid sloth
	Megatheriid Ground sloth
	Mylodont
	Anteater
	Armadillos (3 genera)
	Glyptodont
	Porcupine
	Cavy
	Dinomyids:
	<i>Olenopsis</i>
	<i>Scleromys</i>
	Capromyid
	Echimyid

ness of the narrow barrier may have been the result of the current patterns in the region. One of the principal objections to the proposed sea-level canal across the present day isthmus is the tidal difference between Pacific and Caribbean sides. The former has a 6 m amplitude, the latter an 0.5 m amplitude. If a similar pattern held in the past it is easy to imagine the terrific swirling currents that would sweep through a narrow channel such as the Bolivar Trough as the Atlantic poured into the Pacific twice daily and the Pacific into the Atlantic twice daily. Any mammal attempting to cross the channel would stand an excellent chance of being swept far out to sea, without much possibility of reaching the opposite shore. It seems inescapable that the marine barrier was extremely effective until closure and that most of the mammals

regarded by Hershkovitz as overwater waifs actually are overland immigrants into South America. Contrary to his forceful statements (1969:65), the nature of the water gaps and land bridges and their history, age and extent, best explain the data of present mammal distribution.

#### *The major faunal interchange*

At the beginning of Pliocene, the South American fauna apparently consisted of marsupials, bats, platyrrhine primates, edentates, a series of ungulates, manatees, caviomorph and sigmodontine rodents. Most, if not all, of the genera of these groups were unique to South America. Central America was populated by a variety of northern mammal lines (Table 3) but must have lacked almost all of the South American groups, except some bats, possibly manatees and perhaps a few relic sigmodontine mice or their ancestral stock. The major faunal exchange involved northward movement of many southern genera and the reverse. The families potentially involved in the interchange and their derivation are summarized (Table 5). Included in the table are all living Southern American mammal families and those extinct but recorded from Early Pliocene onward. All northern families with living representatives, and those that are extinct but with Miocene or later records in Middle America are listed. For purposes of discussion the family Cricetidae has been divided into two divisions; each is counted as a family equivalent in the following comparisons: Out of a total of 71 stocks that might have participated in the exchange from the end of Miocene onward, 39 are southerners and 32 northerners. Of the 71, 45 occurred in temperate South America, 52 in tropical South America; 50 in tropical Middle America and 42 in temperate North America. Of the southern families 30 were found in temperate South America, 33 in tropical South America. Twenty-four southern families ranged into tropical Middle America and 12 have reached temperate North America. Of the northerners 26 reached tropical Middle America, 19 tropical South America, and 15 temperate South America. Out of these groups 5 southern families are extinct in Middle America, although known as fossils in Pliocene or Pleistocene. Nine northern families present during the same time span are also no longer represented in Middle America. Five southern families, formerly represented in temperate North America, are extinct there and 2 northern families, formerly occurring in South America, are extinct in the New World.

As nearly as can be determined, the recent New World mammal fauna, exclusive of cetaceans and the West Indian forms, is comprised of 332 genera; 191 of these are southern genera, 141 northern genera. Table 7 summarizes the data for generic distributions (based on Hershkovitz, 1958 and Hall and Kelson, 1959). The first line (N) lists the number of genera in each major geographic region. The second line (%) gives the percentage of the total of each fauna comprised of southern and northern genera. The third line gives the percentage of the total genera for the New World as a whole, represented









by genera in the region. For example, in temperate South America there are 53 southern genera; these comprise 69% of the fauna for the region; the 53 genera represent 28% of the southern genera in the New World. In addition, data for all South American genera are pooled for an overall evaluation and totals for the four mainland regions are pooled and summarized in the same table.

These figures (Tables 5-6-7) provide a basis for testing the conclusion of Simpson (1950) that the major faunal movement was from north to south and the assertion of Hershkovitz (1969) of the reverse.

TABLE 6

## FAMILIAL EXCHANGE BETWEEN MIDDLE AND SOUTH AMERICA ACROSS ISTHMIAN LINK

FAMILIES		TROPICAL SOUTH AMERICA			MIDDLE AMERICA		
		Total	Southern	Northern	Total	Southern	Northern
Prior to	N	33	33	0	25	0	25
Land Bridge	%	100	100	0	100	0	100
Additions	N	19	0	19	25	24	1
Extinctions	N	9	7	2	14	5	9
Net Gain	N	10	-7	17	11	19	-8
Today	N	43	26	17	36	19	17
	%	100	60	40	100	53	47
Enrichment	%	30	-21	51	44	76	-32

At the time the bridge was established 39 southern families occurred in South America, 33 in the region of the marine portal. To the north 25 northern families occurred in the adjacent Central American area. After the faunal exchange and extinctions 43 groups occur in the South American area and 36 in Central America. On this basis (Table 6) both regions were enriched by the interchange, a net gain of 10 families in South America (a 30% enrichment) and a net gain of 11 families in Central America (a 44% enrichment). The figures demonstrate a basically balanced exchange, but 51% of the enrichment in South America comes from northern additions and 76% of the enrichment in Middle America from southern invaders.

At the generic level (Table 7) a similar pattern in faunal composition for the tropic bases of the Isthmian Link is indicated. From south to north (southerners) as a % of total number of southern genera show the following pattern: 28-76-40-17; from north to south the percentage of northerners to total number of northern genera is: 59-44-35-17. On this basis the equivalent of 40% of the southern genera have invaded tropical Middle America; 35% of the northern genera have invaded tropical South America. If the faunas nearest to the Bolivar Trough are used for comparison, the equivalent of 53% of the southern genera invaded Central America from tropical South

TABLE 7  
NUMBERS OF LIVING MAMMAL GENERA IN THE NEW WORLD BY MAJOR REGION

Southern	TEMPERATE SOUTH AMERICA		TROPICAL SOUTH AMERICA		MIDDLE AMERICA		NORTH AMERICA							
	North- ern	Total	South- ern	North- ern	South- ern	North- ern	South- ern	Total						
N	53	24	77	146	49	195	77	3	8	62	139	32	84	116
%	69	31	100	75	25	100	56	2.2	5.8	44	100	28	72	100
% Total	28	17	23	76	35	59	40	1.6	5.7	44	42	17	59	35

Total South American		Total New World	
Southern	Northern	Southern	Northern
N	183	53	236
%	78	22	100
% Total	96	37.5	76
N	191	141	332
%	58	42	100
% Total	100	100	100

America; the equivalent of 79% of the northern genera in Central America immigrated across the land link. Essentially most of the Central American northerners (49 out of 62 genera) have invaded South America and about half of the southerners (77 out of 146 genera) have crossed into Central America. A higher percentage of northern genera moved southward than southerners northward, but many more (actual numbers) southern genera immigrated northward. Any of Simpson's or Hershkovitz', or Darlington's ideas can be supported by these data, depending upon which ones are selected.

As a further attempt to evaluate the situation, I have tried other means of faunal comparison. At the family level (Table 8) 62% of the southern stocks reached Central America, but only half of these reached temperate North America. Of the groups present in tropical South America at the time of Isthmian uplift 73% invaded Central America. Out of the northern families 59% reached South America and 47% passed through the tropical area to South America. Out of the northerners in Central America at the time of connection of the continents 72% ranged into South America. Slightly fewer northern lines (19) invaded South America than South American stocks (24) invaded Central America. In the region of interchange the two elements are almost balanced. Seventy-seven of 146 tropical southern genera have invaded Central America, 49/62 of the northern genera in Middle America have immigrated to South America. Only when temperate North and South America are compared is there any suggestion of one of the two elements being more successful invaders than the other. Out of the total number of northern families a higher percentage (47%) have reached temperate South America than southern families have reached temperate North America. Of the families in the region adjacent to the Isthmian Link at the time of intercontinental connection 14 of 25 (56%) northerners have penetrated into temperate South America and 12 of 33 (36%) southerners have reached temperate North America.

The ratio of southern to northern families in each region (Table 8) provides another measure of the effect of the interchange. In temperate and tropical South America there are 2 southern families to each northern family, in Middle America the families are in a nearly 1:1 ratio and in North America the northerners are 2.5:1 to southern families. These ratios again demonstrate the almost equal familial exchange in the Isthmian region and the slightly greater success of northern families in reaching temperate South America over southern families affecting the North American fauna.

A similar ratio comparison for genera (Table 8) follows an almost identical pattern. In temperate South America southerners are in a ratio of about 2:1 to northerners, 3:1 to northerners in the tropic regions of the continent and nearly 1:1 with northerners in Middle America. In North America the number of northern genera approaches 3:1 southern. This method indicates that somewhat more southern genera have invaded Middle America from tropic areas to the south than northern genera have crossed from Central into South

America. Again fewer southerners contribute to the North American fauna, than northern genera contribute to the mammalian fauna of temperate South America.

Another comparison (Table 8) uses the maximum number of genera of a particular element in one region as a basis for determining faunal exchange. If the number (146) of recent southern genera in tropical South America is taken as 100%, it is seen that 53% have invaded Middle America and 22% have reached North America. If the number (84) of northern genera in temperate North America is taken as 100%, 58% have invaded tropical South America and 29% have reached temperate South America. This comparison supports the concept of a balanced faunal exchange.

TABLE 8  
INCREASE AND DECREASE IN PROPORTIONS OF SOUTHERN AND  
NORTHERN GROUPS OF MAMMALS  
(Recent and Fossil Families, Living Genera)

	TEMPERATE South America	TROPICAL South America	MIDDLE America	NORTH America
% Total Southern Families	77	85	62	31
% Total Northern Families	47	59	81	94
Ratios:				
Southern:Northern Families (maximum)	2:1	1.7:1	1:1.1	1:2.5
Southern:Northern Genera	22:1	3:1	1.2:1	1:2.6
% Southern Genera (100% = 146)	36	100	53	22
% Northern Genera (100% = 84)	29	58	74	100

Certain conclusions emerge from the evaluation of the comparative data. Some data can be interpreted to favor each of the three possible hypotheses: a) primary movement from North into South America (Simpson's view), b) primary movement from south to north (HersHKovitz' position), or c) that the faunal exchange was balanced. Nevertheless the 10 comparisons made in the preceding paragraphs support the following conclusions:

1. a higher proportion of northern families were able to invade South America and penetrate to the temperate zone of the continent than the reverse (47% of northern families, 31% of southern families); almost equal numbers of genera of northerners (24) and southerners (32) reached temperate areas on the opposite continents and each of these values is about 17% of the total northern or southern genera in the New World

2. in the region of the Isthmian Link the picture is mixed but points to a balanced faunal exchange

a. in favor of greatest south to north movement, at the family level, southerners affected Middle America more profoundly than northerners affected tropical South America: 48% of the Middle American families are of southern origin; 37% of the tropical South American families are of northern origin, 56% of the genera in Middle America are of southern origin, only 25% of the genera in tropical South America are of northern origin,

b. in favor of greatest north to south movement at the generic level, northerners invaded tropical South America more than southerners invaded Middle America: 79% of the northern genera in Middle America have reached South America, while 53% of the southerners in tropical South America have reached Central America or beyond

c. all other measures of contributions to the interchange indicate a balanced situation:

24 southern families moved north, 19 northern families moved south; 65% of all southern families now occur in Middle America, 58% of all northern families now occur in tropical South America;

73% of the southern families in tropical South America reached Central America, 72% of the northern families in Central America reached South America;

ratios of southern to northern families for tropical South America compared to Middle America are 1.7:1 and 1:1.1, respectively;

35% of all New World northern genera have reached tropical South America, 40% of all New World southern genera have reached Central America;

ratios of southern to northern genera for tropical South and Middle America are 3:1 and 2:1, respectively;

53% of the southern and 58% of the northern genera, when the greatest number of genera in any one region is used as 100%, are found in Middle America and tropical South America, respectively.

3. faunal enrichment also was generally balanced; in Middle America before faunal exchange and extinction the area had 25 northern families, today the total is 17 northern and 19 southern; in tropical South America before the exchange there were 33 southern families, today there are 26 southern and 17 northern families in the region; the Middle American fauna was enriched by 44%, the South American by 30%. The enrichment in both cases involved a disproportionate extinction of native families and enrichment by invader lines (Table 6).

The hypothesis of Simpson (1950) regarding a greater immigration and effect on South America of northern groups than southern effects on North America is not supported. His views are strongly biased by his comparisons between temperate North America or North and Central America combined versus South America, which obscured the degree to which South American groups contributed to the fauna of tropical Middle America. It is true that 79% of the northern genera in Central America have reached South America

while only 53% of the southern genera in tropical areas have passed into Central America. However, 77 southern genera have moved northward and 48 northern genera southward. Of the 141 northern genera in the New World only 35% have reached South America and only 25% of the tropical South American fauna is of northern origin. Emphasis on the one point of substantial immigration of northern genera into South America from Central America creates a false picture of the situation. Other evidence supports the concept of balanced interchange.

Hershkovitz' (1969) hypothesis that southern immigration northward is dominant also is supported by the following data, at the family level 51% of the Middle American mammal fauna is of southern origin, 35% of the tropical Southern American fauna of northern origin. 56% of the Middle American genera are of southern groups, 25% of the tropical South American genera are from the north. These values are considerably biased, since many southern groups only occur in extreme lower Central America, a region indeed dominated by recent southern invaders. The remaining evidence supports a concept of balanced interchange.

Darlington (1957:367) suggested a possible balanced exchange, but was handicapped by his acceptance of Simpson's views. He finally concluded that the South American fauna was profoundly changed by the exchange, North America much less so. A balanced exchange is strongly indicated by my analysis. At the family level more southern groups moved northward than the reverse; at the generic level the northerners had greater impact. In terms of total New World families and genera, in short the total pattern of mammalian faunal distribution, the exchange was balanced, 62% of all New World southern families and 40% of the genera have invaded Middle America; 59% of all New World northern families and 35% of the genera have reached South America. Other comparisons (Tables 5-6-7) confirm the equilibrium established between northern and southern invaders and endemic stocks. The essential pattern of approximately equal interchange between the continents is reiterated by each comparison (see 2c above). Only in the immediate region of the Bolivar Trough does the general balance seem to break down. The view of this breakdown depends upon the data selected for evaluation. On one basis southern families have been more successful invaders than northern families, 25 southerners to 19 northerners involved in the exchange; 51% of Middle America families are southern in origin, 35% of tropical South American are northern. In terms of total number of families 62% of southern families and 59% of northern families were involved; 73% of the southern families in tropical South America and 72% of the northern families in Central America were involved in the exchange. At the generic level on one basis the apparent breakdown of balance is the reverse of the pattern for families, since 79% of the northern genera in Middle America have crossed into South America and only 53% of the southerners have ranged north, but 77 southern genera occur in Middle America and only 45 northern genera in tropical South

America. Which values indicate the dominant movement and effect? The other comparisons show a balance of generic exchanges when total numbers of New World genera are considered; for example, 34% northerners, 40.5% southerners, are involved in the exchange. When faunal enrichment for tropical America as a whole is evaluated, the enrichment of Middle America at the family level was 44%, for South America 30%, confirming the present overall balance following the interchange and maximum exchange during the last 10-12 million years.

### *The role of Middle America*

When I began this study, it was with the full expectation that the Middle American mammal fauna would prove to be as distinctive and significant to understanding of origins and history as is the herpetofauna (Savage, 1966). In my paper I demonstrated that the Middle American herpetofauna is unique, mostly endemic and only slightly influenced by northern and southern invaders. Of 159 genera of amphibians and reptiles in Central America 67 are Middle American in origin. Only 14% of the genera north of Panama are South American in origin and less than 12% are of northern affinities. The expectation for the mammal fauna has not been fulfilled.

The herpetofauna of Middle America is dominated by autochthonous tropical groups, (Middle American Element) that apparently are allied to South American tropical stocks (South American Element). The two elements underwent independent evolution north and south of the Panamanian Portal during Eocene-Pliocene and have been involved in the intercontinental interchange across the Isthmian Link. Temperate North America has its own herpetofauna made up of stocks (Old Northern Element) associated with the history of temperate forest climates and a more recent series (Young Northern Element) derived from tropical ancestors in association with development of temperate subhumid to arid climates. Neither of these latter two stocks profoundly affected tropical Middle America. Three major recent herpetofaunas occur in the New World, a North and temperate Middle American fauna (Nearctic), a tropical Middle American fauna (Mesoamerican) and a tropical and temperate South American fauna (Neotropical).

The mammal situation is quite different. Two major recent faunas are recognized (Herskovitz, 1958) a North American temperate unit (Nearctic) and a Middle and South American unit (Neotropical). Only two principal historical units, a Southern Element and a Northern Element seem to be involved in mammal history (Table 3). These differences partially reflect the relative ages and evolutionary patterns for amphibians-reptiles and mammals. All orders and probably most families of living amphibians and reptiles were represented in Cretaceous. Some orders (marsupials, insectivores, multituberculates, condylarths, and creodonts) of mammals are known from Early Paleocene, but most do not appear until Eocene. Among Southern Element groups many of the families appeared by Eocene, but most of those still extant

appeared in Oligocene. Many Northern Element families are Oligocene in age, but a number, about 10, did not appear until Miocene or later. The northern mammal lines seem to have had little difficulty in populating and replacing more primitive stocks in Central America. The slower pace of amphibian and reptile evolution allowed *in situ* differentiation of ancient groups in Middle America. The Cenozoic mammal situation conforms to the concept of Matthew (1915), Simpson (1950) and Darlington (1957) of northern origins and southward immigration of higher placental mammal families. The more temperature sensitive amphibians and reptiles do not follow this pattern. Their centers of evolutionary radiation are tropical or warm temperate, with construction of family ranges by Late Cenozoic temperature effects, immigration reduced and more likely to involve south to north movement than the reverse.

Simpson (1950) viewed tropical Middle America as being at present a complex transition zone, barrier and pathway for immigration with its combined roles acting to form a filter to faunal interchange across the Isthmian Link. In his view, during the past, Middle America was populated by tropically adapted northerners that were in position geographically and ecologically to invade South America. He aptly pointed out that most of the groups regarded as North Tropical (Table 3) types by me, were probably differentiated in the Middle American tropics and thus could rapidly and successfully invade South America when the land connection was formed. Darlington (1957:459) also regarded Central America as a transitional zone between temperate North America and tropical South America.

Hershkovitz (1958) concluded that tropical Middle America was dominated by Neotropical groups and that it is not a transitional zone between North and South American faunas. He (1966, 1969) expanded on this view and related it to his idea that the Panamanian Portal was ineffective as a dispersion barrier and that Middle America was a region of differentiation, primarily for southern groups (Table 2, unit 3) and as a staging area for northern groups that invaded South America overwater (unit 2) and overland (unit 8).

Patterson and Pascual (1968) regarded tropical Middle America as the area of differentiation of numerous northern stocks (particularly cricetid mice) that rolled into South America, while disappearing to the North, after an Early Pleistocene land-bridge was established. The data presented in their paper and in the previous sections of this report seem clearly to define the role of Central America in faunal history. From earliest Cenozoic it has been closely tied to North America and populated with tropical groups of northern origins. It is from these latter stocks that additional groups passed across the marine portals to South America from Cretaceous to Miocene (Table 3, Young Southern Complex). These stocks underwent evolution in isolation in South America as their tropical Middle American allies became extinct. Even as early as Late Eocene, Nuclear Central America was almost completely domi-

nated by derivative northern lines. By Late Miocene 25 northern families were in the region, underwent differentiation into groups still present there, and became the earliest post-Miocene invaders of South America (Table 3, North Tropical Complex). All evidence suggests that no southern stocks or a very few were in Middle America at this time. The idea of Patterson and Pascual (1969) that 40 sigmodontine mice genera differentiated in Central America and immigrated *en masse* into South America, leaving behind only 4 or 5 stocks is a drastic overextension of this view. Since the intercontinental connection was established many northern genera in Central America have moved southward and at least 77 southern genera have moved into Central America. No evidence suggests wholesale immigration by one group, but rather movement by representatives of many different genera.

It seems in this instance that tropical Middle America served several functions in the periods just before, during and after formation of the Isthmian Link:

1. North Tropical groups underwent differentiation there prior to uplift;
2. These groups moved southward into tropical South America and new stocks (North American) began to filter into the region after the bridge was established;
3. Southern groups moved northward across the connection;
4. The region today has a mixed fauna: 19 southern families to 17 northern families; 77 southern genera to 62 northern genera; it has acted and continues to act as a barrier, pathway and filter to northward and southward movements by South American and North American mammals, respectively. Its role as a center of differentiation is past, since only 11 genera are endemics, 8 southern and 3 northern.
5. The region today forms a complex filter to faunal interchange and its mammal fauna (families: 53% southern, 47% northern; genera: 56% southern, 44% northern) reflects the modern role as a transitional zone, forming both a barrier and a pathway for immigration.

The distribution patterns of mammals and the actual operation of the filter effects in Middle America have never been analyzed in depth, although Simpson (1950, 1956) realized the need and significance of such a study. It may well be that the apparent transitional nature of the region, at least as far as mammals are involved, is overemphasized by a treatment of it as a single unit. In my study of the herpetofauna (Savage, 1966) the Central American fauna, taken as a whole, appeared to be a transitional mixture of South American post-Miocene immigrants (42% of the genera) and northern groups (58%). Detailed analysis, however, demonstrated that southern genera are predominant only in the southern portion of the Isthmian Link (Panama). In Nuclear Central America less than 15% of the genera are of southern origin.

#### *The mammals of the West Indies*

In the discussion of the major patterns of New World mammal distribu-

tion and history I have not included families and genera from the West Indies, since they are peripheral to the central problem. A summary of living (Herskovitz, 1958) and fossil groups (Simpson, 1956) provides the data for the following observations. It is clear that the islands have been populated by overwater waifs, principally if not exclusively of tropical origins. The lesser Antilles mammal fauna is small, but seems to be mostly derived from northern Venezuela-Trinidad in late Cenozoic. Only the caviomorph heptaxodontid genus *Amblyrhiza* (Anguilla and St. Martin) and the sigmodontine mouse *Megalomys* (Curaçao, Martinique, St. Lucia, Barbuda, and possibly Tobago), are endemic (both are apparently extinct). In addition the phyllostomatid bat genus *Ardops*, with four nominal species, is endemic to the lesser Antilles and the West Indian endemic genera *Brachyphylla* and *Monophyllus* of the same family also occur there.

The situation in the Greater Antilles is very different. The recent fauna consists of endemic insectivores, bats, several endemic caviomorphs and one sigmodontine mouse. In the fossil record an endemic insectivore, several bats, an endemic monkey, several endemic ground sloths and a number of endemic caviomorphs are known from Pleistocene and many of these survived on the island almost to the present (Table 9). Simpson (1956) regarded the fauna as composed of three overwater groups of invaders:

1. the insectivores from North America in Early Tertiary;
2. most of the fauna from South America in Miocene-Pliocene;
3. the sigmodontine mouse from Central America recently. According to his view the ancestors of group 2, arrived by overwater waif dispersion from Colombia.

Darlington (1957) disagreed. He viewed the Greater Antillean mammal fauna as derived primarily by overwater waif dispersal from Central America to Cuba or Jamaica.

Herskovitz developed another hypothesis, associated with his general theme of the inefficacy of the Panamanian Marine Portal as a barrier to intercontinental mammal dispersal. Four separate invasions by overwater transport were suggested:

1. the ancestor of the insectivores from Central America in Cretaceous or early Tertiary (possibly by a land bridge, Fig. 5A);
2. immigrants from the south in Middle Tertiary, while South America was separated from Middle America (endemic bats, edentates, and caviomorphs);
3. bats from Central America, derived from overwater transport from South to Central America in earlier times;
4. recent species from Central America.

Although he stated that the total fauna seems to be South American in origin, Herskovitz (1969:10, Fig. 5) concluded that the Greater Antillean mammal fauna is a relict representative of a tropical Tertiary Middle American fauna. This view is another example of the confusion caused by Herskovitz'

underestimate of the effect of the Panamanian Portal. It is clear that mid-Tertiary mammals in Central America did not include representatives of Southern Element stocks and that the West Indian fauna shows virtually no effect of North Tropical genera.

TABLE 9  
MAMMAL FAUNA OF THE GREATER ANTILLES

GROUP	ORIGIN					Total (Extinct)
	SOUTHERN South American	ELEMENT Young Southern	West Indian	NORTHERN North Tropical	ELEMENT North American	
Insectivores			3(1)			3(1)
Primates		1(1)				1(1)
Bats	15(2)	1		3	4	23(2)
Edentates	5(5)					5(5)
Caviomorphs		18(15)				18(15)
Sigmodontines		1				1
Total	20	21	3	3	4	51
%	39	41	6	6	8	100
Extinct	7	16	1			24
Living	13	5	2	3		27
%	48	18.5	7	11		100

The accompanying table (Table 9) makes the situation clear. The bulk of Greater Antillean genera are South American in origin and most of them probably reached the islands prior to the invasion of Central America by the southern lines in Pliocene onwards. The peculiar insectivores are ancient relicts of North America origin and their ancestors may have crossed to Cuba (portions land positive throughout Tertiary, according to Malfait and Dinkelman, 1972) from Central America or Gulf coastal North America early in Tertiary. For this reason they cannot be grouped with any of the four historical units recognized for continental forms and I have separated them as a West Indian unit. Seven northern bat genera and the very recent sigmodontine invader (*Oryzomys*) seem to have come from Central America. *Oryzomys* is a Young Southern Element genus that spread very rapidly into Central America after the Isthmian Link was established in Pliocene. The Antillean species *O. antillarum* belongs to a Central American species group (*palustris*) that ranges from Panama to New Jersey and is an example of the immigration of southern genera across the land link.

My analysis supports the hypothesis of Simpson (1956) in most respects. If Darlington (1957:510-517) and Hershkovitz (1969:10) are correct that the Greater Antillean fauna came mostly by overwater transport from Central America then this occurred well back in Tertiary. This idea suggests that the insectivores, primate, most bats, edentates and caviomorphs are relicts of a hypothetical ancestral tropical fauna in Central America that gave rise to

Antillean and South American stocks, but is now extinct in Middle America, except for descendant groups that re-invaded from South America. Only the presence of insectivores supports this concept. The Antillean primate, bats, edentates, and caviomorphs all appear to be advanced derivative groups rather than near the ancestral stocks that originally reached South America. One subfamily of phyllostomatid bats and two families of caviomorphs are endemic to the islands, but all close relatives are South American. For terrestrial mammals Simpson's three strata of overwater waifs cited at the beginning of this section agree with available evidence. Perhaps some of the bats of southern derivation have reached the Antilles from Central America since Pliocene.

#### ORIGINS OF NEW WORLD TROPICAL MAMMAL ASSEMBLAGES: A SUMMARY

The purpose of this section is to summarize the ideas developed in the preceding pages in the form of a general theory (Savage, 1960:184).

At the beginning of Cenozoic relatively few major mammal stocks populated the world. In South America marsupials, edentates, condylarths and protonotungulates were already established as an isolated fauna probably derived from the Gondwanaland mammal fauna of Late Triassic. That these stocks were already in South America and did not arrive there from the north as proposed by Simpson (1950, 1969) and Patterson and Pascual (1963, 1968) seems likely (Fooden, 1972). Some question still persists as to whether the basic South American lines reached Central and North America by waif-overwater or overland migration and if the latter where the land connection was geographically located. Evidence from geology, invertebrate paleontology and distribution of the herpetofauna suggests the presence of a Paleocene intercontinental connection but not in the present day Isthmian Link region. The latest new tectonic studies (Freeland and Dietz, 1971; Malfait and Dinkelman, 1972), while equivocal, tend to rule out such a proto-Antillean land-bridge. The original mammal groups underwent independent evolution in isolation in South America until Pliocene, (Fig. 1) since the Panamanian Marine Portal separated Nuclear Central America from South America from Late Cretaceous to Pliocene, their closest allies to the north became extinct during this time interval in Central and North America. The descendent stocks of this ancient assemblage form the South American Complex of the Southern Element (Table 3).

From Cretaceous to Miocene (Fig. 2) a number of additional mammal stocks appear to have invaded South America from Nuclear Central America, across the marine barrier. In chronological order from earliest to latest these are: primates, caviomorph rodents, manatees, bats, and sigmodontine mice of the family Cricetidae. The latter series of waif invaders are grouped as the Young Southern Complex of the Southern Element (Table 3). These stocks also underwent evolution in isolation in South America and the two complexes are responsible for the unique composition of the mammal fauna on

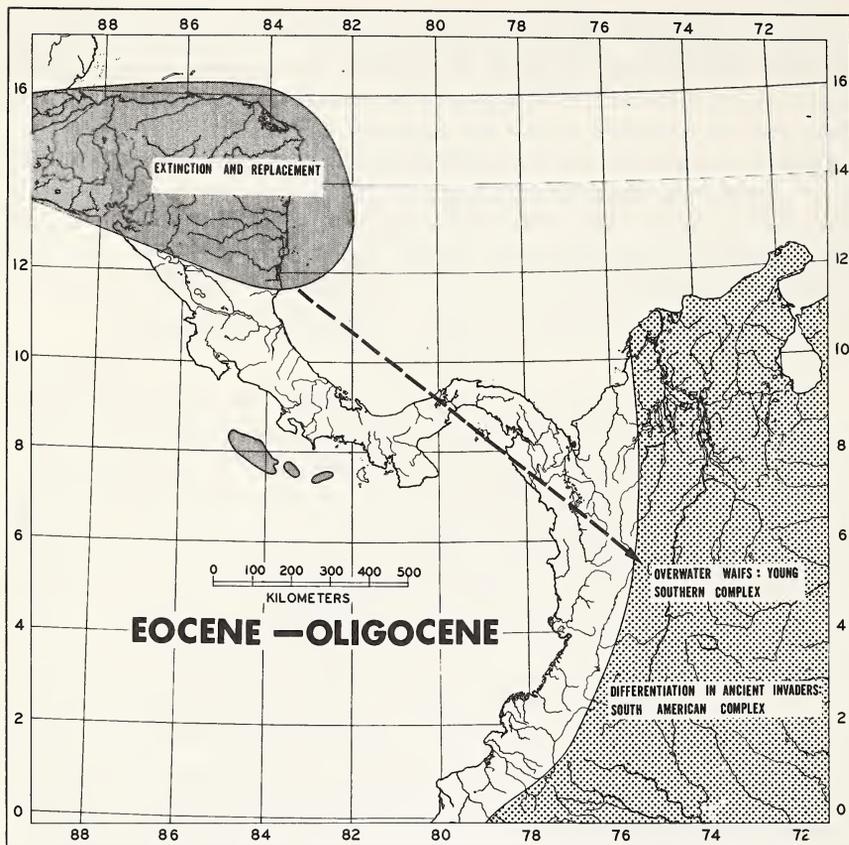


FIGURE 1. Probable Eocene-Oligocene distribution of historical units of Neotropical mammal fauna, indicating events taking place concurrently in Nuclear Central America and South America. Dashed arrow indicates source of overseas waifs.

that continent. These stocks too were replaced and disappeared in Central America.

During mid-Tertiary a series of northern mammal groups invaded Middle America and underwent some differentiation there to form the North Tropical Complex of the Northern Element (Table 3). Contrary to the views of Hershkovitz (1966, 1969) the Panamanian Portal prevented any substantial overwater interchange between South America and Nuclear Central America. Thus, until Pliocene, Northern and Southern Elements remained geographically isolated from one another. In Miocene the portal became reduced from north to south and an elongate peninsula was established. The final waterway to be closed was the Bolivar Trough. The evidence of fossil Miocene mammals in Panama and northern Colombia demonstrates that even

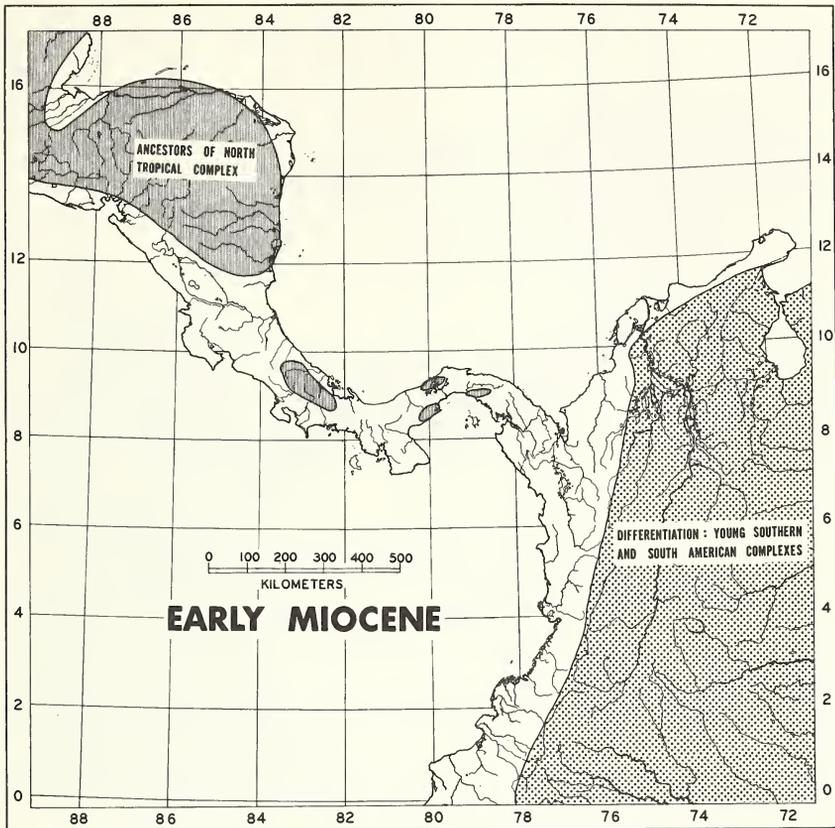


FIGURE 2. Probable Early Miocene distribution of historical units of tropical American mammal faunas.

this relatively narrow (100 km) marine barrier was extremely effective, since no southern groups occurred north of it and no northern groups to the south.

In earliest Pliocene (Fig. 3) the Isthmian Link was completed with the uplift of the Bolivar Trough region. At this time began a dramatic and rapid faunal interchange that continues today. Although Simpson (1950, 1969), Darlington (1957), and Patterson and Pascual (1968) place the time of intercontinental connection as Early Pleistocene, the geologic data, invertebrate paleontologic evidence, distribution of recent herpetofaunas and the South American mammal fossil record with northern groups (procyonids, a skunk and two peccaries) present in Pliocene make it clear that an Early Pliocene connection occurred.

The interchange was complex and continuous from Pliocene onwards and involved both Southern complexes, the North Tropical Complex and in

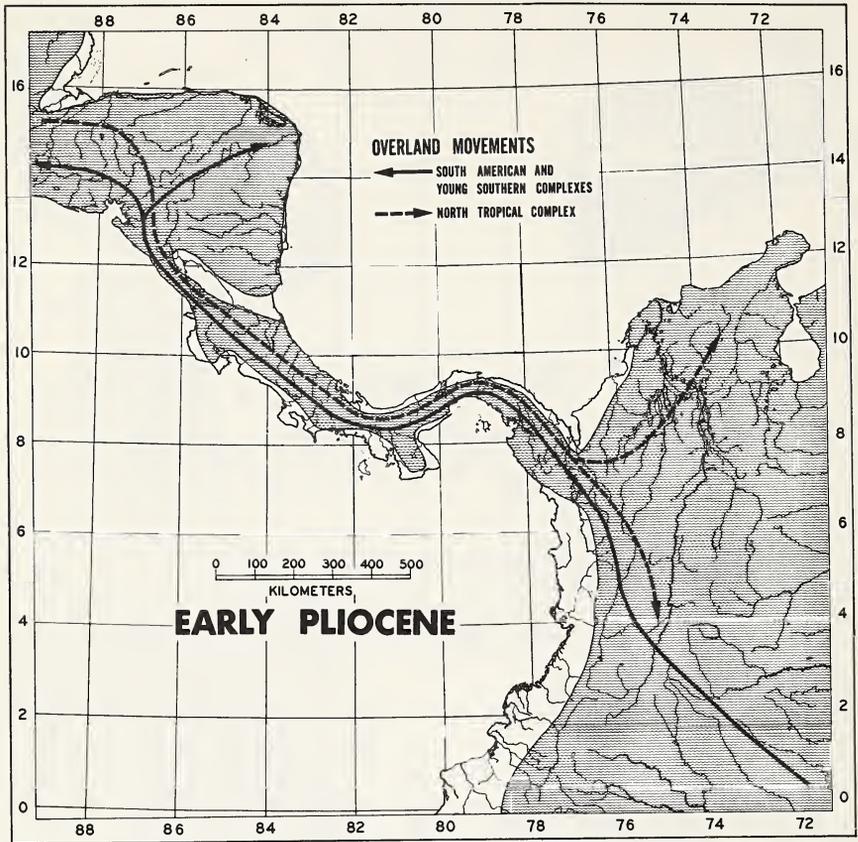


FIGURE 3. Probable Early Pliocene overland movements of historical units of tropical American mammal faunas.

Pleistocene a second northern faunal unit, the North American Complex (Table 3). Members of this complex are allied to the tropical northerners, but are derived from temperate stocks established in North America no later than the time the land connection was formed in the Isthmian region, or are Pleistocene invaders from eastern Asia (Fig. 4). Derivatives of these lines comprised a second wave of northerners that penetrated the tropics of Middle America in Pleistocene and some have extended their ranges into South America (Table 3).

Following the establishment of the Isthmian Link 24 southern families have entered Central America, 12 reached temperate North America; 19 northern families entered South America, 15 reached the temperate areas of the continent. Today, out of 191 southern genera, 40% occur in Central America, 17% in temperate North America; of 141 northern genera, 44% occur in Middle America, 35% in tropical South America and 17% to the

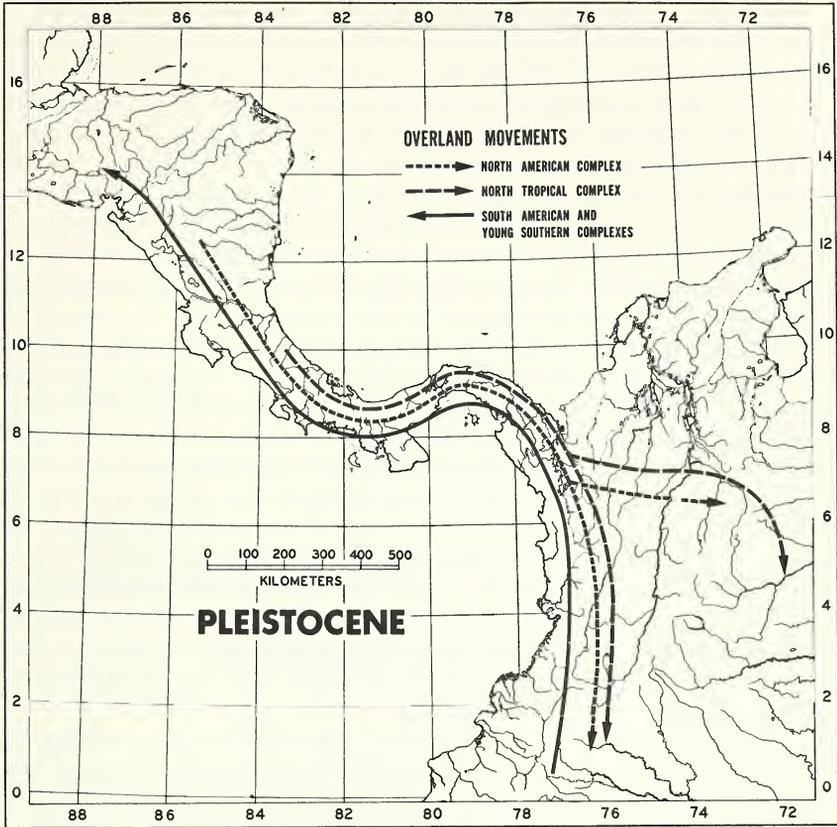


FIGURE 4. General patterns of overland migrations in Pleistocene for historical units of tropical American mammal faunas.

south. Contrary to the views of Simpson (1950), Darlington (1957), and Patterson and Pascual (1968) the immigration has not been predominantly from north to south. Nor can I agree with Hershkovitz (1969) that the heaviest flow was from south to north. Taken in totality, northern families and genera contribute to about the same degree to the fauna of South America as southern families and genera to the fauna of tropic Middle America. The most impressive feature of the interchange is the almost equal effects of north-south and south-north post-Miocene immigrations in modifying the faunal structure in both regions.

In terms of the controversy between the views of Simpson (1950), as supported by Patterson and Pascual (1968) and those of Hershkovitz (1966, 1969) as reviewed in an earlier section of this paper, my analysis indicates:

A. That the time of reconnection between the continents was early

Pliocene, *not* early Pleistocene, a timing that allows for the invasions of northerners with some differentiation in South America, without presuming extensive and continuous overwater immigration during mid-Tertiary. This point is critical and in it I disagree with the Simpsonian hypothesis of Pleistocene connection. Although Hershkovitz (1969) favors a Miocene-Pliocene link, he missed its significance entirely and failed to see that most of the groups of northerners for which he postulated overwater immigration to South America (Table 2, unit 2) must have used this overland route instead. His principal arguments for south-north overwater invasions by southerners (unit 3) are also vitiated by a Pliocene connection. Since the amount of differentiation in Middle and North American extinct ground sloths, primates, *Oryzomys*, (14 species) and *Sigmodon* (about the same number) and Echimyidae required earlier entry than Pleistocene into Central America, overwater transport seemed to Hershkovitz a reasonable view. I agree that entry was pre-Pleistocene, but an overland route was available and was doubtless used by these stocks in Pliocene movements into Central America. Hershkovitz' prime argument against overland invasion by most northern and southern groups in Pleistocene is the degree to which they have differentiated after reaching the new land area. He attempts to show that the Pleistocene connection was of little significance as a result. The realization that the land connection was established 10 million years earlier destroys any basis for his concept that continuous overwater exchanges took place between the continents in Tertiary. The revised timing completely eliminates the basis for his objections to the idea of extensive overland exchange.

B. That the extensive Panamanian Marine Portal was an extremely effective barrier to mammal dispersion from Cretaceous to Late Miocene; only five stocks succeeded in crossing the barrier (Table 3, Young Southern Complex) from north to south, none in the opposite direction; even the reduced portal, restricted to the Bolivar Trough, of Late Miocene was a remarkable barrier to mammal dispersion. In this regard I concur completely with Simpson. Much of Hershkovitz' theory of the history of mammals in his region is negated by his failure to appreciate the barrier effect of the 1000 km extent of the great seaway of Eocene to Miocene and the amazing effectiveness of the 100 km wide Bolivar Trough of Miocene times.

C. That Middle America was an area of differentiation for groups of mammals at infrafamilial levels during middle Tertiary, but not as a center for the origin of new families of northerners; it was clearly isolated from the south during this time, contrary to Hershkovitz (1969), by the seaway and did not have any, or had at most a few southern overwater waif components. The Tropical Northern Complex developed here and formed the initial wave of southward invaders when the Isthmian Link was forged. These views do not substantiate either Simpson (Middle America a major center of differentiation) or Hershkovitz (Middle America with a mixed fauna) in their ideas of tropical Middle America in pre-Pliocene times.

D. That the effect of Isthmian connection produced a dramatic and rapid faunal interchange in both directions with profound effects on the composition and structure of the faunas of North, Middle, and South America and that these effects were essentially balanced. Simpson claimed an even more dramatic change (Pleistocene) with northerners affecting South America much more than the reverse. Hershkovitz minimized the extent and amount of overland exchange after the linkage and thought that maximum movement was of southerners into the north.

The role of the Isthmian Link in these events is summarized (Fig. 5).

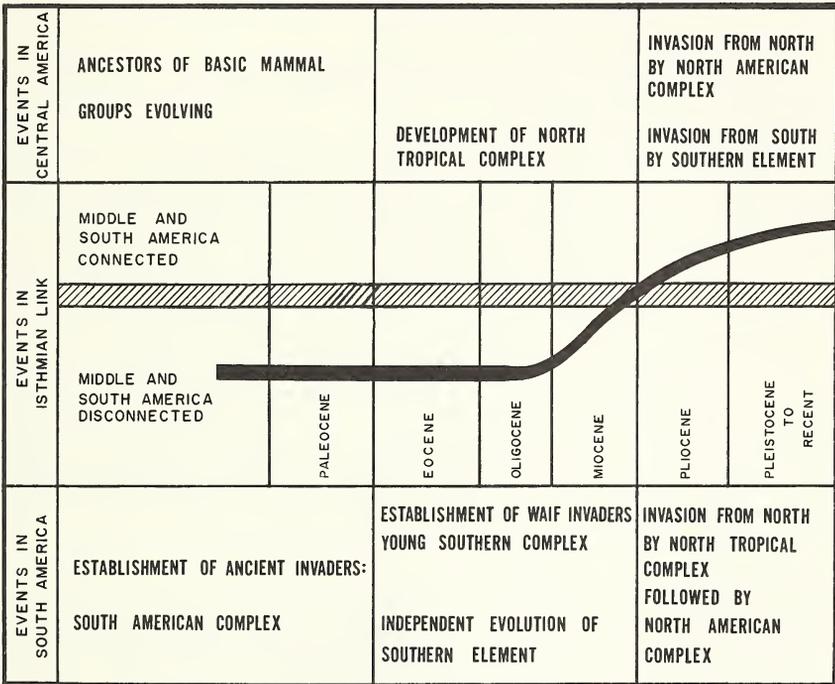


FIGURE 5. Geological history of Isthmian Link—Panamanian Portal region and effects on historical units of tropical American mammal faunas.

The present day South American mammal fauna is composed of two major historical elements, each with two components. The South American and Young Southern groups have a long independent history on the continent. Two waves of Northern Element lines have invaded South America since Miocene across the Isthmian Link. The first, North Tropical groups, were in Central America when the connection was established; the second is a more recent wave of temperate North American stocks that arrived in Early Pleistocene in Middle America, and some continued southward. In the total South

American fauna 60% of the families and 78% of the genera are of the Southern Element; 40% of the families and 22% of the genera are of the Northern Element.

The Middle American mammal fauna contains groups from both Southern Element complexes and both Northern Element complexes. Since Early Pliocene it has had invaders from the south (South American and Young Southern groups) and north (North American groups) add to its basic structure of North Tropical stocks. The southern invaders crossed the Isthmian Link, the northern stocks the land mass of Central America. Many more southern groups reached Central America than did North American types. Nevertheless, since the core of the Middle American mammal fauna was of North Tropical origin the fauna is balanced. In Middle America, 53% of the families and 56% of the genera are southerners; 57% of the families and 44% of the genera are northerners.

The fauna of temperate North America contains predominantly North American complex forms. A limited number of southern families (12) have crossed the Isthmian Link and reached this region where five have become extinct. At present out of 29 living families 24% are southerners, 76% are northerners; at the generic level 28% are Southern Element genera, 72% are of the Northern Element. By way of contrast in temperate South America 30 families occur: 57% are Southern Element, 43% are Northern Element stocks; at the generic level 69% are southerners, 31% northerners.

The mammal fauna of the West Indies is derived from these sources, but Southern Element stocks predominate: a) ancient overwater waifs from North America, ancestors extinct—insectivores; b) Southern groups arriving by overwater transport from South America in Miocene—Pliocene times—endemic bats, edentates and caviomorph rodents; c) recent species by overwater transport from Central America—bats and *Oryzomys*, a rice rat.

In conclusion, the mammal fauna of South America was extremely different from that of tropical and temperate areas north of the Panamanian Portal, during most of Tertiary. Upon connection of the continents extensive overland immigrations profoundly affected the faunas of South and Middle America from Early Pliocene onward. Today both southern and northern faunas have been significantly modified by the increments, but the effects are essentially equalized. Both faunas have been substantially enriched by the exchange, but neither has been disproportionately influenced by the recent immigrants.

The role of Middle America in the history of the mammal faunas has been overemphasized by most authors. It served as a staging ground for North Tropical differentiation (no more than generic or species group level in most cases) and invasion across the link; also as the region most strongly affected by southern invaders. It is today primarily a complex, transitional zone, forming both a barrier to and a pathway for immigration and acting within these combined roles as a filter to faunal interchange across the link region. A

complete analysis of the distributions of Middle American mammals at the species level offers a tremendous opportunity for someone to clarify and evaluate the operation of the filter. The significance of such a study as a contribution toward understanding the dynamics of the intercontinental exchange cannot be overestimated and it should provide new biogeographic, ecologic, and evolutionary insights as well. It is a crucial next step in fully elucidating the historical and current role of Middle America and the Isthmian Link in mammal evolution.

### RESUMEN

La fauna tropical de mamíferos del Nuevo Mundo comprende cuatro importantes unidades y fuentes históricas. La más antigua de estas unidades (la Sud Americana) está compuesta de marsupiales, xenartidos edentados, condilártidos, protonotungulados y algunos murciélagos cuyos ancestros estuvieron en Sud América al principio del Terciario y evolucionaron, se diversificaron y en muchas ocasiones se extinguieron, *in situ*. Una segunda unidad (la Joven del Sur) comprende primates, roedores cavimorfos, manatíes, algunos murciélagos y ratones sigmadontidos, cuyos ancestros llegaron de Norte América errando sobre el agua en varias ocasiones del Paleoceno al Plioceno. No existe sólida evidencia de la presencia de una conexión entre Norte y Sud América en el Cretácico o temprano Terciario que se pueda aducir de la disponible evidencia de los mamíferos.

Recientemente (Eoceno-Mioceno), una serie de mamíferos modernos evolucionaron en Meso América (la unidad Nor Tropical) los cuales invadieron Sud América cuando la Conexión Istmica entre los dos continentes se estableció en el temprano Plioceno. Una unidad final (la Norte Americana) son mamíferos que solo recientemente han migrado hacia el sur al través de los trópicos Meso Americanos a norte Sud América. Siguiendo el establecimiento de la Conexión Istmica, 24 familias de mamíferos del sur migraron hacia el norte a Centro América, 12 de estas llegaron a Norte América templada; 19 familias del norte entraron a Sud América, 15 de estas llegaron a zonas templadas de este continente. Hoy ambas faunas, la del norte y la del sur han sido significativamente modificadas por estos incrementos, pero el intercambio ha sido balanceado sin un desproporcionado efecto en cualquier dirección. América Meso Tropical es esencialmente una compleja zona transicional entre elementos del sur y norte. Y no es ahora ni fue en el Cenozoico un centro significativo de evolución de mamíferos. La presente fauna de mamíferos de las Indias Occidentales se deriva casi en su totalidad del norte de Sud América.

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HYDROGRAPHY AND MIDWATER FISHES  
OF THREE CONTIGUOUS OCEANIC AREAS  
OFF SANTA BARBARA, CALIFORNIA

*By* DAIL W. BROWN

CONTRIBUTIONS IN SCIENCE



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# HYDROGRAPHY AND MIDWATER FISHES OF THREE CONTIGUOUS OCEANIC AREAS OFF SANTA BARBARA, CALIFORNIA<sup>1</sup>

By DAIL W. BROWN<sup>2</sup>

**ABSTRACT:** The continental shelf or borderland off southern California is characterized by a complex of basins varying in their depth and nearness to the coast. The biota of these basins are influenced by major water masses that converge and mix over the borderland, subarctic water from the north, central water from the west, and equatorial water from the south. Faunal studies were conducted in two basins and in an area over the continental shelf off Santa Barbara that constitute three contiguous but oceanographically distinct borderland environments. Midwater fish faunas were sampled with a six-foot Isaacs-Kidd midwater trawl during cruises of the General Motors Research Vessel SWAN, 1964-1967. The three areas sampled are separated from each other by an undersea ridge and island chain and are differentially affected by the land and by the prevailing oceanic currents. Intense upwelling occurred in the Santa Cruz and Santa Barbara basins, due to a seasonal redistribution of mass in the complex California Current system off southern California.

The midwater fish fauna of the inshore Santa Barbara Basin was the least diverse but the most abundant of the three. The comparative shallowness of this basin excluded most bathypelagic species. The intermediate-deep Santa Cruz Basin contained a typical bathypelagic fauna, including relatively many southern species. The fish fauna of the Rodriguez Dome area over the continental slope was most diverse, including many exotic central and northern species. The faunas of the two offshore areas resembled each other more than either resembled the fauna of the Santa Barbara Basin. The Santa Barbara Basin is physiographically and hydrographically isolated from the offshore areas and is enriched by coastal runoff from the land. This isolation and enrichment has produced a relatively eutrophic environment, containing a somewhat provincial fish fauna. The Santa Cruz Basin contains a fauna more typical of the greater borderland environment, while the Rodriguez Dome area, which is directly influenced by the California Current, contains a typically oceanic fauna.

## INTRODUCTION

The oceanic environment off the west coast of North America is influenced by the interaction of three major water masses in the eastern north Pacific

### <sup>1</sup>REVIEW COMMITTEE FOR THIS CONTRIBUTION

Alfred W. Ebeling  
Robert J. Lavenberg  
Theodore W. Pietsch

<sup>2</sup>U.S. Department of Commerce, National Oceanic and Atmospheric Administration, Rockville, Maryland 20852.

Ocean. Subarctic water of low salinity moves southward between the west coast of North America and the warmer, more saline central water mass offshore. This subarctic water is formed in high latitudes and is characterized by low salinity, high oxygen, and abundant nutrients. Eastern north Pacific central water occurs to the west and is associated with a clockwise gyre between Hawaii and the coast. This water is warm and has a high salinity (Sverdrup et al., 1942). Equatorial water, formed in the lower latitudes, is warmer, more saline, and denser than the subarctic water. Some of this relatively dense water flows inshore northward along the coast of southern California, usually under the mixed, southward flowing subarctic water. This circulation has been extensively studied by oceanographers associated with the California Cooperative Oceanic Fisheries Investigations (e.g., Reid et al., 1958; Wyllie, 1966).

Brinton (1962) recognized each of these three water masses as primary faunal regions and pointed out that a transitional or secondary faunal region is created off the west coast by their mixing. An area of oceanographic transition constitutes an ecotone of faunal mixing. This mixing has been documented in several zoogeographical studies: e.g., of euphausiids by Brinton (1962, 1967), of deep-sea fishes by Ebeling (1962), of chaetognaths by Alveríño (1965), of copepods by Fleminger (1964), of mesopelagic fishes and euphausiids by Pieper (1967). The transitional water also supports an endemic fauna (e.g., Brinton, 1962).

The California Current is the major eastern boundary current of the north Pacific Ocean. This current transports subarctic water southeastward along the coast of North America. When the California Current turns west at about 10°N to join the north Equatorial Current, the subarctic water has been modified by mixing and by increasing insolation and evaporation. In fact, only a small salinity minimum remains to indicate its origin (Reid et al., 1958).

The intensity of the California Current is greatest during the late spring when the northwesterly winds are strongest off Washington and Oregon. The long shore component of the wind stress and the earth's rotation cause extensive upwelling along the coast. This upwelling brings to the surface pockets of cool, nutrient-rich, and saline water, which mixes with the subarctic water. This upwelled water is derived partly from lower subarctic water and partly from the modified equatorial water of the submerged countercurrent (Reid et al., 1958). During fall and winter, the winds are less intense and shift to the west and southwest. Then, the California Current weakens, upwelling subsides, and the countercurrent develops at the surface between the California Current and the coast.

Point Conception has generally been recognized as a zoogeographical boundary between littoral biotas (Hedgpeth, 1957; Neushul et al., 1967). North of this boundary the subarctic component of the California Current dominates environmental conditions, while to the south and inshore, intrusions of southern water over the continental shelf predominate. This relatively

narrow and basin-pitted continental shelf off southern California was designated continental borderland by Shepard and Emery (1941).

Vertically, the water column may be divided into three zones (Lavenberg and Ebeling, 1967). The lighted epipelagic zone of locally-warmed and wind-mixed surface water extends to some 50-100 m. Between 100 and 500-600 m subarctic water and, to a lesser extent, central water dominate the weakly-lighted mesopelagic zone of rapidly changing temperature with depth. Southern water occupies the aphotic bathypelagic zone. Over the borderland, this zone extends from 500-600 m to the bottom (Emery, 1960). This bathymetric zonation has its biological counterpart. Many mesopelagic fishes are relatively strong-bodied; have well-developed eyes, photophores and swimbladders; are countershaded; and undergo extensive diel vertical migrations. Bathypelagic fishes, on the other hand, are weak swimmers. They have reduced or no eyes, photophores, and/or swimbladders. Most are uniformly brown or black and undergo restricted or no diel migrations (Marshall, 1960).

The objective of the present study was to compare the midwater fish faunas off Santa Barbara relative to the hydrography and physiography (1) of the shallow inshore Santa Barbara Basin between the coast and the Channel Islands some 20 miles offshore, (2) of the intermediatedeep Santa Cruz Basin immediately seaward of these islands, and (3) of the slope area about the Rodriguez Dome seamount to the northwest. The faunas in these three areas

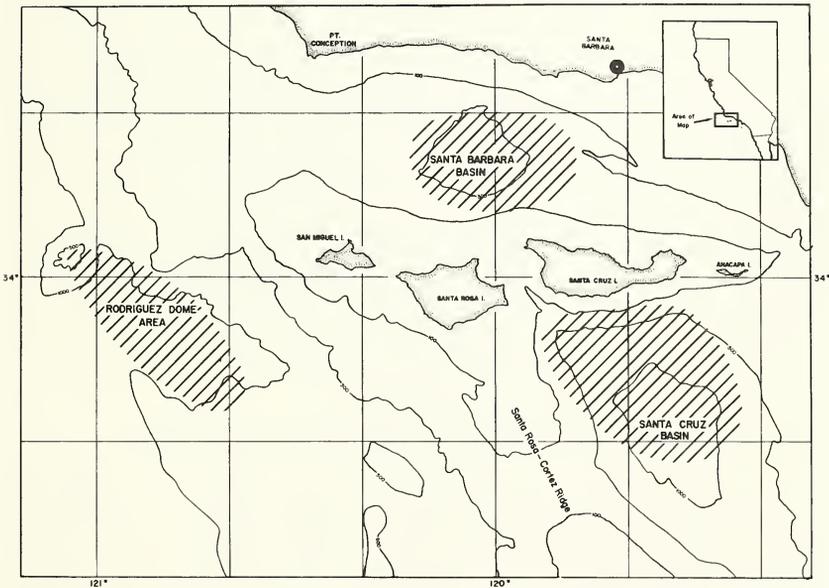


FIGURE 1. Deep water areas of the continental shelf off Santa Barbara, California. The three areas sampled are hatched.

were compared in terms of the abundance, diversity, composition, and distribution of their included species. Abundance reflects the productivity of the environment; diversity indicates its complexity; composition reflects the adaptations of its species; and distributions indicate its heterogeneity in space and time.

The Santa Barbara Basin is a relatively shallow, inshore basin with a maximum depth of 600 m and a still at 475 m opening to the west (Fig. 1). The Santa Cruz Basin has a maximum depth of 2000 m with a still at 1075 m opening on the borderland to the south.

## MATERIALS AND METHODS

### Sampling the midwater environment

To investigate the oceanography and midwater faunas off Santa Barbara, 28 cruises were made aboard the General Motors Research Vessel SWAN by personnel from the University of California at Santa Barbara Marine Laboratory. Only the Santa Barbara and Santa Cruz basins were sampled during the first 13 cruises, beginning in the fall of 1964. In July, 1966, a third area to the southeast of the Rodriguez Dome seamount was added to the study. This area is over the continental slope between the 1000 and 2500 m bottom contours. During the 28 cruises, 204 midwater trawl stations were occupied and 568 separate successful collections were made (Table 1). Less than three per cent of the total number of collections were rejected as unsuccessful because of presumed or actual failures in the trawling and monitoring gear.

Collections were made in a 6-foot Isaacs-Kidd midwater trawl lined with half-inch stretch bait netting and equipped with a special four-chambered discrete depth sampler and with sensors of ambient depth, temperature, light, and water flow through the net opening (Clarke, 1966; Aron et al., 1964; Bercaw, 1966; Bourbeau et al., 1969). The outputs of the sensors were multiplexed up the single-conductor trawl cable to digital and strip recorders on shipboard. The chambers were closed in sequence by reversing the polarity of the depth channel and thereby activating piston solenoids to close the gates between the chambers.

For each collection, trawl depth and water temperature were recorded

TABLE 1  
Summary of trawl activities in each of the three study areas

	<i>Santa Barbara Basin</i>	<i>Santa Cruz Basin</i>	<i>Rodriguez Dome area</i>
Number of collections	210	267	91
Number of cruises	28	25	11
Total effort as km linear flow	520.7	826.8	316.8
Fish volume (ml)	24,675	10,891	3,859
Number of individuals (fish)	13,800	11,415	2,999

from the digital display that accompanied the strip recording. Surface water temperature was measured at each trawl station with a bucket thermometer, and a bathythermograph cast was made with each series of trawls in an area. Bottom depth and the depth of the Deep Scattering Layer were monitored by a Precision Depth Recorder.

Hydrographic casts were made near the centers of each of the three areas during the last 15 cruises, weather permitting (see hatched areas, Fig. 1). Water samples were collected in a vertical series of ten Nansen bottles with reversing thermometers. In the Santa Barbara Basin the bottles were usually placed on the hydrographic wire at 0, 25, 50, 75, 100, 150, 200, 300, 400, and 500 m. In the two offshore areas, the bottles were placed at 0, 30, 60, 100, 200, 350, 500, 650, 800, and 1,000 m. These intervals assured measurements from the three main bathymetric zones; epipelagic, mesopelagic, and bathypelagic.

Oxygen samples were drawn first, preserved within 15 minutes, and analyzed using the Winkler titration method as outlined by Strickland and Parsons (1965). Titration volumes were converted to ml/liter, and percent saturation at *in situ* temperatures and salinities was determined using the tables of Green and Carriet (1967). Salinities were analyzed later with a Hytech Portable Laboratory Salinometer. Temperatures were recorded as the average reading of two observers. Temperature, salinity, and oxygen were contoured as vertical profiles for each month of 1967.

The three major depth zones were sampled. The trawl was set with all gates between the chambers in the open position so that no sample was taken during the lowering. The trawl was lowered to the first sampling depth, the first gate was closed, and a horizontal (discrete) collection was made. The second gate was then closed and an oblique collection was made while the trawl was retrieved to a shallower depth for the second horizontal sample. A fourth, oblique sample was made as the trawl was brought to the surface.

Each trawl haul usually provided four collections, which were sorted into groups of fishes and invertebrates. After measuring the liquid displacement volume of each group, it was preserved separately in 10 percent buffered formalin and later transferred to 55 percent isopropyl alcohol. Only the fish collections were used in the present study. As the fishes were identified to species, the numbers of individuals and their ranges in standard length were recorded for each collection. Individuals of *Stenobranchius leucopsarus*, *Leuroglossus stilbius*, and *Cyclothone acclinidens* were separated into categories of young (individuals shorter than 50, 50, and 25 mm in standard length, respectively) and adult. The number of individuals of each species and displacement volume per collection were standardized by dividing each value by the kilometers of linear effort for that collection, measured as the average distance between ticks on the depth trace recorded on shipboard from the trawl's flow meter. Each tick represented 1000 revolutions of the propeller in the flow meter. Obviously, this linear measurement is proportional to the

volume of water filtered by the trawl net. A total of 28,214 individuals were captured, belonging to 81 species in 39 families (Table 1; Appendix). All station and collection records are on file at the Natural History Museum of Los Angeles County.

#### Faunal analyses

All environmental and collection data were punched on two sets, respectively, of computer cards for sorting and analysis at the Computer Center at UCSB.

There are two main sources of variation among the samples. Variation in the abundances of fishes may represent fluctuations in the actual densities of their populations or merely fluctuations in the sampling effectiveness of the trawl caused by distributional patchiness, net avoidance, escape, and contamination of captures among depth zones (Harrison, 1967).

To estimate sources of variability in subsequent analyses, collections were initially pooled by area. They were then grouped within each area by cruise, and finally considered as individual samples. Initially all samples from an area were treated as one large collection. Cruise collections pool those samples taken in an area during each cruise. (Monthly collections used in the analysis of abundance combine the cruise collections taken during the same months over the several years of the study.) Within each area, the collections were also analyzed individually. In this way, for example, vertical and seasonal variation could be estimated.

The standardized fish displacement volumes were used as the index of faunal abundance.

Several types of observations were used to describe faunal diversity: the number of species in a collection; the number of dominant species; the number of frequently captured species; and a probability index of diversity. The species contributing the greatest number of individuals to a collection was considered to dominate that collection. In each area, the number of collections dominated by a particular species and the number of collections in which the species was present were both expressed as percentages of the total number of collections made in the area. The diversity index was computed both for each individual collection and for the pooled collections constituting each cruise collection: Simpson's diversity index as modified by McGowan and Fraundorf (1966).

$$d = 1 - \left[ \frac{\sum n(n-1)}{N(N-1)} \right]$$

where:  $n$  = no. individuals of each species

$N$  = total individuals of all species in each collection

The index "d" gives the probability that any two individuals selected randomly and independently from a sample will *not* be of the same species.

The faunal composition was contrasted among the areas by considering

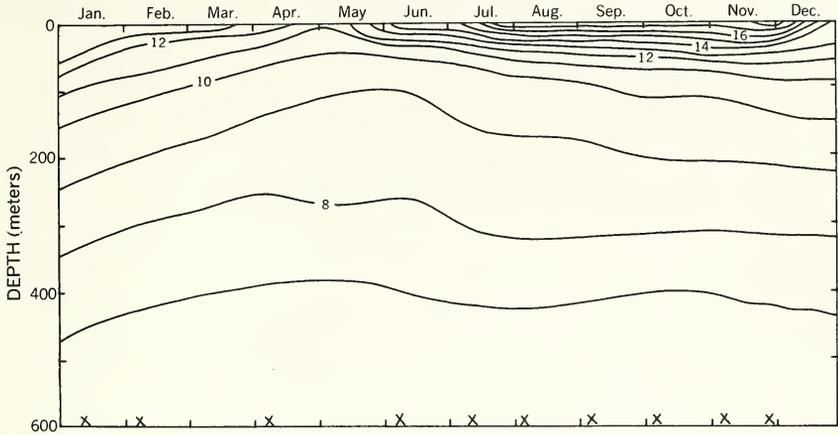


FIGURE 2. Seasonal profile of temperature in the upper 500 m for the Santa Barbara Basin during 1967. The contour interval of isotherms is  $1^{\circ}\text{C}$ .

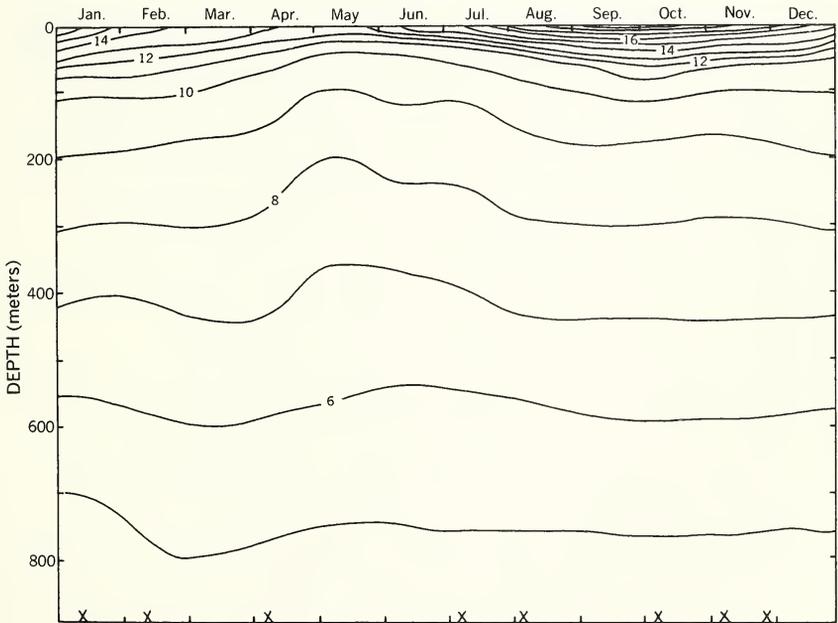


FIGURE 3. Seasonal profile of temperature in the upper 900 m for the Santa Cruz Basin during 1967. Contour interval,  $1^{\circ}\text{C}$ .

the particular species that dominated the collections or that were frequently captured.

To analyze the vertical distribution of either the total displacement volumes of all fishes or numerical density of a particular species, samples were integrated over arbitrary bathymetric intervals. First, the water column from the surface to 1000 m was treated as comprising 50, 20 m intervals. A computer program was written that distributed equal proportions of the total displacement volume or of the number of individuals captured of a particular species among the intervals transgressed by the trawl. The values for each interval were then summed over all collections within each area. The total kilometers of effort for each depth interval were determined in a similar way. The total displacement volume or frequency of a species within each interval was then standardized by dividing either of these two values by the effort expended within that interval.

## RESULTS

### Hydrography

*Temperature, salinity, oxygen.* In the Santa Barbara Basin, the coldest surface water was measured during May when the 11° isotherm reached the

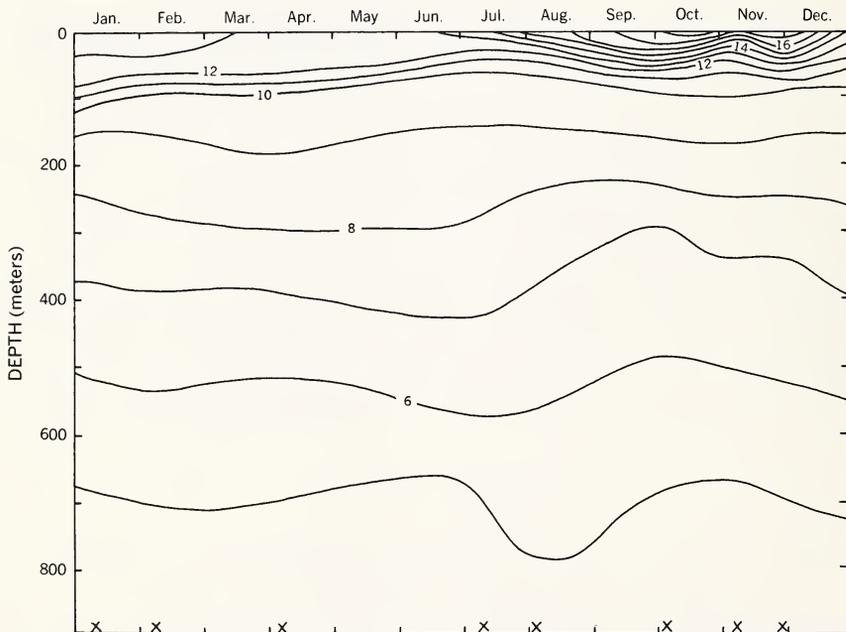


FIGURE 4. Seasonal profile of temperature in the upper 900 m for the Rodriguez Dome area during 1967. Contour interval, 1°C.

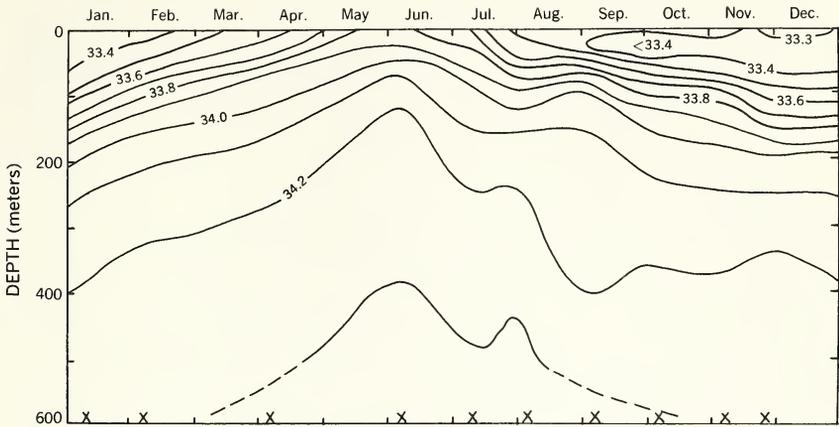


FIGURE 5. Seasonal profile of salinity in the upper 500 m for the Santa Barbara Basin during 1967. Contour interval, 0.1‰.

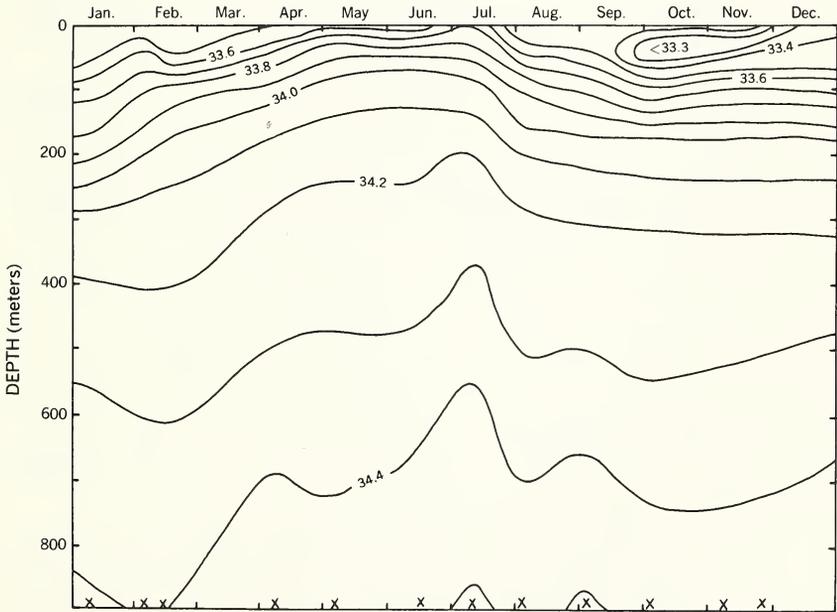


FIGURE 6. Seasonal profile of salinity in the upper 900 m for the Santa Cruz Basin during 1967. Contour interval, 0.1‰.

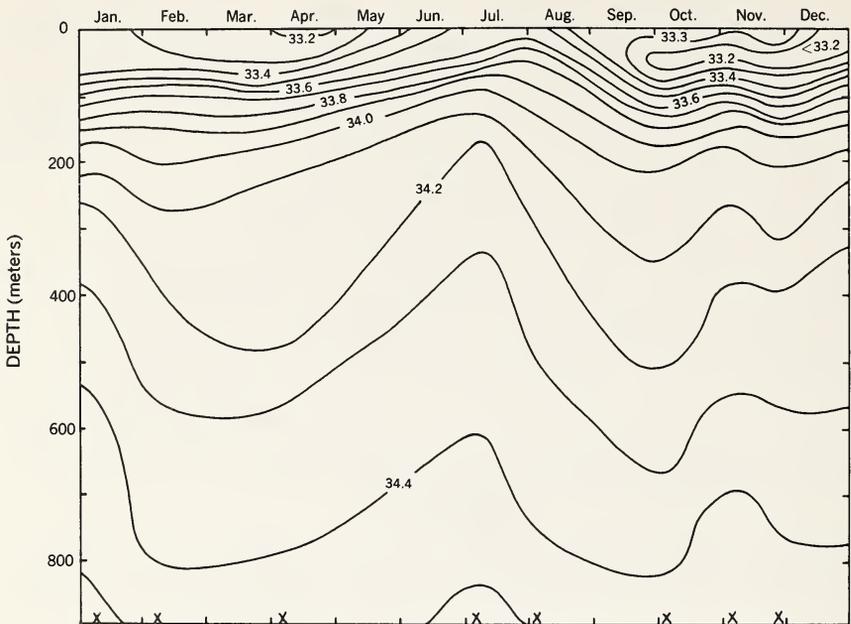


FIGURE 7. Seasonal profile of salinity in the upper 900 m for the Rodriguez Dome area during 1967. Contour interval, 0.1‰

surface (Fig. 2). Below 75 m, coldest water was recorded in June. Surface warming continued from June until December. The resulting thermal stratification preceded surface mixing from January to March, when the seasonal thermocline disappeared. In the Santa Cruz Basin (Fig. 3), the coldest surface water was also measured during May when the  $12^{\circ}$  isotherm approached the surface. Since no hydrographic observations were made during May and June at Rodriguez (Fig. 4), it is possible that measurements here did not include those of the coldest surface waters. Contours of average monthly temperatures presented by Reid (1965) for an area south of Point Arguello showed the coldest surface temperatures in April ( $12^{\circ}$ ). Below 30 m, the coldest water was recorded from May to July. Between 100 and 300 m the isotherms fluctuated much less at Rodriguez than in the other two areas. For example, in the Santa Barbara Basin the  $9^{\circ}$  isotherm was displaced 130 m, from 230 m in January to 100 m in June. At Rodriguez, the vertical displacement of this isotherm was only 60 m.

In the Santa Barbara Basin, maximum surface salinities were observed in June ( $33.8^{\circ}/00$ ), when minimum temperatures were recorded between 100-300 m (Fig. 5). No water samples were taken during May. The isohalines gradually deepened from June until January. In the Santa Cruz Basin, the maximum surface salinity was  $37.7^{\circ}/00$ , recorded in July (Fig. 6). At

Rodriguez, the isohalines below 200 m approached the surface in both July and January (Fig. 7). Maximum surface salinities just exceeding  $33.6^{\circ}/00$  were recorded in July and August.

With minor exceptions, seasonal fluctuations of the contours showing the percent saturation of dissolved oxygen generally coincided with changes in salinity in all three areas (Figs. 8-10).

*Upwelling.* The contours of salinity, temperature, and oxygen suggest the occurrence of three hydrographic periods analogous with those of Monterey Bay (Barham, 1957): May through July, the "upwelling" period; August through December, the period of stratification; and January through April, the period of surface mixing.

The upward slope of the temperature, salinity, and oxygen isopleths indicated intensive upwelling in the Santa Cruz and Santa Barbara basins during the late spring. Mr. Joseph L. Reid, Jr. (personal communication) suggested that this upwelling occurs when a geostrophic low moves toward the coast during this period. This low, which characterizes the hydrography off southern California, constitutes the center of a counterclockwise gyre associated with the borderland. In general, geostrophic lows are identified by surface anomalies expressing central cores of dense water surrounded by less dense water. The redistribution of mass occurs when water moves from the center to the periphery of the gyre. Upwelling is replacement in the central core. Therefore, the movement of the core itself into the study areas causes the observed vertical displacement of isopleths.

At Rodriguez during this period, there occurred little deflection of isotherms, although salinity increased. Mr. Reid suggested that continuously

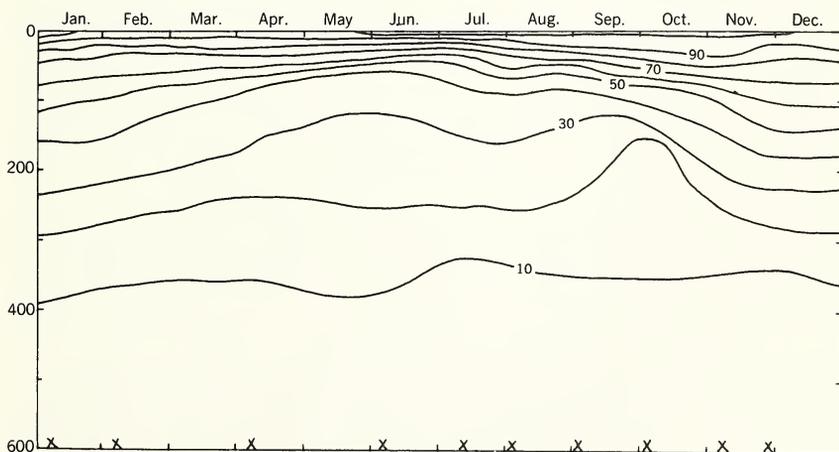


FIGURE 8. Seasonal profile of oxygen concentration percentage in the upper 500 m for the Santa Barbara Basin during 1967. Contour interval, 10% saturation.

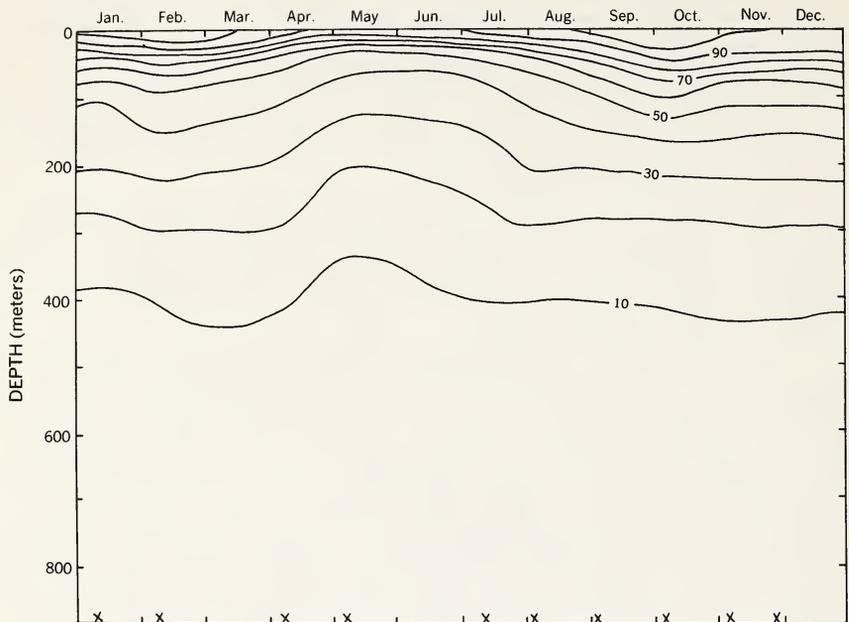


FIGURE 9. Seasonal profile of oxygen concentration percentage in the upper 900 m for the Santa Cruz Basin during 1967. Contour interval, 10% saturation.

warm, more saline central water follows the inshore movement of the hydrographic low.

The southward-flowing California Current is deflected offshore at Point Conception. Emery (1960) pointed out that as the California Current passes Point Conception, it entrains or "pulls with it" a large body of surface water lying over the borderland. The seaward edge of the northern borderland is delimited by the Santa Rosa-Cortez Ridge, which generally rises above 200 m. Obviously, this entrainment of borderland water by the California Current can only occur above this depth in this region.

Emery (1960) showed that the volume of water at 300 m flowing northward past San Diego greatly exceeds that which could possibly escape through the few depressions in the Santa Rosa-Cortez Ridge. This water rises in Santa Cruz Basin to replace the surface waters entrained by the California Current.

The apposition of the California Current and the deeper countercurrent together with the above mentioned entrainment causes a redistribution of mass resulting in the creation of a semi-permanent gyre off southern California between Point Conception and northern Baja California (Reid et al., 1958). Usually centered in the vicinity of the Santa Rosa-Cortez Ridge, this gyre comprises water typical of the upwelled water—high in salinity and inorganic nutrients and low in temperature and oxygen (Emery, 1960).

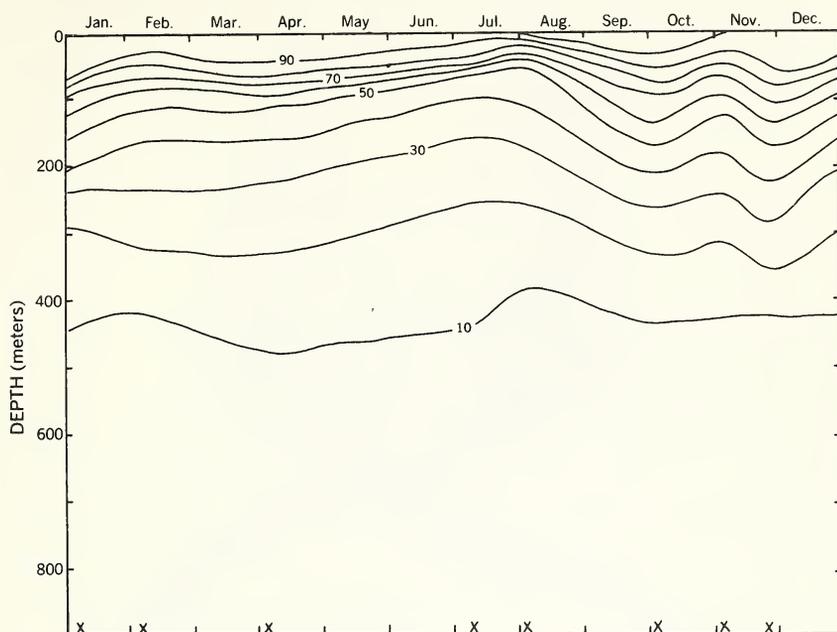


FIGURE 10. Seasonal profile of oxygen concentration percentage in the upper 900 m for the Rodriguez Dome area during 1967. Contour interval, 10% saturation.

These concepts are mutually compatible in that entrainment as conceived by Emery is simply the outward peripheral flow from the geotrophic low as conceived by Reid. Furthermore, the upwelled water replacing that in the center of the low most logically comes from a deep source to the south.

Curves of temperature plotted against salinity substantiate these conclusions. Water mass envelopes were defined for each of the three oceanographic periods by families of these T-S curves (Figs. 11-13). These were compared with T-S relationships from Tibby (1941) which define 30% and 50% equatorial water. Envelopes for all three areas show an increase in a southern component during the upwelling period. In the Santa Barbara and Santa Cruz basins, this probably indicates an influx of deep water from the south. In the Rodriguez area, however, this salinity maximum may indicate an influx of central water as well.

#### Faunal comparisons

*Abundance.* The Santa Barbara Basin was the richest area sampled, in terms of fish biomass measured by the standardized displacement volumes. The volumes here were three to four times as large as those from the two offshore areas (Table 2; Figs. 14, 15). Collections from the Santa Barbara Basin were also the most variable, including the most highly successful and empty collec-

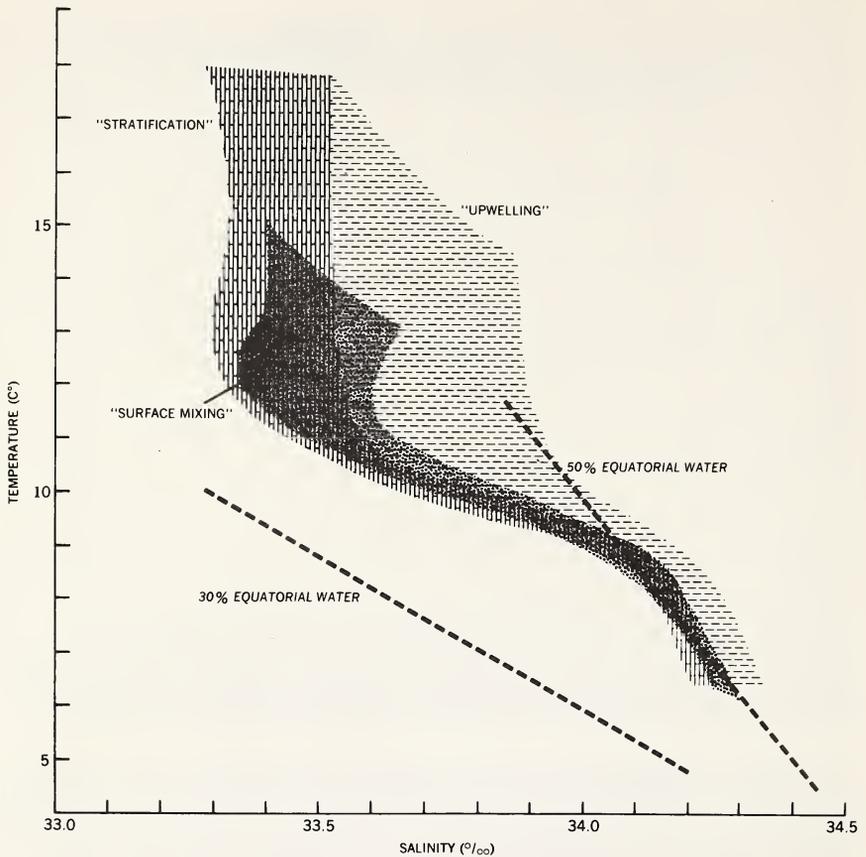


FIGURE 11. Water mass envelopes for three seasonal periods defined by temperature-salinity (T-S) curves for the Santa Barbara Basin: May-June, upwelling period; August-December, stratification period; January-April, period of surface mixing.

tions. They contained the greatest abundance of fish at all depths sampled, although an abundance minimum between 100 and 120 m may separate diel concentrations near the surface at night and at depth during the day (Fig. 14). Seasonally, the collections indicated two periods of maximum abundance in July and November (Fig. 15). The single maximum for the Rodriguez Dome area coincided with the July maximum, while that for the Santa Cruz Basin was one month later than the November maximum.

*Diversity.* The total number of species captured in each area indicated that the two offshore areas contained a considerably more diverse fish fauna than the Santa Barbara Basin (Table 3; Fig. 16). When the individual collections were pooled by cruise, the increase in the average number of species from Santa Barbara to Rodriguez was accentuated. These averages, but not the total

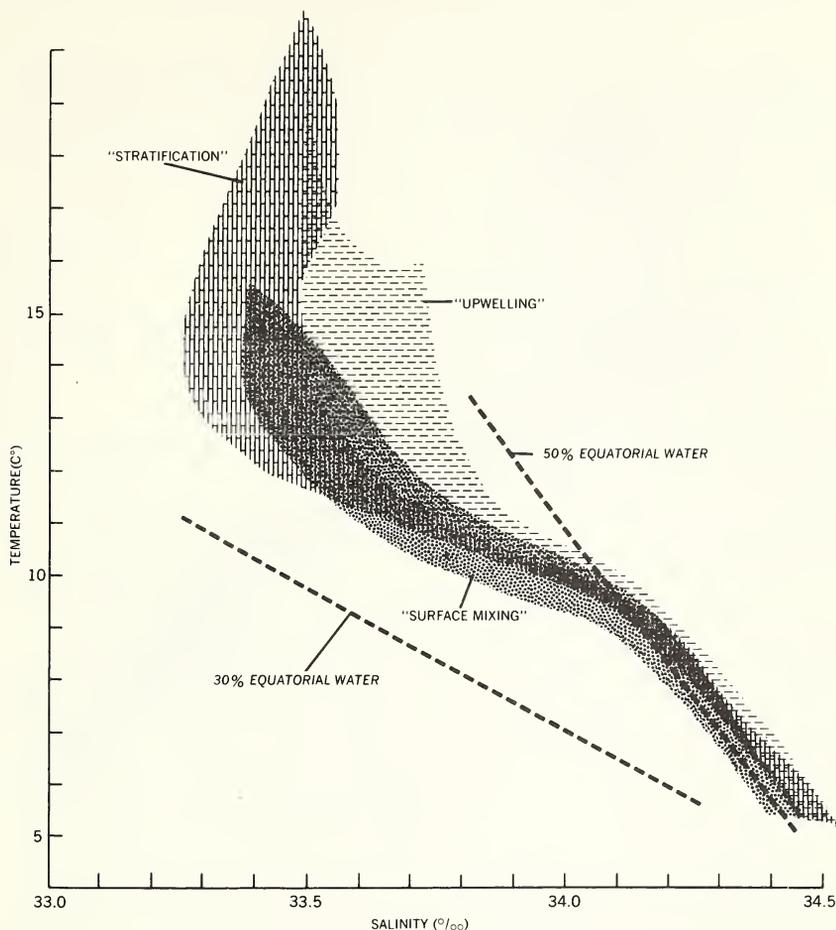


FIGURE 12. Water mass envelopes for three seasonal periods defined by temperature-salinity (T-S) curves for the Santa Cruz Basin (see Fig. 11).

species taken, indicated that Santa Cruz is intermediate in species number. That a greater total number of species was captured in Santa Cruz is probably due to the greater number of collections taken in that area. This would increase the probability of capturing rare species. Also, the relatively steep slope for Rodriguez of a regression of the cumulative total of species captured on the cumulative number of cruises shows that further cruises would undoubtedly take additional species (Fig. 16).

The index of diversity, capture frequency, and dominance hierarchy of species also indicated increased diversity offshore. The diversity index averaged among collections increased from 0.46 for the Santa Barbara Basin, through

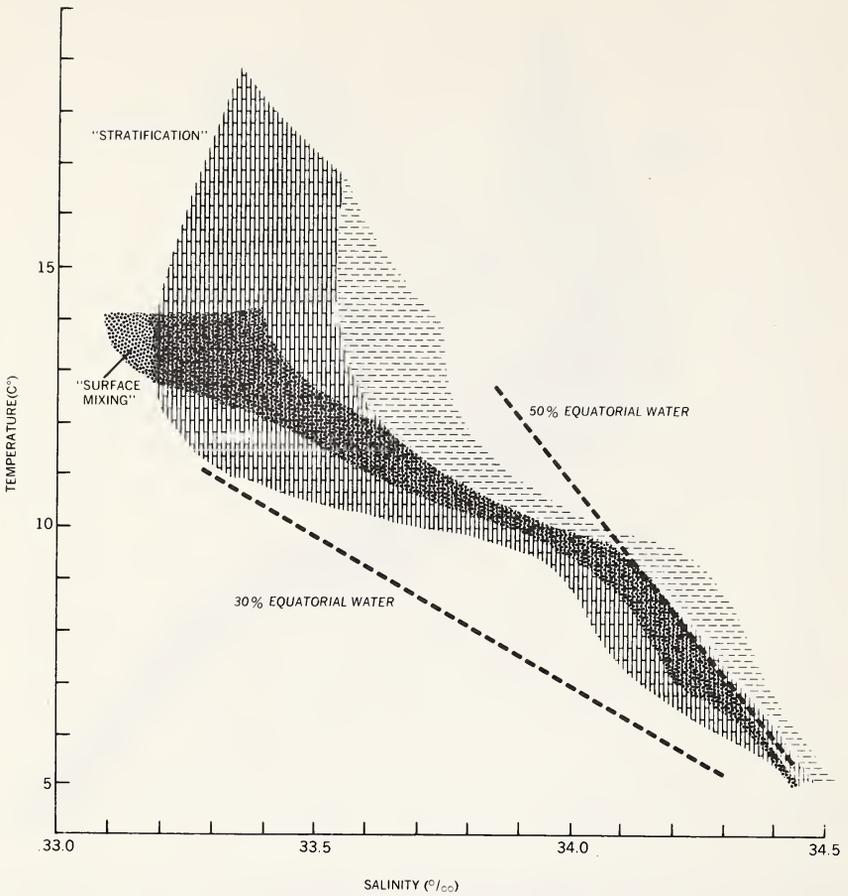


FIGURE 13. Water mass envelopes for three seasonal periods defined by temperature-salinity (T-S) curves for the Rodriguez Dome area (see Fig. 11).

0.58 for the Santa Cruz Basin, to 0.66 for the Rodriguez Dome area. Similarly, the cruise average (pooled among collections) increased from 0.53, through 0.74, to 0.82, respectively. The average collection diversity indices as well as the average numbers of species differed significantly among all three areas ( $p < .01$ ). Furthermore, 12, 19, and 36 species were captured in at least 50% of the collections from Santa Barbara, Santa Cruz and Rodriguez, respectively, while 9, 12, and 21 species were captured during at least 50% of the cruises. Species-abundance curves indicated that relatively few species dominated the Santa Barbara collections, while several species dominated the offshore collections; i.e., the offshore areas showed the more even distributions of species abundance (Fig. 17). In addition, the number of species that constituted 90%

TABLE 2

Displacement volumes of midwater fishes from the three study areas. For each area, the total volumes over all collections are divided by the total trawling effort expended, the volumes per cruise are divided by effort per cruise, and the volumes per each collection are divided by the effort per each collection and averaged over all collections

	<i>Santa Barbara</i>	<i>Santa Cruz</i>	<i>Rodriguez Dome</i>
Total volume standardized by total effort	47.39	13.17	12.18
Cruise average	55.42	14.19	17.56
Collection average	57.46	14.82	17.75

of the individuals in each of the three areas was 3, 7, and 15, respectively (Table 4).

*Composition.* The faunal overlap between the two offshore areas was much greater than that of either area with the Santa Barbara Basin. Some 39% of 81 species occurred in all three areas, while 61% occurred in the Santa Cruz and Rodriguez areas only.

The seven most abundant species comprised more than 90% of the individuals in the Santa Barbara and Santa Cruz basins, but only 78% in the Rodriguez Dome area (Table 4). Only two species, the deepsea smelt *Leuroglossus siilbius* and lanternfish *Stenobranchius leucopsarus* made up over 90% of the captures in the Santa Barbara Basin. In the Santa Cruz Basin, however, they, along with the bristlemouth *Cyclothone signata* and lanternfish *Triphoturus mexicanus*, made up about equal proportions of the total fish catch: 11–17% of the total number of individuals captured, taken in 58–69% of the collections. The bathypelagic bristlemouth *Cyclothone acclinidens* was the most abundant and most frequently captured species at Santa Cruz. Two other lanternfishes, *Diaphus theta* and *Lampanyctus ritteri*, were taken less frequently in smaller numbers.

The seven species mentioned above also dominated the Rodriguez fauna, but in a different order. *Cyclothone signata* was the most abundant species

TABLE 3

Total number of species captured among all areas and average number of species captured during each cruise and for each collection

	<i>Santa Barbara Basin</i>	<i>Santa Cruz Basin</i>	<i>Rodriguez Dome Area</i>
Total number of species captured	44	67	57
Cruise average	9.92	17.83	24.27
Collection average	3.49	5.66	7.20

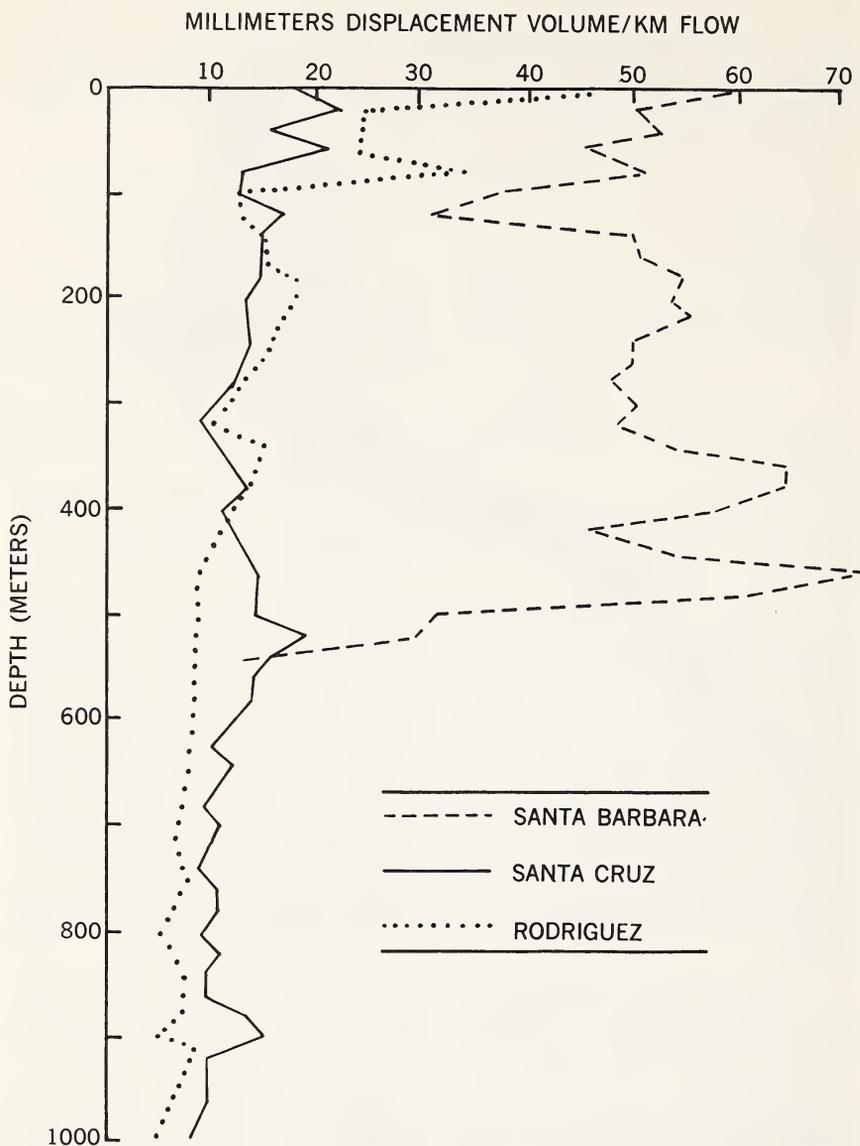


FIGURE 14. Vertical profiles of fish abundance (millimeters displacement volume) for each of the three study areas. Values plotted were computer generated by integrating the displacement volumes over 20 meter depth intervals for the upper 1000 m (see text). The profile for the Santa Barbara Basin is, of course, restricted vertically in this shallow basin.

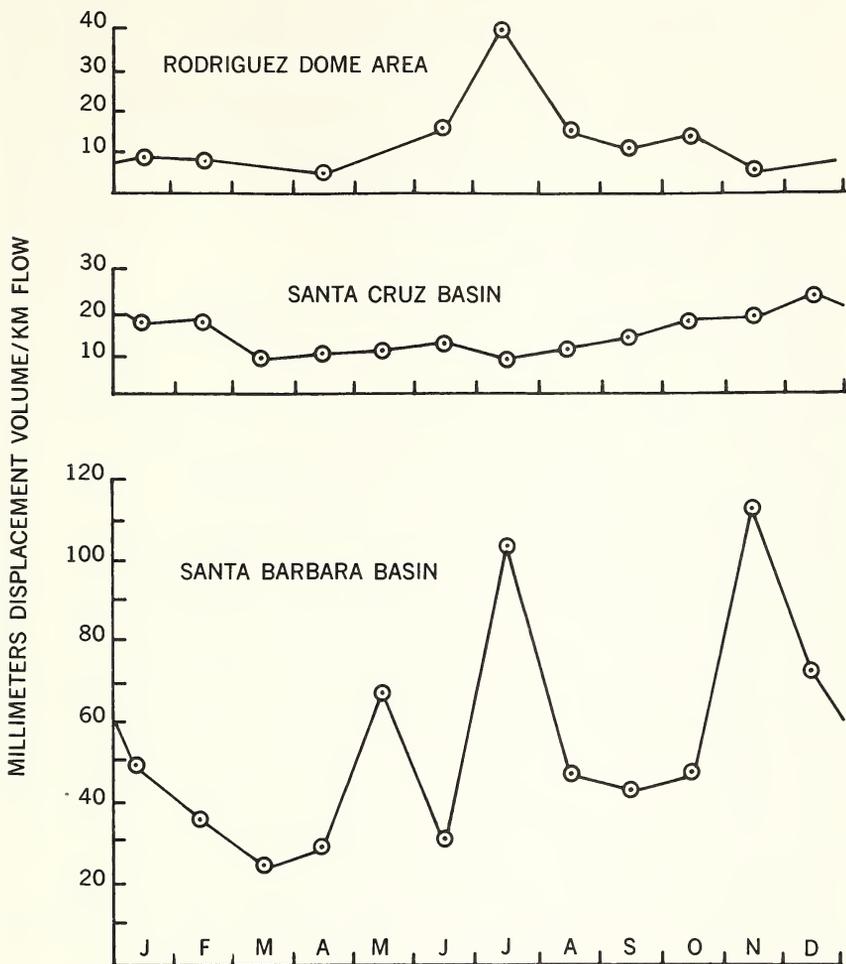


FIGURE 15. Seasonal distribution of fish displacement volumes for the three study areas. Values plotted are the average of the collections pooled by "cruise" for each month in each of the three study areas.

(28%). Next in order, *C. acclinidens* and *S. leucopsarus* comprised 19 and 15% of the total captures, respectively. The other four species comprised much smaller proportions.

Unique and rare species are often quite important in determining faunal intrusions. For example, the distributional center of the alepocephalid *Pel-lisolus facilis*, taken only in Santa Cruz during the present study, is probably equatorial (Berry and Perkins, 1966). The deep-sea anglerfish *Oneirodes acanthias* and the spookfish *Dolichopteryx longipes* are two other southern

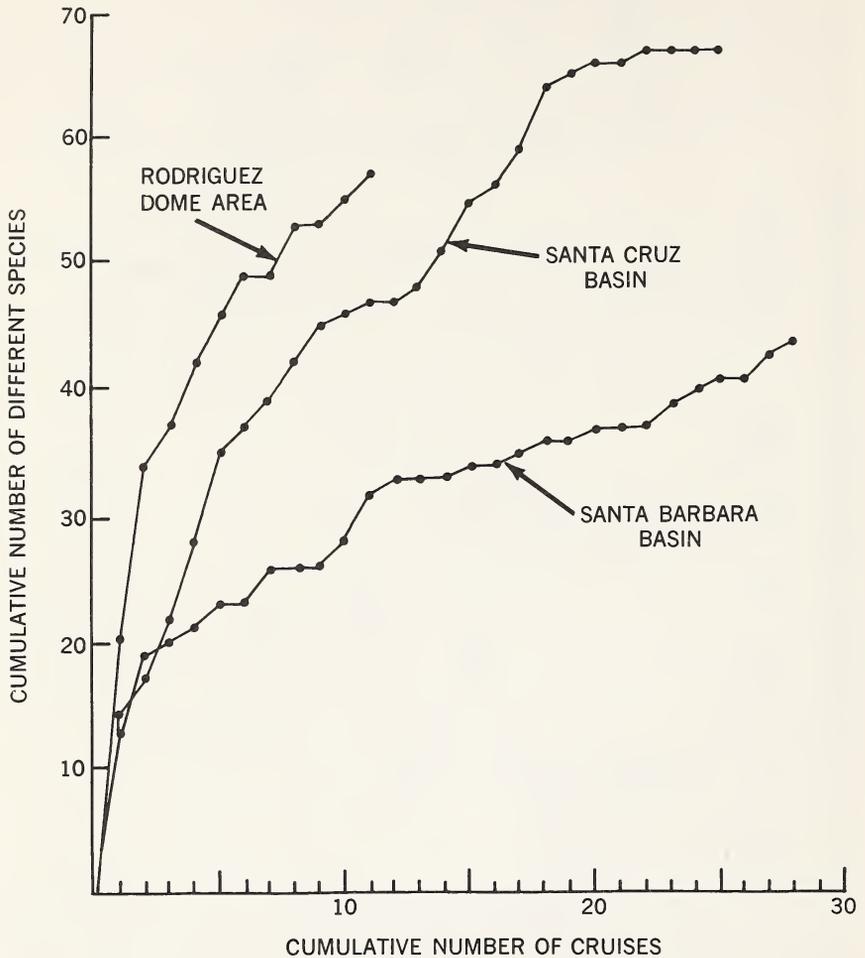


FIGURE 16. Cumulative number of different species plotted against the cumulative number of cruises for each of the three study areas.

species rarely captured as far north over the borderland as the Santa Cruz Basin. However, both species seaward of the borderland are known to occur further north. The stomiatoid *Tactostoma macrops*, three specimens of which were taken at Rodriguez, was among the four most abundant midwater fishes that Percy (1964) reported from off the Oregon coast. *Bathylagus ochotensis*, *Icichthys lockingtoni* and *Macropinna microstoma* are three other northern species occasionally taken at Rodriguez. Among the species taken in but one

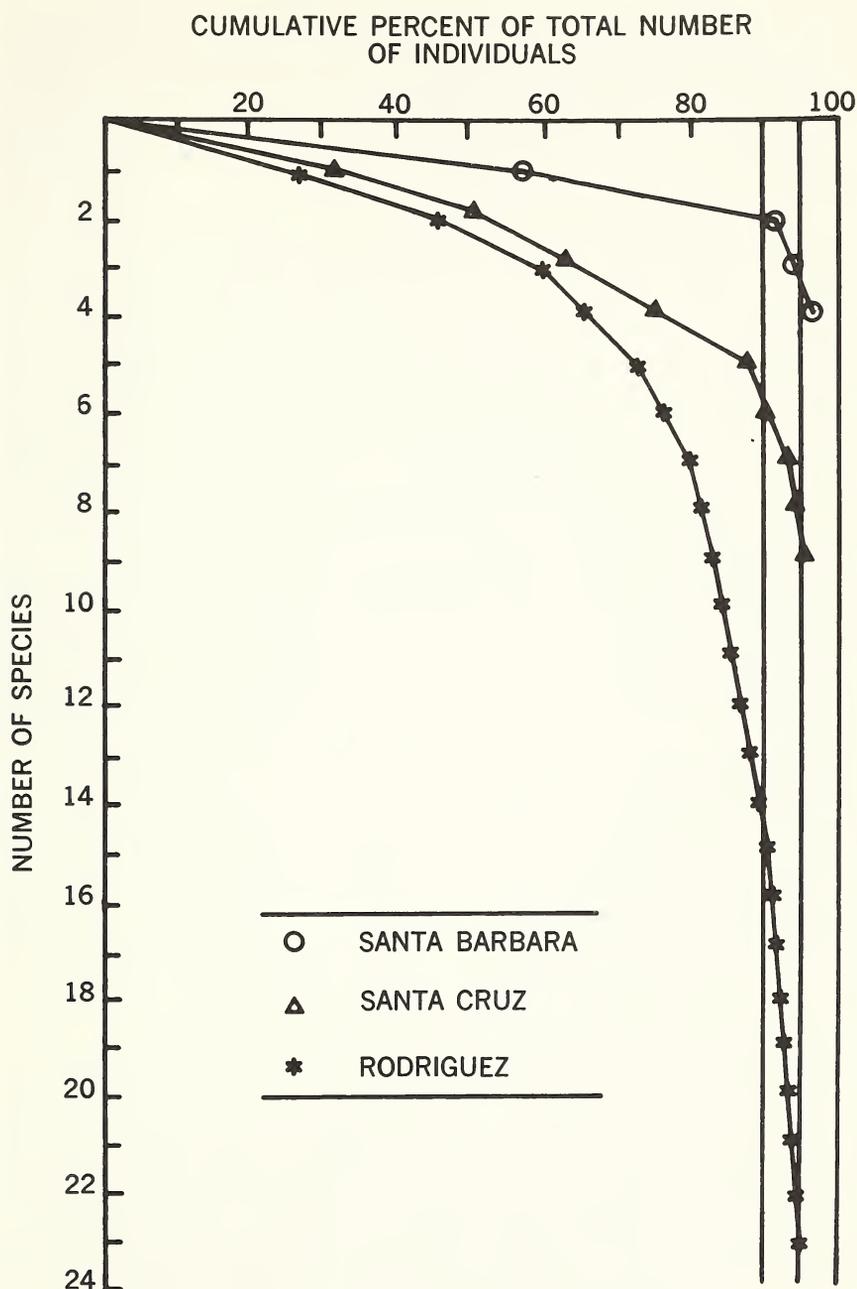


FIGURE 17. Number of species accounting for 95% of the individuals, ranked in descending abundance and plotted as the cumulative percent of total abundance from each of the three study areas.

TABLE 4

Capture frequencies of species that comprised 90% of the individuals or that were captured in more than 50% of the collections

	<i>Santa Barbara Basin</i>				<i>Santa Cruz Basin</i>				<i>Rodriguez Dome area</i>			
	Rank in terms of total abundance	% total no. of individuals	% collection in which captured	% cruises during which captured	Rank in order of total abundance	% total no. of individuals	% collections in which captured	% cruises during which captured	Rank in terms of total abundance	% total no. of individuals	% collections in which captured	% cruises during which captured
<i>Leuroglossus stilbius</i>	1	58	81	100	3	16	62	100	9	2	31	91
<i>Stenobranchius leucopsarus</i>	2	33	71	100	5	11	64	100	3	15	74	100
<i>Cyclothone signata</i>	3	4	50	100	4	15	69	100	1	28	85	100
<i>Cyclothone acclinidens</i>					1	27	73	92	2	19	88	82
<i>Triphoturus mexicanus</i>					2	17	58	100	8	2	31	82
<i>Diaphus theta</i>					6	4	30	96	5	6	31	91
<i>Lampanyctus ritteri</i>					7	2	34	92	4	6	43	100
<i>Sebastes</i> sp.									6	3	20	82
Larval myctophids									7	2	17	45
<i>Protomyctophum crockeri</i>									10	2	21	82
<i>Bathylagus wesethi</i>									11	2	23	82
<i>Argyropelecus lychnus</i>									12	1	25	73
<i>A. sladeni</i>												
<i>Argyropelecus pacificus</i>									13	1	21	82
<i>Tarletonbeania crenularis</i>									14	1	23	100
<i>Danaphos oculatus</i>									15	1	19	73

of the three areas, only the cat shark *Parmaturus xaniurus* of the Santa Barbara Basin was captured in any abundance.

Several other important differences were the absence of melamphoids in the Santa Barbara Basin, the relative abundance of hatchetfishes in the offshore areas, and the regularity of captures of the lanternfish *Tarletonbeania crenularis* at Rodriguez. Melamphoids are characteristically bathypelagic fishes (Ebeling, 1962). Ebeling et al. (1970) suggested that the hatchetfishes taken in low numbers off California are waifs on the periphery of their tropical distributional centers. Obviously, therefore, their occurrences will increase seaward toward their main ranges. *Tarletonbeania crenularis* is quite abundant

in Monterey Bay to the north of Point Conception (Barham, 1957) and off Oregon (Pearcy, 1964). The zoarcid *Melanostigma pammelas* was frequently captured in the Santa Barbara and Santa Cruz basins, but was rare at Rodriguez. It is probably derived from more generalized eelpouts adapted to a benthonic habit on the continental shelf. This may account for its abundance in the borderland basins, which are obviously influenced by benthonic and near shore processes.

*Distribution.* Among the seven most abundant species, *Leuroglossus stilbius* was about four times more numerous in the Santa Barbara Basin (ca. 20 individuals per km flow effort) than in the Santa Cruz Basin (ca. 5 ind./km flow). In the Santa Barbara Basin it was most abundant between 150-450 m, with a maximum at about 380 m. In the Santa Cruz Basin, it was most abundant between 350-650 m, maximally at 520 m. The several major and minor maxima in the Santa Barbara Basin may represent different age classes and/or diel fluctuations in abundance (Clarke, 1966). Although about equal numbers of young and adult individuals were captured in Santa Barbara, over 70% of the captures were of young individuals in Santa Cruz. Perhaps *L. stilbius* breeds to a greater extent in the offshore areas, then enters the rich Santa Barbara Basin as adults. Young also outnumbered adults at Rodriguez, although all stages were relatively rare there. It has usually been considered as a southern transitional species (Lavenberg and Ebeling, 1967). Barham (1957) and Pearcy (1964) did not record it from Monterey Bay or from off Oregon, respectively. Berry and Perkins (1966) depicted its distributional center over the borderland, to the south of Point Conception.

The second most abundant species, *Stenobranchius leucopsarus*, was also about four times more abundant in the Santa Barbara Basin (ca. 12 ind./km flow) than in the offshore areas (ca. 3 ind./km flow). An abundance minimum at 120 m in Santa Barbara may separate diel maxima and/or age classes. Separate analysis of young and adults, however, revealed similar inflections, which probably distinguish diel concentrations at different depths: shallow at night, deep during the day. Paxton (1967) reported concentrations at 500-700 m during the day and at 100-400 m at night in the San Pedro Basin to the south. At Rodriguez, in contrast, it was always concentrated above 400 m. At Santa Cruz it occurred somewhat deeper, while it was concentrated at only about 250 m in Santa Barbara. Fast (1960) reported a diurnal concentration of adults between 300-500 m, the larvae being restricted to the upper 100 m. The young of *S. leucopsarus*, defined as specimens shorter than 50 mm standard length, comprised approximately 45, 50, and 64% of all individuals of this lanternfish captured in Santa Barbara, Santa Cruz, and Rodriguez, respectively. Like those of *Leuroglossus stilbius*, the young were most abundant offshore. Rodriguez provided the greatest number of unidentifiable larval lanternfishes; Santa Barbara the least. *Stenobranchius leucopsarus* comprised 45% of the individuals reported off Oregon by Pearcy (1964). Aron (1959) noted its abundance in the Gulf of Alaska.

The tiny, light-colored bristlemouth *Cyclothone signata* was captured during every cruise in each of the three areas. At Rodriguez, it was concentrated between 300-500 m (ca. 11 ind./km flow). Similar concentrations were less well defined in the other two areas (ca. 3 ind./km flow at Santa Cruz, ca. one ind./km flow at Santa Barbara). It was always least abundant in the Santa Barbara Basin. Aughtry (1953) described a similar vertical distribution for it in Monterey Bay.

The somewhat larger, black species *Cyclothone acclinidens* was most abundant in the Santa Cruz Basin, with a maximum of ca. 15 ind./km flow at 700-900 m, compared with a maximum of ca. 5 ind./km flow at Rodriguez. The relatively deep bathymetric restriction of this bathypelagic bristlemouth apparently precludes its establishment in the Santa Barbara Basin, even though young and halfgrown individuals were occasionally captured there. The Santa Cruz Basin may serve to concentrate the breeding population. Water flowing into the borderland at depth from the south is funneled between the Santa Rosa-Cortez Ridge and the coast into the Santa Cruz Basin. In the process, bathypelagic and lower mesopelagic species may be concentrated at depth in Santa Cruz as the water finally rises and passes over the northward extension of this ridge. Resident breeding populations would be restrained by the relatively shallow ridge and island chain to the north and west.

The lanternfish *Triphoturus mexicanus* was captured during every cruise in the Santa Cruz Basin, where it was almost 10 times more abundant (ca. 5 ind./km flow at two maxima) than at Rodriguez (ca. 0.5 ind./km flow). Concentrations marked by sharp abundance maxima near the surface and at 500 m indicated that it ascends as relatively dense shoals toward the surface at night. It was seldom captured in the Santa Barbara Basin. It has a southern distribution; very few captures have been noted north of Point Conception.

*Diaphus theta* was equally abundant in Rodriguez and Santa Cruz (ca. 2.5 ind./km flow at maxima), although its vertical distributions appeared to be quite different between the two areas. It had a relatively shallow distribution in the Santa Cruz Basin at all times, with a distinct abundance maximum between 0-100 m and a lesser maximum at about 200 m (ca. 1.0 ind./km flow). At Rodriguez the order was reversed, with a lesser shallow maximum between 0-250 m (1.5 ind./km flow) and a distinct greater maximum at about 400 m (2.5 ind./km flow). Paxton (1967) concluded that it ascends from 400-600 m into the upper 50 m at night. Although such extensive vertical migrations were suggested by the observed bimodal vertical distribution at Rodriguez, the general pattern was obscure. This somewhat confused diel pattern of movement may reflect what has been called the dynamic nature of the species (Barham, 1957). It may randomly move into and out of the area. Like *Triphoturus mexicanus*, this offshore lanternfish was seldom captured in the Santa Barbara Channel. It has an antitropical distribution, being confined to transitional waters between 25-55°N in the Northern Hemisphere and between equivalent latitudes in the Southern Hemisphere (Bussing, 1965). It comprised 21% of

all individuals captured off Oregon during a similar trawling study (Pearcy, 1964).

*Lampanyctus ritteri* was most abundant at Rodriguez, where it was captured at a rate of ca. 2.5-4.0 ind./km flow, as compared with ca. 1.0 ind./km flow in Santa Cruz at a near-surface maximum. Like the other offshore lanternfishes, it was rarely captured in the Santa Barbara Basin. It appears to be confined to the upper 400-500 m and has a lesser abundance maximum between 100-300 m (ca. 1.5 ind./km flow) in Rodriguez. Berry and Perkins (1966) depicted this species as ranging from Baja California, Mexico to San Francisco, California. Aron (1959) reported captures from the Gulf of Alaska. It may have its distributional center offshore in the transitional water bordering the tropical central region to the west (Pieper, 1967).

#### DISCUSSION

The Santa Barbara Basin contains a relatively large standing crop of fishes composed of relatively few species. Both offshore areas contain more characteristically oceanic species and a noticeably smaller standing crop. Because the offshore areas are deeper, they support a typical bathypelagic fauna, which cannot invade the relatively shallow Santa Barbara Basin. Brown (1969) showed that more factors, which defined groups of associated species and environmental measures, were needed to describe adequately the offshore faunal assemblages of fishes than to describe the simpler assemblage in the Santa Barbara Basin. Also, in an analysis of both fishes and invertebrates, Ebeling et al. (1971) showed that more "transitory groups" of animals and resident communities were represented in the Santa Cruz Basin than in the Santa Barbara Basin. Both studies showed that fish volumes were invariably correlated with increasing abundances of animals characteristic of the inshore Santa Barbara Basin.

Thus, there is an offshore increase in faunal diversity with contributions from more exotic species. Similarly, Ebeling et al. (1970) showed that the intermediate-deep Santa Catalina Basin to the south has a more diverse and typical oceanic fauna than the shallow inshore San Pedro Basin, which occupies a position analogous to that of the Santa Barbara Basin. Although in the present study the faunas of the two offshore areas resemble each other more than either resembles that of the Santa Barbara Basin, collections from the Rodriguez Dome area did average slightly more species in less abundance than did those from the Santa Cruz Basin. This basin is the northern terminus of a chain of basins progressively filled by deep water flowing up from the south. Therefore, it recruits deep water species from the south more readily than those from the oceanic realm to the west. Central and northern species have more direct access to Rodriguez.

Subsequent collections not included here substantiate the faunal trends discussed above (Brown, 1969). A series of collections taken during Novem-

ber, 1967, generally show the offshore trend in abundance and diversity. Of the 44 collections in this series, 32 were from the offshore areas and 12 were from the Santa Barbara Basin. The cumulative frequencies of displacement volumes and diversities for the test fish collections from inshore and offshore areas were calculated and plotted against the expected frequencies obtained from graphs of cumulative frequency vs all previous collections. The distributions of abundance and diversity based on the 44 test collections, in fact, generally coincided with the distributions based on all the rest. And, as in all previous collections, the 12 inshore test collections were dominated by the deep-sea smelt *Leuroglossus stilbius* and the lantern fish *Stenobranchius leucopsarus*, while the 32 offshore collections were dominated by the bathypelagic bristlemouth *Cyclothone acclinidens*, mesopelagic *C. signata*, or the southern lanternfish *Triphoturus mexicanus*.

Multivariate statistical analyses by Brown (1969) and by Ebeling et al. (1971) resolved a discrete group of intercorrelated measures of water mass change—temperature at given depths, season, and upwelling—which lacked biological correlates of species abundances or total standing crop measured by displacement volumes. Among the physical measures of the environment used, only those of position, such as locality, bottom depth, trawl depth, and trawl temperature, which was a strong correlate of trawl depth, had biological correlates. Depth and physiography, therefore, seem to explain the observed local faunal differences better than major water mass characteristics, which may influence the transitional fauna as a whole, but which are modified locally by nearshore processes. Also, Riley (1963) pointed out that causal relationship among different environmental measures may not be simple, i.e., may not be expressed by a simple linear correlation, because of time lags and complex phase interactions. Therefore, the distinctions among the three faunas are rationalized in terms of four local “positional” characteristics of the three study areas: physiographic isolation; local hydrography; depth differences; and nearness to the coast.

In the relatively rich Santa Barbara Basin, the regeneration and replacement of inorganic nutrients in the surface waters is facilitated by upwelling from the relatively shoal bottom. The presumed high productivity of the surface waters is reflected by a pronounced decrease in dissolved oxygen content below the thermocline to almost zero near the bottom. The adjacent coastal zone is an additional important source of nutrients. The chain of Channel Islands partially isolates the Santa Barbara Basin from the open ocean and thereby inhibits mixing of the inshore water mass with the offshore waters. Therefore, the nutrients are concentrated in this “eutrophic” basin (Robert W. Holmes, personal communication). The physiographic isolation and relatively shallow bottom depth of the basin limit faunal diversity in Santa Barbara. Reduced interaction with surrounding areas restricts faunal intrusions. Bathymetric confinement excludes a true bathypelagic fauna. The wide fluctuation in abundance and diversity observed at Santa Barbara may be due to local

effects within the semi-isolated circulation of the area, which is least buffered by the open ocean.

The offshore areas communicate more directly with the open sea. But the relatively high Santa Rosa-Cortez Ridge prevents unlimited oceanic exchange of the deeper Santa Cruz Basin water. Located over the continental slope, the Rodriguez Dome area is directly influenced by the open ocean. Consequently, the primary faunal regions to the north, south, and west contribute exotic species to the area's heterogenous fauna. Its direct contact with the California Current accounts for the regular occurrence of northern and central species in this area, so that the Rodriguez fauna is characteristically the most typical of the open ocean.

#### ACKNOWLEDGMENTS

I thank the students and staff of the Marine Laboratory, University of California, Santa Barbara, who assisted in the trawling operations aboard the R/V SWAN and in the sorting and identification of the specimens. In particular I appreciate the encouragement and advice of my graduate advisor, Dr. A. W. Ebeling. I also acknowledge the help and cooperation of Greg Cailliet, Floyd Dewitt, Henry Genthe, and Norman Lammer.

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## APPENDIX

List of fishes collected during trawling studies  
off Santa Barbara, California, 1964-67

(Rare species—except for the cat shark *Parmaturus xaniurus*, which was taken 48 times—captured in but one of the three sampled areas: Santa Barbara Basin\*, Santa Cruz Basin\*\*, and Rodriguez Dome area\*\*\*)

Scyliorhinidae (young)	Alepocephalidae (mostly young)
<i>Parmaturus xaniurus</i> *	<i>Bajacalifornia burragei</i>
Serrivomeridae	<i>Sagamichthys abei</i>
<i>Serrivomer sector</i> **	<i>Pellisulus facilis</i> ***
Nemichthyidae	<i>Holtbyrnia macrops</i>
<i>Nemichthys scolopaceus</i> **	<i>Holtbyrnia melanocephala</i>
Clupeidae (larvae)	Paralepididae (larvae and young)
<i>Sardinops caeruleus</i> *	<i>Lestidium ringens</i>
Engraulidae (larvae)	<i>Lestidium</i> sp.
<i>Engraulis mordax</i>	<i>Macroparalepis</i> sp.**
Argentiniidae	Myctophidae
<i>Argentina sialis</i> *	<i>Protomyctophum crockeri</i>
<i>Nansenia</i> sp.**	<i>Diogenichthys atlanticus</i> ***
Bathylagidae	<i>Symbolophorus californiensis</i>
<i>Leuroglossus stilbius</i>	<i>Tarletonbeania crenularis</i>
<i>Bathylagus ochotensis</i> ***	<i>Diaphus theta</i>
<i>B. wesethi</i>	<i>Stenobranchius leucopsarus</i>
<i>B. milleri</i>	<i>Triphoturus mexicanus</i>
Opisthoproctidae	<i>Lampanyctus ritteri</i>
<i>Macropinna microstoma</i> ***	<i>Lampanyctus regalis</i>
<i>Dolichopteryx longipes</i> **	<i>Parvilux ingens</i>
Gonostomatidae	Myctophid larvae
<i>Cyclothone signata</i>	Scopelarchidae (larvae)
<i>C. acclinidens</i>	<i>Benthalbella linguidens</i>
<i>C. pallida</i>	<i>Benthalbella dentata</i>
<i>Cyclothone</i> sp.	<i>Benthalbella</i> sp.
<i>Danaphos oculatus</i>	Neoscopelidae
<i>Vinciguerria lucetia</i>	<i>Scopelengys tristis</i> **
<i>Ichthyococcus irregularis</i>	Oneirodidae
Sternoptychidae	<i>Oneirodes acanthias</i> **
<i>Argyrolepeceus affinis</i>	Gadidae (larvae and young)
<i>A. hemigymnus</i>	<i>Merluccius productus</i>
<i>A. lychnus</i>	Zoarcidae
<i>A. sladeni</i>	<i>Melanostigma pammelas</i>
<i>Sternoptyx diaphana</i>	Macrouridae
Melanostomiidae	<i>Nezumia stelgidolepis</i>
<i>Tactostoma macropus</i> ***	Prejuvenile macrourid**
<i>Bathophilus flemingi</i>	Scomberesocidae
Malacosteidae	<i>Cololabis saira</i> **
<i>Aristostomias scintillans</i>	Melamphaidae
Chauliodontidae	<i>Scopelogadus mizolepis bispinosus</i>
<i>Chauliodus macouni</i>	<i>Poromitra crassiceps</i>
Stomiidae	<i>Melamphaes acanthomus</i>
<i>Stomias atriventer</i>	<i>Melamphaes lugubris</i>
Idiacanthidae	Anoplogasteridae
<i>Idiacanthus antrostomus</i>	<i>Anoplogaster cornuta</i>

Syngnathidae (young)	Brotulidae (larvae)
<i>Syngnathus californiensis</i>	<i>Cataetyx rubrirostris</i> *
Scorpaenidae (larvae and young)	Blenniidae* (larvae)
<i>Sebastolobus altivelis</i>	Stromateidae (larvae and young)
<i>Sebastolobus</i> sp.	<i>Icichthys lockingtoni</i> ***
<i>Sebastes</i> sp.	<i>Peprilus simillimus</i>
Zaniolepididae (larvae)	Bothidae (larvae)
<i>Zaniolepis</i> sp.*	<i>Citharichthys sordidus</i>
Cottidae (larvae)	<i>Citharichthys xanthostigma</i>
<i>Scorpaenichthys marmoratus</i>	<i>Citharichthys stigmaeus</i>
Agonidae (larvae and young)	Pleuronectidae (larvae)
Cyclopteridae (young)	<i>Microstomus pacificus</i>
<i>Paraliparis</i> sp.*	<i>Glyptocephalus</i> sp.
<i>Nectoliparis pelagicus</i>	Flatfish larvae
Carangidae (larvae)	
<i>Trachurus symmetricus</i>	

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