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CONTENTS

Numbers 380–409

1971

No. 380. The Taxonomic Position of the Genus *Petria* Semenow (Coleoptera: Alleculidae). By John F. Lawrence. 9 pp. June 15.

No. 381. Tetraploidy in a Hybrid Lizard of the Genus *Cnemidophorus* (Teiidae). By William B. Neaves. 25 pp. December 20.

1972

No. 382. Osteology and Description of *Thrattidion noctivagus*, a Minute, New Freshwater Clupeid Fish from Cameroon, with a Discussion of Pellonulin Relationships. By Tyson R. Roberts. 25 pp. February 25.

No. 383. Two New Genera of Bembidiine Carabid Beetles from Australia and South America with Notes on their Phylogenetic and Zoogeographic Significance (Coleoptera). By Terry L. Erwin. 19 pp. February 25.

No. 384. An Attempt to Determine the Systematic Position of *Ellopostoma megalomycter*, an Enigmatic Freshwater Fish from Borneo. By Tyson R. Roberts. 16 pp. February 25.

No. 385. The Chañares (Argentina) Triassic Reptile Fauna. XII. The Postcranial Skeleton of the Thecodont *Chanaresuchus*. By Alfred Sherwood Romer. 21 pp. February 25.

No. 386. A Review of the Australian Species of *Elaphrosyron* and *Telostegus*, with Notes on Other Genera (Hymenoptera, Pompilidae). By Howard E. Evans. 18 pp. February 25.

No. 387. Growth Changes in *Amphilimna olivacea* (Lyman) and the Systematic Status of *Amphitarsus spinifer* Schoener. By Lowell P. Thomas and Amy Schoener. 9 pp. March 15.

No. 388. Intense Low-Frequency Sounds from an Antarctic Minke Whale, *Balaenoptera acutorostrata*. By William E. Schevill and William A. Watkins. 8 pp. April.

No. 389. The Chañares (Argentina) Triassic Reptile Fauna. XIII. An Early Ornithosuchid Pseudosuchian, *Gracilisuchus stipanicicorum*, Gen. et Sp. Nov. By Alfred Sherwood Romer. 24 pp. August 11.

No. 390. The Chañares (Argentina) Triassic Reptile Fauna. XIV. *Lewisuchus admixtus*, Gen. et Sp. Nov., a Further Thecodont from The Chañares Beds. By Alfred Sherwood Romer. 13 pp. August 11.

No. 391. The Relationship of Island Area and Isolation to Color Polymorphism in *Liguus fasciatus* (Pulmonata, Bulimulidae). By Michael A. Rex. 15 pp. August 11.

No. 392. A Fossil Pelomedusid Turtle from Puerto Rico. By Roger Conant Wood. 13 pp. August 11.

No. 393. Minute Jamaican Prosobranch Gastropods: *Stoastoma* and its Congeners. By Kenneth J. Boss. 13 pp. August 11.

No. 394. The Chañares (Argentina) Triassic Reptile Fauna. XV. Further Remains of the Thecodonts *Lagerpeton* and *Lagosuchus*. By Alfred Sherwood Romer. 7 pp. August 11.

No. 395. The Chañares (Argentina) Triassic Reptile Fauna. XVI. Thecodont Classification. By Alfred Sherwood Romer. 24 pp. November 6.

No. 396. The Chañares (Argentina) Triassic Reptile Fauna. XVII. The Chañares Gomphodonts. By Alfred Sherwood Romer. 9 pp. November 6.

No. 397. *Xyloredo*, a New Teredinid-like Abyssal Wood-borer (Mollusca, Pholadidae, Xylophagainae). By Ruth D. Turner. 19 pp. November 6.

1973

No. 398. *Pseudobeaconia*, a Perleidiform Fish from the Triassic Santa Clara Formation, Argentina. By Peter Hutchinson. 24 pp. March 6.

No. 399. The Evolution of Mammalian from Reptilian Dentitions. By J. W. Osborn and A. W. Crompton. 18 pp. March 6.

No. 400 The Carolina Salt Marsh Snake: a Distinct Form of *Natrix sipedon*. By Roger Conant and James D. Lazell, Jr. 13 pp. March 6.

No. 401. The Chañares (Argentina) Triassic Reptile Fauna. XVIII. *Probelesodon minor*, a New Species of Carnivorous Cynodont; Family Probainognathidae Nov. By Alfred Sherwood Romer. 4 pp. March 6.

No. 402. Speciation in the Genus *Ochthoeca* (Aves: Tyrannidae). By John W. Fitzpatrick. 13 pp. June.

No. 403. A New Late Paleocene Phenacodont (Mammalia: Condylarthra) from Western Colorado. By Bryan Patterson and Robert M. West. 7 pp. June.

No. 404. New Studies on a Montane Lizard of Jamaica, *Anolis reconditus*. By Robert Hicks. 23 pp. June.

No. 405. A Fossil Trionychid Turtle from South America. By Roger Conant Wood and Bryan Patterson. 10 pp. September 20.

No. 406. Two New Lygosomine Skinks from New Guinea with Comments on the Loss of the External Ear in Lygosomines and Observations on Previously Described Species. By Allen E. Greer, Jr. 25 pp. September 20.

No. 407. The Chañares (Argentina) Triassic Reptile Fauna. XIX. Postcranial Materials of the Cynodonts *Probelesodon* and *Probainognathus*. By Alfred Sherwood Romer and Arnold D. Lewis. 26 pp. September 20.

No. 408. A Taxonomic Comparison of the American *Upogebia* (Decapoda, Thalassinidea), Including Two New Species from the Caribbean. By David Thistle. 23 pp. September 20.

No. 409. The Classification of the Cotingidae (Aves). By D. W. Snow. 27 pp. September 20.

BREVIORA

Museum of Comparative Zoology

INDEX OF AUTHORS

Numbers 380–409

1971–1973

	No.
Boss, Kenneth J.	393
Conant, Roger	400
Crompton, A. W.	399
Erwin, Terry L.	383
Evans, Howard E.	386
Fitzpatrick, John W.	402
Greer, Allen E.	406
Hicks, Robert	404
Hutchinson, Peter	398
Lawrence, John F.	380
Lazell, James D.	400
Lewis, Arnold D.	407
Neaves, William B.	381
Osborn, J. W.	399
Patterson, Bryan	403, 405

Rex, Michael A. 391

Roberts, Tyson R. 382, 384

Romer, Alfred Sherwood 385, 389, 390, 394, 395, 396, 401, 407

Schevill, William E. 388

Schoener, Amy 387

Snow, D. W. 409

Thistle, David 408

Thomas, Lowell P. 387

Turner, Ruth D. 397

Watkins, William E. 388

West, Robert M. 403

Wood, Roger Conant 392, 405

08

B R E V I O R A

Museum of Comparative Zoology

Cambridge, Mass. 15 June, 1971 Number 380

THE TAXONOMIC POSITION OF THE GENUS *PETRIA* SEMENOW (COLEOPTERA: ALLECULIDAE)

John F. Lawrence[1]

Abstract. The beetle genus *Petria* Semenow includes a few species inhabiting the Kara-Kum Desert, U.S.S.R. They are known only from males, which are soft-bodied, with short elytra, long antennae, and large eyes. The genus is usually placed in a separate family, the Petriidae, within the section Heteromera, but some Russian workers have included it within the family Alleculidae. A detailed study of *Petria antennata* Semenow provides abundant evidence supporting the inclusion of *Petria* within the subfamily Omophlinae of the Alleculidae. Brief descriptions and figures are given for the prothorax, metendosternite, hindwing, tarsal claw, abdomen, and male genitalia, and comparisons are made with members of the Alleculidae and other heteromeran families. Speculations are made concerning the habits and habitat of the larva and female based on knowledge of related omophlines and analogous types of desert-inhabiting Coleoptera.

The genus *Petria* Semenow includes a few species of peculiar looking beetles that inhabit the Kara-Kum, a desert east of the Caspian Sea (Turkmen S.S.R.). The group is known only from males, which are attracted to lights at night. They are relatively small (3.0–4.25 mm), soft-bodied, and lightly pigmented insects, with shortened elytra, long antennae, and large, prominent eyes (*see* illustrations in Jacobson, 1913, 1915; Ogloblin and Znoiko, 1950; and Znoiko, 1936). The genus has been placed in a separate family, the Petriidae, which is considered in most general texts to be of uncertain phylogenetic position within the section Heteromera (Crowson, 1955).

Although Semenow (1893, 1896) made *Petria* the type of a new family, he considered the genus to be related to members of the

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Alleculidae and particularly the omophline genus *Stenervx* Reitter, also from Central Asia. Most later authors recognized the family Petriidae, but Znoiko (1936) presented evidence for the inclusion of *Petria* within the alleculid subfamily Omophlinae and pointed out a transition in general form, eye size, wing venation, tarsal claws, and antennal structure, among the species of *Petria, Stenervx,* and a third genus, *Cnecosochara* Reitter, also known from males only. In spite of Znoiko's conclusions, the Petriidae is still treated as a heteromeran family of doubtful affinities, and Crowson (1955) made no attempt to place it, since specimens for dissection were not available to him.

The major problem in classifying *Petria* on the basis of superficial characters is that, while it closely resembles several Alleculidae, it has been thought to lack the main diagnostic features of that family, namely, the closed procoxal cavities, connate basal abdominal sternites (3–5), and pectinate tarsal claws. In order to obtain material for dissection, I wrote to Leningrad, and, through the kindness and cooperation of Dr. G. S. Medvedev of the Zoological Institute, Academy of Sciences, U.S.S.R., received three specimens from Semenow's series of *P. antennata,* collected at Utshadzhi in May of 1889. Sincere thanks are due to Dr. Medvedev and the Zoological Institute. I am also grateful to R. A. Crowson for his continual inspiration, comments, and criticisms, and to P. J. Darlington, Jr., and T. F. Hlavac for their useful suggestions and critical review of the manuscript. Although specimens of *Stenervx* and *Cnecosochara* were not available for study, dissections were made of *Cteniopus flavus* (Scopoli) and examinations were made of several alleculids and other Heteromera.

A study of the above material revealed the following features of *Petria antennata* that shed some light on its phylogenetic relationships:

1) The procoxae are subconical, projecting, and almost contiguous, the intercoxal process of the prosternum being laminate (Fig. 1), but each coxa bears a relatively large articular region (a), which is concealed by the coxal cowling (c), so that the articulation with the pleuron is internalized (Fig. 2).

2) The pleuro-coxal mechanism of the prothorax is of the tenebrionoid type, with the endopleuron fused to the notal wall and the trochantin apparently absent.

3) The procoxal cavities are closed internally and open externally or posteriorly (Fig. 1).

4) The mesocoxal cavities are not closed outwardly by the meso- and metasterna and are thus contiguous laterally with the mesepimera.

5) The metendosternite is of the tenebrionoid type, with a narrow stalk, no laminae, and the anterior tendons out near the apices of the lateral arms (Fig. 3).

6) The tibial spurs are neither serrate nor pubescent.

7) The tarsal claws each have two or three toothlike projections (Fig. 5).

8) The hindwing is similar to that of most tenebrionoids, with four well-developed anal veins (in the main group), an anal or wedge cell (w) present, and a short stalk of R_s extending basad of the radial cell (not shown in Znoiko, 1936) (Fig. 4).

9) Abdominal sternites 3, 4, and 5 are connate. This is not easily observed without sectioning, since all the segments are broadly overlapping (Figs. 6 and 7).

10) Abdominal sternite 7 has a pair of posterolateral gland openings (Fig. 9) similar to those found in *Cteniopus* (*see* Kendall, 1968).

11) Abdominal sternite 8 is developed into a pair of claspers (Figs. 6 and 8) that are similar to those of alleculids (*see* Campbell, 1966; Champion, 1888; Kaszab, 1969; McDonald, 1960; and Ogloblin and Znoiko, 1950).

12) The aedeagus is of the normal (not inverted) heteromeroid type, with a long basal piece (b), short tegmen (apical or cap piece) (t), and the median lobe (m) membranous except for a ventral strut (or two fused struts) at the apex (Fig. 10). This is a typical alleculid aedeagus as illustrated in Campbell (1966, 1968); McDonald (1960); Marshall (1970a, 1970b); and Sharp and Muir (1912).

Except for the lack of an external coxal closure, the condition of the prothorax in *Petria* is strongly suggestive of a relationship to the tenebrionoid complex of the Heteromera (Tenebrionidae, Lagriidae, Alleculidae, and Nilionidae). The internalization and concealment of the pleural articulation, fusion of the endopleuron to the notum, and reduction of the trochantin are characteristic of the tenebrionoid families and a few related groups, such as the Colydiidae, Zopheridae, Monommidae, Prostomidae, and Dacoderidae; a similar condition also occurs in certain Clavicornia (Propalticidae, cerylonoid complex) (Crowson, 1955; Hlavac, personal communication; Watt, 1967). The internal closure of the procoxal cavities occurs in most Heteromera, but is absent in the Mycetophagidae, Ciidae, Pterogeniidae, Tetratomidae, Perimylopidae, Zopheridae, Monommidae, Pythidae, and Pyrochroidae. The development of conical, projecting procoxae and a laminate intercoxal process has taken place in various members of the tenebrionoid association (*Lagria, Mycetochara, Cteniopus*), but externally open procoxal cavities are unknown in this large group, except in a few sub-Antarctic forms that are doubtfully included or have been removed (Crowson, 1955; Watt, 1967).

The laterally open mesocoxal cavity is a fairly common feature in the Heteromera, but in the families Prostomidae, Zopheridae, Monommidae, Elacatidae, Mycteridae, Inopeplidae, and Salpingidae the cavity is closed by the meeting of the meso- and metasterna (Crowson, 1955; 1967).

The metendosternite of *Petria* is also of the tenebrionoid type, with no laminae and with laterally placed tendons, and differs from that found in most groups of Heteromera. A similar structure may be found, however, in certain Melandryidae and Scraptiidae, which differ from *Petria* by having serrate or pubescent tibial spurs and free abdominal sternites (Crowson, 1938, 1944, 1955, 1966).

The wing venation also points to the tenebrionoid complex, being almost identical with that of certain omophline Alleculidae and a number of Tenebrionidae; in most Melandryidae, the venation is simpler with the anal cell absent, but in *Melandrya* it is essentially the same as that of *Petria* (Bernet-Kempers, 1923; Crowson, 1955, 1966; Forbes, 1922; Znoiko, 1936).

The fusion of the basal three abdominal sternites and the presence of glands on the seventh sternite are probably the strongest pieces of evidence for the association of *Petria* with the Tenebrionidae and their relatives. The fusion of sternites is not uncommon in the Heteromera and has probably occurred several times, but the connation of the first three appears to be restricted to the tenebrionoids, certain Colydiidae, (*Mrymechixenus, Pycnomerus, Anchomma*) and *Meryx* (Merycidae). Two sternites are united in the Pterogeniidae, Prostomidae, Cononotidae, Mycteridae, *Lagrioida* (Anthicidae), and a few other genera of doubtful affinities, while four are actually or apparently fused in the majority of Colydiidae, Zopheridae, Monommidae, and Dacoderidae (Crowson, 1955, 1967; Watt, 1967). The situation is complicated by the fact that fusions are not always visible from the surface (as in *Petria*) or intersegmental membranes are concealed (as in *Dacoderus, see* Watt, 1967). The apparent fusion of three basal abdominal sternites, however, is a consistent feature of the tenebrionoid families and is almost always correlated with several other adult and larval characters.

The presence of defense glands on the seventh abdominal sternite is known, according to Kendall (1968), only in the families Lagriidae, Alleculidae, and Tenebrionidae. Although the actual glandular reservoirs were not seen in my material, openings and ducts, similar to those of *Cteniopus sulphuripes* (Linnaeus) and *C. flavus* (Scopoli), were present at the posterior angles of the sternite.

The presence of small teeth on the tarsal claws, the modification of the eighth sternite into abdominal claspers, and the form of the aedeagus all argue for the inclusion of *Petria* in the family Alleculidae, especially when coupled with the several tenebrionoid features mentioned above. Male claspers may be found in other groups, such as the Oedemeridae and Cephaloidae, but the structure of these organs is entirely different and the other tenebrionoid characters are lacking (Arnett, 1951; 1953).

The arguments presented above, when added to the comparisons of Znoiko (1936), leave little doubt that *Petria* belongs in the family Alleculidae and is related to *Stenerya*, *Cnecosochara,* and their allies in the subfamily Omophlinae. It represents an adaptive extreme characterized by the loosely built and lightly sclerotized body, shortened elytra, large eyes, loss of the combs on the tarsal claws, loss of the external coxal closure, and sexual wing dimorphism. The last feature is not actually known in *Petria* but may be postulated by analogy with other groups known from males only (see below).

Semenow (1893) speculated that the females of *Petria,* since they were never collected along with males, might be wingless parasites of Hymenoptera or Orthoptera, as is the case in certain Meloidae and Rhipiphoridae. In other omophlines, however, such as *Omophlus, Podonta,* and *Cteniopus,* the larvae are soil inhabitants, feeding on various roots and tubers, while the adults are usually found on flowers and fruits (Aguilar, 1962; Kaszab, 1969). A more reasonable hypothesis, then, would be that *Petria* larvae are root feeders and that the wingless females live either in the soil or at the bases of shrubs or grasses. This particular type of wing dimorphism and habitat selection is known in at least two other xerophilous beetles, the males of which resemble those of *Petria,* namely *Vesperus* (Cerambycidae) and *Anorus* (Dascillidae). Species of *Vesperus* inhabit the Mediterranean Region; the wingless female deposits her eggs above the ground, and the fast moving, triungulinlike larvae enter the soil and are transformed into radically different grubs, which feed on roots (Balachowsky, 1962). *Anorus* species occur in the deserts of southwestern North America and Chile; the larvae are unknown (but those of the related *Dascillus* are root feeders), and the only known female is wingless and subterranean (Blaisdell, 1934). It is likely that the females and larvae of *Petria,* when they are discovered, will have similar habits.

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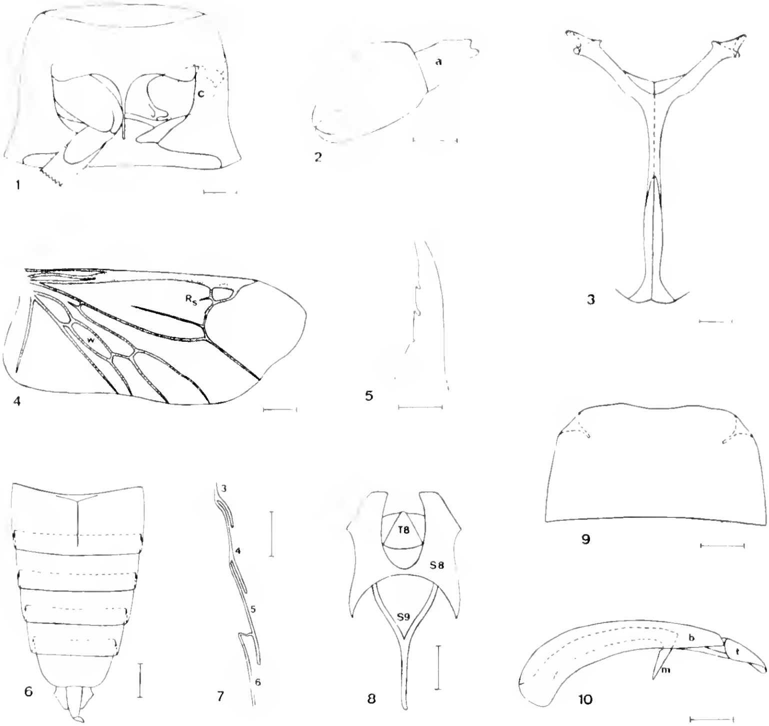

Figures 1–10. *Petria antennata* Semenow, male (1 line = 0.125 mm unless otherwise indicated). Fig. 1. Prothorax, ventral view, with left coxa removed. Fig. 2. Procoxa, showing internal articular area (a). Fig. 3. Metendosternite, dorsal view. Fig. 4. Hindwing (0.50 mm). Fig. 5. Tarsal claw (0.038 mm). Fig. 6. Abdomen (0.25 mm). Fig. 7. Cross section of abdominal sternites 3–6 (0.076 mm). Fig. 8. Abdominal claspers and associated structures, ventral view. Fig. 9. Abdominal sternite 7, showing glandular ducts and openings. Fig. 10. Aedeagus, lateral view.

B R E V I O R A

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TETRAPLOIDY IN A HYBRID LIZARD OF THE GENUS *CNEMIDOPHORUS* (TEIIDAE)

William B. Neaves[1]

Abstract. An apparent hybrid between triploid, parthenogenetic *Cnemidophorus exsanguis* and diploid, sexual *C. inornatus* is shown to possess a tetraploid chromosome complement. Evidence suggests that this tetraploid karyotype resulted from the fusion of a haploid sperm pronucleus of *C. inornatus* with an egg pronucleus carrying the unreduced triploid chromosome complement of *C. exsanguis*. Observations of captive *C. inornatus* males show their propensity to engage in mating behavior with *C. exsanguis* parthenogenones. These findings are discussed with regard to the origin and genetic mechanism of parthenogenesis in *Cnemidophorus*.

INTRODUCTION

The hypothesis that parthenogenetic species of *Cnemidophorus* arose from the offspring of interspecific hybridizations (Lowe and Wright, 1966) has been supported by evidence from studies of lactate dehydrogenase (Neaves and Gerald, 1968) and adenosine deaminase (Neaves, 1969). A particular aspect of that hypothesis, namely, that triploid parthenogenones originated in crosses between males of a sexual species and females of a diploid, parthenogenetic species, has received support from reports that such hybridizations occur in nature. Taylor and Medica (1966) described apparent hybrids between *Cnemidophorus inornatus*, a sexual species, and *C. neomexicanus*, a diploid parthenogenone.

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Wright and Lowe (1967a) verified the occurrence of *C. inornatus* x *C. neomexicanus* hybrids, conveniently designated *C. "perplexus,"* at several localities in New Mexico where the two parental species are sympatric.

The question arises as to whether or not hybridization in *Cnemidophorus* ends with the attainment of triploidy. Although triploid parthenogenones are common (of seven parthenogenetic species in the *sexlineatus* group, five are triploid), no tetraploid species are known in the genus. Lowe and Wright (1966) mention a suspected tetraploid individual that they considered to represent a hybrid of *C. inornatus* and *C. uniparens,* the latter a triploid parthenogenone, but no evidence, karyotypic or otherwise, was presented to verify their suspicion. My report describes in detail a documented instance of tetraploidy in a *Cnemidophorus* hybrid and seeks to explain why there are as yet no tetraploid species in nature. Observations of interspecific mating behavior involving male *C. inornatus* and females of various parthenogenetic species are included in this report. Finally, these findings are discussed with regard to the origin and genetic mechanism of parthenogenesis in *Cnemidophorus.*

MATERIALS AND METHODS

Animals used in these studies were captured alive in their native habitats in Colorado, New Mexico, and Texas during the summers of 1967 and 1968. Soon after capture, these lizards were shipped to Boston and Cambridge. Upon arrival in the laboratories, they were housed either in a rectangular pen 12 feet by 14 feet or in oval pens 3.5 feet by 5 feet. The pens had sand floors with tiles and sheets of cardboard scattered about for shelter. Sun lamps installed over the pens were automatically controlled to provide a twelve-hour daily photoperiod. A constant supply of open water and available food, in the form of mealworms and crickets, was provided.

Aspects of lizard behavior reported here were observed and photographed among the captive inhabitants of the large rectangular pen described above. Most incidents were recorded during the winter of 1968–1969 when the pen held approximately 150 *Cnemidophorus* distributed among five sexual and five parthenogenetic species.

The tetraploid karyotype illustrated in this report was obtained from a phenotypically aberrant lizard captured at Alamogordo, New Mexico, in August, 1967. This lizard was maintained alive until May, 1968, when it was used for karyotypic study. Mitotic figures were obtained from tissue cultures of 1 mm cubes of heart tissue according to the following procedure. Small Falcon flasks were loaded with 5.0 ml of a mixture containing 80 percent Eagle's Minimum Essential Medium (Microbiological Associates) and 20 percent fetal calf serum. With the flask in an upright position, tissue explants were placed against the dry wall of the flask. The flask was slowly lowered to its side so that the explants were covered by the medium but not dislodged from the plastic surface. The flasks were incubated at 33° C. without agitation. The cultures were examined regularly with an inverted phase contrast microscope in order to follow cell proliferation. On the ninth day of incubation, when mitotic activity was intense, 0.25 microgram of Velban (Grand Island Biological Co.) was added to each flask. Twenty-four hours later, the medium was discarded and 5.0 ml of 0.1 percent trypsin in 0.8 percent sodium citrate was added to each flask. Following a twenty-minute incubation at 37° C., the flasks were shaken vigorously to free the dissociating cells from one another and from the plastic. From this point, the cultures were processed according to a modification of the method outlined by Moorhead *et al.* (1960). The solution from each flask was decanted into a centrifuge tube and spun at 1000 g for five minutes. The cell pellet was fixed in two changes of ethanol:acetic acid (3:1) and was suspended in 45 percent acetic acid. Drops of this suspension were placed on cold, wet slides and flame dried. The chromosomes on these slides were stained with 1 percent toluidine blue in 1 percent borax and were photographed with an Olympus photomicroscope.

THE DISCOVERY OF THE TETRAPLOID

In the course of a collecting trip to New Mexico in August, 1967, I visited an exceptionally dense *Cnemidophorus* population within the city limits of Alamogordo in Otero County. The population was largely restricted to a weed bed approximately 20 meters wide and over 1000 meters long, bounded on the west by the roadbed of the Southern Pacific Railroad and on the east by the Alamogordo City Park. Two *Cnemidophorus* species were found in the area described. *C. exsanguis,* a triploid parthenogenone, was most abundant, occurring at a density of approximately 50 animals per acre; *C. inornatus,* a sexual species, occurred at a density of about 10 animals per acre. No lizards were seen in the park itself, which had a cover of closely mown grass. West of the roadbed, the cover consisted of mesquite shrub and cactus on an eroded surface virtually devoid of weeds or grass. Here both *C. inornatus* and *C. tigris,* a second sexual species, were abundant. In two days of collecting west of the roadbed, only a single *C. exsanguis* was seen. No *C. tigris* were found east of the roadbed in the weeds where *C. exsanguis* was so abundant.

Forty-three *C. exsanguis* and eleven *C. inornatus* were captured in the Alamogordo weed bed in 1967. In addition, two aberrant *Cnemidophorus* were taken. One of these, MCZ*100080, was the size of *C. inornatus,* with partially fused paravertebral stripes, a white ventral surface, and a rusty tint on its dorsum, causing it to resemble *C. exsanguis.* The day after its capture, this animal died. Its abdomen was opened to expose the gonads, which appeared rudimentary. The nature of this specimen remains a mystery. A second aberrant specimen, MCZ 101991 (Plate 1), resembled a typical *C. exsanguis* except that its paravertebral stripes were fused and its ventral surface and tail were suffused with a brilliant blue characteristic of the same surfaces in *C. inornatus* males. This *exsanguis*-like animal was maintained alive for almost nine months before it was sacrificed for a study of its chromosomes.

It was immediately suspected that MCZ 101991 might represent a cross between the sympatric species of the weed bed, *C. inornatus* and *C. exsanguis.* This lizard clearly possessed attributes characteristic of both suspected parental species. A decision was reached to allow the animal to remain alive as long as possible so that its behavior might be observed, but at the same time, an assessment of its ploidy was desired. Accordingly, blood smears were prepared from the *exsanguis*-like animal and from other *Cnemidophorus* known to be either diploid or triploid on the

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* Museum of Comparative Zoology

basis of karyotypic evidence (Lowe and Wright, 1966; Wright and Lowe, 1967b). These were sent to N. B. Atkin for densitometric estimation of DNA in the nucleated erythrocytes. Dr. Atkin reported (in litt.) that karyotypically triploid species (3n = 69±1) possessed about 50 percent more DNA per nucleus than karyotypically diploid species (2n = 46) and that the aberrant specimen (MCZ 101991) possessed about 20 percent more DNA per nucleus than triploids such as *C. exsanguis*. The details of erythrocyte DNA analysis in *Cnemidophorus* will be reported elsewhere. Although a true tetraploid should have demonstrated approximately 30 percent more DNA per nucleus than a triploid, the results of Atkin's survey encouraged the suspicion that the aberrant specimen represented a hybrid carrying some genetic elements characteristic of *C. inornatus* in addition to the basic triploid complement characteristic of *C. exsanguis*.

In December 1967, Professor C. H. Lowe examined the aberrant lizard and declared it unlike any *Cnemidophorus* he had ever seen. Lowe agreed that it might represent a tetraploid hybrid between *C. inornatus* and *C. exsanguis*. Meanwhile, this lizard thrived in captivity and proved itself a vigorous competitor for food; it commonly robbed typical *C. exsanguis* of mealworms.

In January 1968, the aberrant lizard laid two eggs, thus confirming the suspicion that it was female and suggesting that its ovaries were functional. Attempts were made to provide suitable conditions for ovoposition, but she did not take advantage of them, and the eggs were dessicated by the time I discovered them in my daily check. She produced no more eggs during her captivity, which extended through May, 1968.

When the aberrant lizard was eventually sacrificed for karyotypic analysis, the results (Plates 2 and 3 and Table 1) confirmed its suspected status as a tetraploid hybrid. The modal chromosome number, based on examination of eight apparently complete chromosome spreads, is 91. The karyotype in Plate 2 is from the single spread showing 92 chromosomes. Considering the large number of chromosomes in the karyotype, the small size of many, and the probability of overlap, it is not surprising that fewer than 92 chromosomes are evident in most spreads. The tetraploid karyotype can be divided into four apparently identical haploid complements, each closely resembling the haploid chromosome complement of *C. inornatus* (Lowe and Wright, 1966). Three *inornatus*-like haploid sets constitute the typical triploid karyotype of *C. exsanguis*, which is similar to that of another triploid parthenogenone, *C. uniparens* (Lowe and Wright, 1966). The fourth haploid chromosome complement seen in the aberrant lizard's karyotype may have been contributed by *C. inornatus* itself, through an interspecific mating with *C. exsanguis*.

OBSERVATIONS OF CAPTIVE SPECIMENS: INTERSPECIFIC MATING

Observations of captive *Cnemidophorus* during autumn and winter of 1968–1969 suggest that *C. inornatus* males may be unusually disposed to interspecific mating with parthenogenetic females. Dozens of courtship encounters, including attempted copulation, were recorded between *C. inornatus* males and parthenogenetic females from the species *C. exsanguis* and *C. tesselatus* (Plate 4, figs. 5–9).

The sequence of sexual behavior involved pursuit of a subject, often a parthenogenetic female but sometimes an individual of a sexual species, including other *C. inornatus,* for five to twenty seconds at a speed depending on the movement of the subject, the male apparently trying to stay near the tip of the subject's tail. Suddenly, the *C. inornatus* male would close with the subject, mount its back, and grasp in his jaws a fold of skin on the back of the subject's neck. If the subject acquiesced, the male would immediately execute sinuous movements while pressing its abdomen against the subject's dorsum. With the subject still quiescent, the male would loosen its grip on the subject's skin and caress the back of the subject's head and neck with his jaw while continuing the sinuous body movements. The male seemed particularly intent on rubbing his ventral pelvis and tail base against the dorsal pelvis of the subject. Meeting no resistance, the male would maneuver his vent into the area between the subject's rear limb and tail base. When the subject was a large parthenogenetic female, this maneuver required the male to creep back from his original position in which his jaw touched the subject's head and neck (Plate 4, figs. 5–7). While struggling to approximate his vent to the subject's, the male would constantly stroke the subject's dorsal pelvis and tail base with his rear limb. At times, the male's hemipenis was visibly erect, but in spite of observed close apposition of the participants' vents, unequivocal intromission was not seen.

It did not appear as though *C. inornatus* males met with any real cooperation, beyond mere quiescence, in their courtship efforts, but *C. exsanguis* and *C. tesselatus* at least permitted the sequence of events to proceed as far as described above. Other *C. inornatus,* particularly other males, made real efforts to escape the attentions of an ardent but misguided suitor. Perhaps as a result, *C. inornatus* males exhibited a definite preference for the larger, parthenogenetic females over their conspecific females. Attempted intromission was observed only between *C. inornatus* males and parthenogenetic females.

DISCUSSION

The existence of a tetraploid lizard in a mixed population containing triploid parthenogenones and diploid, sexual lizards argues that tetraploid hybrids are synthesized in nature, although the genus *Cnemidophorus* apparently contains no tetraploid species.[1] That the tetraploid lizard described here is a hybrid and not an autopolyploid is suggested by its possession of phenotypic traits characteristic of both suspected parental species, by the propensity of the suspected male parent, *C. inornatus,* to engage in interspecific mating behavior with parthenogenetic females such as *C. exsanguis,* and by the occurrence in nature of another interspecific hybrid, *C. "perplexus,"* which is considered to be the result of crosses between sexual and parthenogenetic lizards (Wright and Lowe, 1967a).

Two questions are raised by the existence of the tetraploid hybrid. First is the question of the cytological events in gametogenesis and fertilization that permit a tetraploid to arise from a mating between a sexual male and a triploid, parthenogenetic female. This question, which is essentially concerned with genetic mechanisms operative in parthenogenesis, will be considered at some length in order to provide a background for the second question. The second question concerns the absence of tetraploid species in spite of the synthesis of hybrid tetraploids in nature.

The first question has a trivial aspect, namely cytological events in the sexual male. Nothing more is required of the male lizard

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[1] See also the discussion of two tetraploid lizards in a mixed population of *C. sonorae* and *C. tigris* (Lowe et al., 1970).

than the production of typical sperm that carry a haploid chromosome complement and that are capable of delivering this genome to the female pronucleus in a mature egg. A more complicated aspect of the question involves the cytological events that lead to the production of a mature egg whose pronucleus contains the unreduced somatic chromosome complement characteristic of the mother. This, in essence, is the question of the mechanism of parthenogenesis in *Cnemidophorus,* and it deserves detailed consideration.

In *Cnemidophorus,* with the possible exception of *C. lemniscatus* (Vanzolini, 1970; Hall, 1970), interspecific hybridization is implicated in the origin of parthenogenesis. Oogenesis in parthenogenones arising from interspecific hybridization must solve two major problems: 1) the maneuvering of potentially, and sometimes obviously, nonhomologous chromosome sets at meiosis, and 2) the production of a mature egg possessing the somatic chromosome number characteristic of the mother. Several solutions have been proposed: 1) mitotic egg production replaces the normal meiotic mechanism (Lowe and Wright, 1966), 2) failure of either first or second polar body formation, or fusion of one of these bodies with the egg nucleus after its formation (Beatty, 1957), 3) suppression of the first cleavage division (Beatty, 1957), or 4) endomitosis in the oogonium prior to the onset of meiosis (MacGregor and Uzzell, 1964).

Solutions 2 and 3 cannot compensate for difficulties in bivalent formation that arise when nonhomologous chromosome sets are present at the onset of meiosis, nor can they compensate for situations in which more than two homologous chromosome sets enter meiosis. Since some diploid parthenogenones, such as the four *Lacerta* parthenogenones studied by Darevsky (1966), may be derived from closely related sexual species possessing fairly homologous karyotypes, solutions 2 and 3 cannot be ignored. In fact, Darevsky's (1966) study of parthenogenetic *Lacerta* suggests that the second meiotic division is incomplete, with a diploid restitution nucleus resulting from the fusion of the daughter pronuclei during anaphase. Solutions 2 and 3 can, however, be discounted in all self-perpetuating triploids, such as *C. exsanguis,* and in diploids containing grossly nonhomologous haploid chromosome complements, such as *C. neomexicanus.* If only solution 2 or 3 were operative in these cases, bivalent formation should fail, owing to the absence of homologues, or, in those triploids that appear to have homologous haploid chromosome sets, owing to a tendency toward trivalent formation.

Solution 1, mitotic egg production, overcomes difficulties in bivalent formation by avoiding the issue completely. This solution suffers from a lack of supporting evidence; no instance is known in which the germ line of a higher organism can facultatively abandon the meiotic theme. Furthermore, solution 1 is rendered dubious in *Cnemidophorus*, the group for which it was originally proposed (Lowe and Wright, 1966), by evidence (personal observations) that the nuclei of oocytes approximately 1 mm in diameter from ovaries of parthenogenetic species such as *C. exsanguis*, *C. neomexicanus*, and *C. tesselatus* contain bivalent lampbrush chromosomes characteristic of meiotic diplotene. Hence, at least some components of typical meiosis occur in the ovaries of parthenogenetic *Cnemidophorus*.

Solution 4, pre-meiotic endomitosis in the oogonia, has been shown to work in one group of parthenogenetic vertebrates, the ambystomatid salamanders (MacGregor and Uzzell, 1964), and appears likely in triploid poecilid fish (Schultz, 1967). Since pre-meiotic endomitosis can solve the problems of increased ploidy and nonhomologous chromosome complements, it is the most probable mechanism operative in parthenogenetic *Cnemidophorus* as well.[1] This probability justifies discussion of its known features and its genetic implications.

While studying preparations of diplotene lampbrush chromosomes, MacGregor and Uzzell (1964) found 42 bivalents in each germinal vehicle from triploid parthenogenones ($3n = 42$), but in germinal vesicles from closely related, diploid sexual species ($2n = 28$), they found the expected 14 bivalents. This finding was explained by the postulation that endomitosis precedes meiosis in parthenogenetic oocytes, so that such oocytes enter meiosis with a hexaploid ($6n = 84$) chromosomal constitution. Meiotic DNA replication would then give an oocyte that is dodecaploid with respect to DNA, and meiosis would operate on

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[1] A recent paper by Orlando Cuellar verifies the occurrence of this mechanism in the triploid parthenogenone *Cnemidophorus uniparens*.

42 tetrads (bivalents) to yield a pronucleus with 42 chromosomes, which is the somatic complement for triploid ambystomatids.

MacGregor and Uzzell (1964) suggest that only sister chromosomes resulting from the endomitotic duplication associate to form bivalents. The genetic status of all parthenogenones that may rely on pre-meiotic endomitosis hinges on the question of bivalent formation, making a critical assessment of the MacGregor-Uzzell proposition necessary. The method of bivalent formation will determine whether the parthenogenetic lineage will retain the heterozygosity inherent in its hybrid origin or will experience an ultimate tendency toward homozygosity. While this question is not directly relevant to the issue of tetraploid hybrids, it is important to an understanding of parthenogenesis in *Cnemidophorus*.

Should sister chromosomes pair exclusively, a most conservative pattern of inheritance would result; each offspring would, neglecting mutation, emerge with an exact copy of its mother's genome. Should homologous chromosomes also pair, independent assortment at first meiotic metaphase would cause the offspring to deviate from the mother's genotype, owing to the loss of alternative alleles in the first polar body. In triploid parthenogenones relying on pre-meiotic endomitosis, the probability of losing both representatives (sisters) of a single chromosome from a homologous set of three in a single generation can be calculated ($p = 0.066$), assuming random pairing of sister and homologous chromosomes, no crossing-over, and independent assortment. Similarly, after only two generations, $p = 0.0066$ that two chromosomes from a homologous set of three will be lost, leaving complete homozygosity at all loci on that chromosome.

A diploid parthenogenone in which sister and homologous chromosomes pair randomly experiences an even stronger tendency toward homozygosity. The probability is 0.33 that one of a set of two homologous chromosomes will be lost in a single generation if crossing-over does not occur. In either diploidy or triploidy, crossing-over will only randomize the occurrence of homozygosity with respect to all loci on a single chromosome and will not delay the trend of the entire genome toward homozygosity. The ultimate consequence of participation of homologous chromosomes in bivalent formation is homozygosity at all loci in the genome.

The most sensitive test devised to assess the genetic status of parthenogenones, namely tissue grafts to determine histocompatibility (Kallman, 1962; Maslin, 1967), does not discriminate between uniform clonal heterozygosity, which would be preserved in the case of exclusive pairing of sisters, and established clonal homozygosity resulting from independent assortment of bivalents formed from random pairing of both sister and homologous chromosomes. Only the transient period of developing homozygosity characteristic of the latter situation would be revealed as frequent failure of parent-to-offspring grafts and sibling-to-sibling grafts.

In order to judge if pairing is restricted to sisters, as suggested by MacGregor and Uzzell (1964), one is left with the task of examining directly the composition of bivalents, or of inferring the degree of homo- or heterozygosity that a given parthenogenetic clone might possess. The former possibility, direct determination of bivalent composition, is smple enough in principle. The administration of ^{3}H-thymidine to a parthenogenone at the synthetic phase of mitosis immediately preceding endomitosis would result in the presence of radioactive label in one member of each sister pair arising from endomitotic duplication. Autoradiography of lampbrush bivalents would then show label in half of each bivalent, should strict sister pairing be the rule. Random pairing of sisters and homologues would result in some bivalents unlabeled, some half labeled, and some wholly labeled. Crossing-over would not complicate interpretation. Although such an experiment would clearly resolve the question of bivalent composition, practical problems, such as finding the proper time in the animal's life cycle for ^{3}H-thymidine administration, make this a difficult exercise.

Judgement of the degree of homo- or heterozygosity in a parthenogenetic clone, and hence, inference of the composition of meiotic bivalents, can be based on studies of phenotypic variation. While some good studies of phenotypic variation in parthenogenones and in their sexual relatives have been performed (Zweifel, 1965), results are not easily interpreted in favor of either homo- or heterozygosity. For example, groups of *C. tesselatus* from a given locality were found to exhibit a range of variation in many characters that approximated half that seen in local populations of the sexual lizard, *C. tigris* (Zweifel, 1965). Does the relatively smaller variation seen in parthenogenones reflect the existence of homozygous clones, or does it indicate the importance of recombination in freeing variation inherent in heterozygous genomes? Complicating this question is a fundamental ignorance of the genetic regulation of most phenotypic expression. One could resort to the doctrine of superior fitness in heterozygotes and argue that parthenogenones that compete successfully with their sexual counterparts must necessarily be heterozygous. This begs an interesting question and ignores an opportunity to test notions of fitness that have become a foundation of evolutionary theory. Furthermore, such reasoning is contradicted by Darevsky's (1966) observations on the cytology of parthenogenesis in *Lacerta.* Darevsky maintains that failure of second meiotic division is the parthenogenetic mechanism operative in these lizards. Under this mechanism, crossing-over will temporarily maintain some heterozygosity, particularly at loci far from the centromere. However, the ultimate tendency is toward complete homozygosity of the genome (Beatty, 1957). Hence, if Darevsky's observations are correct, one must expect the competitively successful *Lacerta* parthenogenones to exhibit a high degree of homozygosity relative to their sexual counterparts.

Assuming that pre-meiotic endomitosis facilitates parthenogenesis in *Cnemidophorus,* a reliable indication that pairing may be strictly limted to sister chromosomes comes from studies that have deduced genotypes for certain enzymes. Parthenogenetic *Cnemidophorus* exhibit a striking incidence of heterozygosity at genetic loci determining phenotypes for lactate dehydrogenase, adenosine deaminase, phosphogluconate dehydrogenase, and NADP-dependent malate dehydrogenase (see Table 1 in Neaves, 1969). Most impressive are the genotypes for adenosine deaminase; every parthenogenetic species studied showed heterozygosity at the *ada* locus. This is clear evidence in favor of fixed heterozygosity in parthenogenetic *Cnemidophorus,* and hence, in favor of strict sister pairing at meiosis.

With the question of parthenogenetic mechanisms aired, it appears that pre-meiotic endomitosis provides a basis for understanding how a triploid, parthenogenetic *C. exsanguis* could produce an egg whose pronucleus carried an unreduced somatic chromosome complement, and how the union of this pronucleus with a haploid pronucleus from male *C. inornatus* could result in an offspring carrying the chromosomes seen in Plates 2 and 3. A precedent for these events is established in the occurrence of such a fertile union of pronuclei from parthenogenetic females and sexual males in the genus *Poecilia* (Rasch *et al.*, 1965).

There remains the question of the absence of tetraploid species of *Cnemidophorus* in spite of the existence of tetraploid hybrids in nature. Probing this question requires some indulgence in speculation, which the novelty of the subject will hopefully excuse.

The most likely reason for the absence of tetraploid species may be the failure of tetraploid hybrids to reproduce parthenogenetically. There is no evidence that the tetraploid lizard described in this study was parthenogenetically competent. The fact that it laid fully yolked eggs does not imply that these eggs either, 1) carried an unreduced chromosome complement, or 2) were capable of undergoing spontaneous embryonic development. These are two basic criteria that must be met if an interspecific hybrid is to achieve the reproductive success characteristic of existing parthenogenetic species in the genus *Cnemidophorus*. If one prefers to assume that tetraploid hybrids can reproduce parthenogenetically, then one must account for their absence as species on the grounds that no suitable ecological niche is available to them or that they cannot successfully compete with other species for a mutually suitable niche. However, the similarity of the known tetraploid hybrid to other *Cnemidophorus* suggests that it might compete with them for a currently available niche, and the behavior of the tetraploid lizard in captivity suggests that it could be successful in this regard. It seems that one must attempt instead to justify reproductive failure.

One possibility is that tetraploidy is incompatible with the mechanism of parthenogenesis operative in *Cnemidophorus*. However, the suspected mechanism, which is pre-meiotic endomitosis, has the important virtue of theoretically permitting any karyotype, regardless of ploidy, to function normally at meiosis. Given the suspected mechanism of parthenogenesis, tetraploidy itself should not be a barrier to reproduction.

The most attractive possibility is that only a small proportion of interspecific hybrids meets the basic requirements of parthenogenetic reproduction. In other words, the genetically determined compensatory events, such as pre-meiotic endomitosis and spontaneous embryonic development, which are presumably needed for parthenogenesis, may be frequently absent in F_1 hybrids. This possibility is particularly attractive, owing to the apparent genetic uniformity within existing parthenogenetic species of *Cnemidophorus*.

Maslin (1967) has demonstrated a pattern of histocompatibility in *C. tesselatus* that suggests that all diploid members of the species, even when taken from localities hundreds of miles apart, are genetically identical. Similarly, all triploid *C. tesselatus* are reciprocally histocompatible, and what is more, can accept tissue grafts from the diploids but cannot reciprocate. Biochemical evidence (Neaves, 1969) suggests that diploid *C. tesselatus* arose from interspecific hybridization between *C. tigris* and *C. septemvittatus,* two sexual species, and that triploid *C. tesselatus* resulted from the addition of a haploid genome from *C. sexlineatus,* a third sexual species, to the diploid *C. tesselatus* genome. Coupled with this evidence, Maslin's (1967) findings suggest that all existing populations of *C. tesselatus* arose from the offspring of a single hybrid individual representing a cross between *C. septemvittatus* and *C. tigris* and that all triploid *C. tesselatus* are derived from a single hybrid lizard representing a cross between *C. sexlineatus* and diploid *C. tesselatus*. The genetic uniformity in *C. tesselatus* could not exist if the species contained offspring of more than one parthenogenetic hybrid, since each individual hybrid resulting from a *C. septemvittatus* x *C. tigris* cross will carry a unique recombinant genotype.

The genetic uniformity of *C. tesselatus* points to either one or both of two possibilities, namely that interspecific hybrids are rare or that parthenogenetic competence in an interspecific hybrid is rare. The first possibility cannot be ruled out in the case of *C. tesselatus,* as no evidence is available that might suggest the frequency at which hybrids between either *C. septemvittatus* and *C. tigris* or *C. sexlineatus* and diploid *C. tesselatus* occur in nature. The first possibility can be eliminated in the case of *C. "perplexus,"* the hybrid between *C. inornatus* and *C. neomexicanus*. *C. "perplexus"* was first collected in New Mexico in 1841 (Maslin *et al.,* 1958), and since 1962, at least six of these hybrids have been captured at sites where both *C. inornatus* and *C. neomexicanus* are sympatric (Wright and Lowe, 1967a). This is a case where hybrids are rather common in nature and where they have occurred for at least 130 years without developing a parthenogenetic species. This case supports the view that genetic uniformity in existing parthenogenetic species and the absence of tetraploid species are both due to the rarity with which parthenogenetic competence is achieved in interspecific hybrids.

The establishment of a parthenogenetic species in *Cnemidophorus* may require a lengthy period of experimentation in which thousands or more individual hybrids are synthesized before a reproductively successful hybrid gene combination occurs. Nevertheless, the result may still be termed saltatory speciation, in that the divergence of the new species from its progenitors is instantaneous, deriving as it does from a single, reproductively fit individual, rather than from cumulative changes in a population over long periods of time. It seems that both *C. "perplexus"* and the tetraploid hybrid illustrated here could represent previews of species that might eventually become established in the New Mexico deserts, if a gene combination facilitating parthenogenetic reproduction ultimately occurs in one of these hybrids.

SUMMARY

A tetraploid lizard resembling *C. exsanguis* but bearing traits characteristic of *C. inornatus* is considered to have resulted from a hybrid mating in which a haploid sperm pronucleus of *C. inornatus* fused with an egg pronucleus carrying the unreduced somatic chromosome complement of *C. exsanguis*, a triploid parthenogenone. Production of such an egg by *C. exsanguis* may have relied on endomitosis in the oogonium, followed by normal meiosis operating on bivalents composed of paired sister chromosomes. This modification of oogenesis is compatible with all known aspects of parthenogenesis in *Cnemidophorus*, including the existence of apparently fixed heterozygosity within parthenogenetic species.

Most cases of parthenogenesis in *Cnemidophorus* began with the synthesis of interspecific hybrids. However, several considerations suggest that many hybrids may be generated before a parthenogenetically competent individual, capable of giving rise to a species, is produced. Among these suggestive considerations

are: 1) the synthesis of many hybrid individuals in nature, i.e., *C. "perplexus,"* without the appearance of a corresponding species, and 2) the apparent genetic uniformity of parthenogenetic species, which indicates their origin from a single hybrid individual. Thus, the appearance of a new parthenogenetic species in *Cnemidophorus* may be preceded by a period of hybridization during which large numbers of reproductively incompetent prototypes of the new species are generated.

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Table 1

	chromosome number					
	87	88	89	90	91	92
frequency	2	0	1	1	3	1

Table 1. Eight apparently complete chromosome spreads from MCZ 101991, the tetraploid hybrid *Cnemidophorus*, were studied. The frequency with which various chromosome numbers were observed in these spreads is indicated in this table.

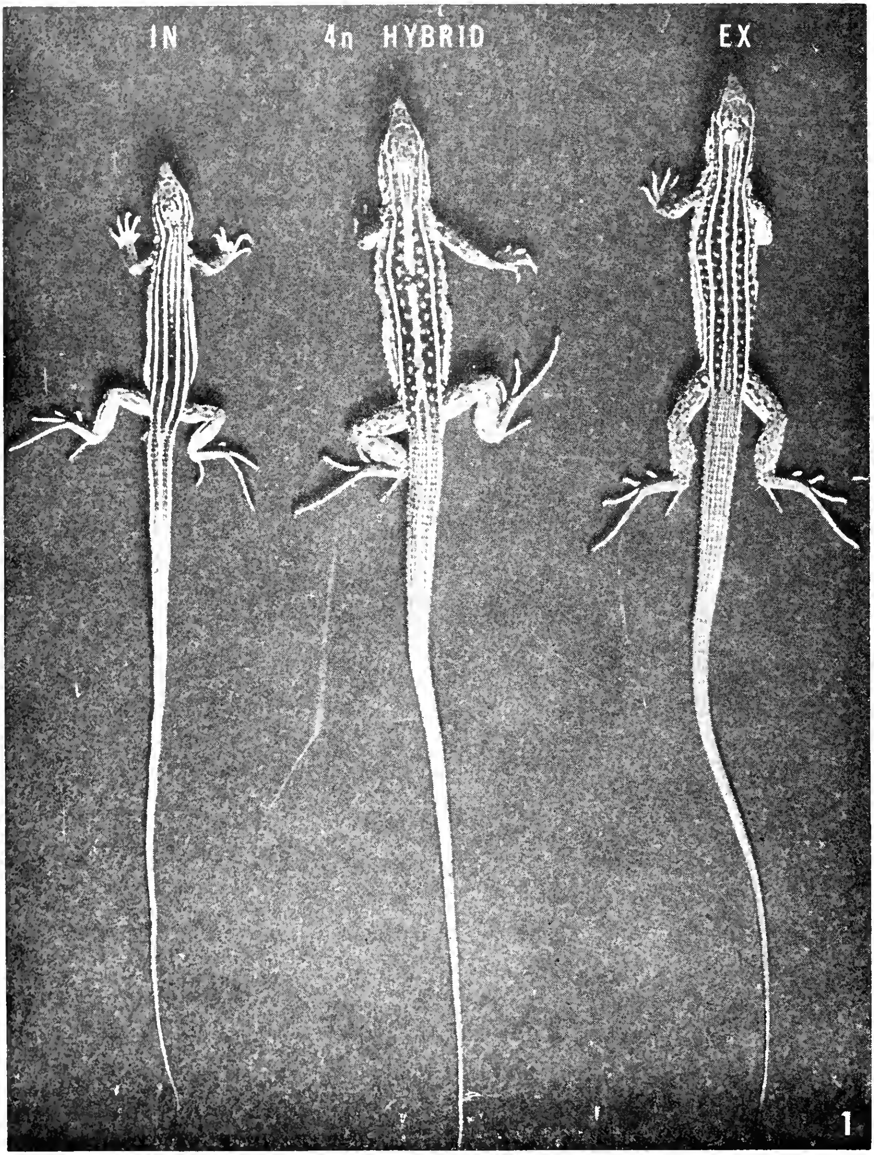
IN
4n HYBRID
EX
1

Plate I

Figure 1. A tetraploid hybrid (MCZ 101991) is shown between its suspected parental species, *C. inornatus* (IN) and *C. exsanguis* (EX). Unlike typical *C. exsanguis*, the hybrid has fused paravertebral stripes and blue on its tail and ventral surfaces. *C. inornatus* also has vivid blue on these surfaces.

2.

Plate II

Figure 2. An apparently complete set of 92 chromosomes from the tetraploid hybrid (MCZ 101991) is shown. The technique for obtaining chromosome spreads is described in the text.

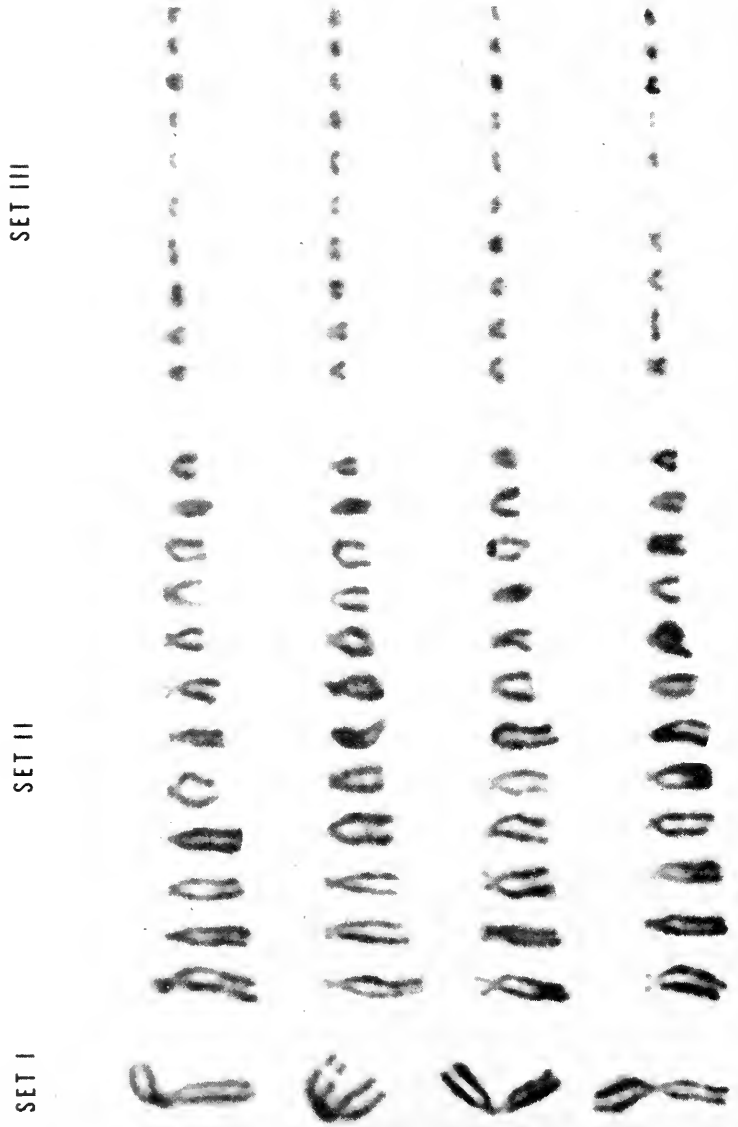

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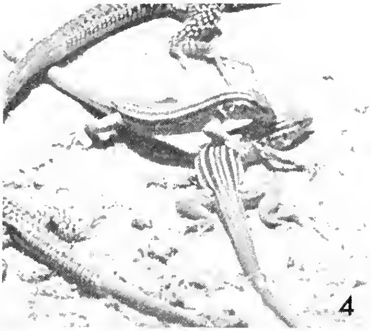
Plate III

Figure 3. A karyotype prepared from chromosomes in Fig. 2 is shown. The chromosomes have been sorted into four similar haploid complements, each resembling the haploid chromosome complement of *C. inornatus*. According to established procedure for this genus (Lowe and Wright, 1966), each haploid complement has been subdivided into three sets on the basis of chromosome size and centromere position.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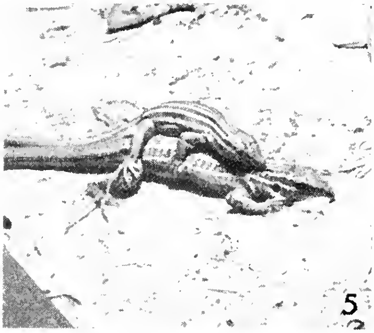
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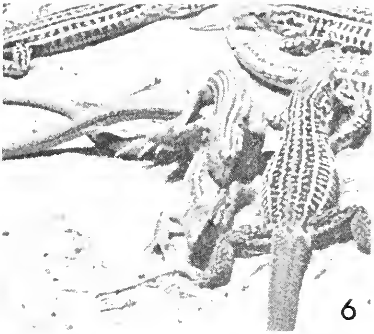
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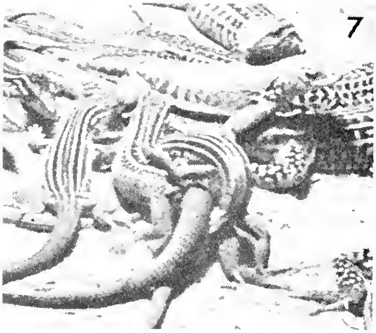
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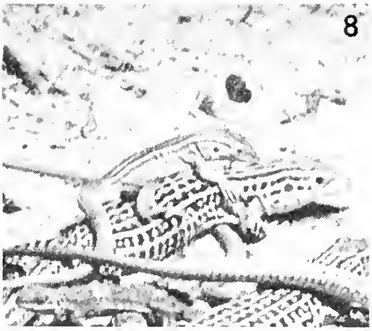
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Plate IV

Figure 4. Courtship behavior between two *C. inornatus*. The male strokes the subject's neck and head with his jaw.

Figure 5. Courtship behavior between a male *C. inornatus* and a parthenogenetic *C. exsanguis*. The male executes sinuous movements against the dorsum of the female.

Figure 6. As in Fig. 5. The male retreats along the female's dorsum, still executing sinuous movements while approaching the copulatory position.

Figure 7. As in Fig. 5. The male wedges his tail between the female's hind limbs and tail and attempts copulation.

Figure 8. Courtship behavior between a male *C. inornatus* and a parthenogenetic *C. tesselatus*. The male strokes the female's neck and head with his jaw.

Figure 9. As in Fig. 8. The male executes sinuous movements against the dorsum of the female.

B R E V I O R A

Museum of Comparative Zoology

Cambridge, Mass. 25 February, 1972 Number 382

OSTEOLOGY AND DESCRIPTION OF *THRATTIDION NOCTIVAGUS*, A MINUTE, NEW FRESHWATER CLUPEID FISH FROM CAMEROON, WITH A DISCUSSION OF PELLONULIN RELATIONSHIPS

Tyson R. Roberts[1]

Abstract. *Thrattidion noctivagus*, a new genus and species of Pellonulinae, is described from the Sanaga River in Cameroon, and an account given of its osteology. Although it agrees with *Congothrissa* in having no supramaxillary bone, the two appear not to be closely related. The ecology of African freshwater Pellonulinae is reviewed. Feeding habits range from planktophagous to insectivorous and piscivorous, with piscivores feeding largely on other species of Pellonulinae. Most or all of the species undergo diel migrations, moving upwards or shorewards at nightfall in mixed aggregations with other small fishes, chiefly translucent schilbeid catfishes and cyprinids of the subfamily Bariliinae.

Sierrathrissa Audenaerde (1969) is evidently the larva of either *Pellonula* or *Cynothrissa*. *Congothrissa* Poll (1964) is referred to the Pellonulinae. Relationships of round herrings (Dussumieriidae) that seem close to Pellonulinae are also discussed; *Laeviscutella* should be placed in the Pellonulinae.

INTRODUCTION

During fieldwork on the Sanaga River in Cameroon, I collected a minute clupeid which is clearly a member of the Pellonulinae but defies placement in any described genus. In lacking a supramaxillary bone in the upper jaw it differs from all other known clupeoids excepting *Congothrissa* (Poll, 1964) from the Congo basin. Consequently the distinctions between *Congothrissa* and

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other clupeids are not so great as they at first appeared, and it may now be referred with some confidence to the Pellonulinae. Nevertheless these two minute clupeids are not more closely related to each other than to other forms, and their relationships within the Pellonulinae are unclear. The description of this new form from Cameroon is accompanied by an account of its osteology in the hope that this will contribute to its eventual placement in a phyletic classification.

Acknowledgments. I wish to thank Mr. Thomason Newcomb for providing a congenial lodging place during my stay at Edea, and Prof. George S. Myers for reading the manuscript. The field-work was assisted financially by the Office of Environmental Sciences (contract no. RC 717634).

THRATTIDION, new genus

Type species. Thrattidion noctivagus, new species.

Diagnosis. Minute (largest specimen 21.4 mm), largely translucent Pellonulinae with direct development. Four to seven keelless prepelvic abdominal scutes and three to five (usually four) strongly keeled postpelvic abdominal scutes. All scutes with well-developed lateral (ascending) arms; pelvic scute with bifurcate or trifurcate lateral arms in larger specimens.

Supramaxillary bones absent. Maxillary toothless. Branchiostegal rays 5,5 or 5,4. Lower limb of first gill arch with 10–11 and upper limb with four short, widely spaced gill rakers.

Anal fin considerably longer than dorsal, with 23–25 rays. Origin of dorsal fin about one-third of distance between verticals through pelvic and anal fin origins. Origin of anal fin on a vertical through base of eighth or ninth dorsal fin ray. Pectoral rays usually ten.

Squamation restricted to a patch of about a dozen scales just behind head, a double row of scales on either side of prepelvic abdominal scutes, and a single row of scales on either side of postpelvic abdominal scutes. Vertebrae 45–47, about equally divided between abdominal and caudal (preural centrum 1 counted as last vertebra). Epurals three.

Remarks. If the largest specimens in my material are fully grown, *Thrattidion* is the smallest clupeoid yet described. Next smallest is *Congothrissa,* with specimens recorded up to 27.7 mm (here and throughout this paper lengths referred to are standard lengths). Almost all African freshwater clupeids have nine or more prepelvic scutes and at least seven postpelvic scutes; in these forms the prepelvic as well as postpelvic scutes are invariably serrated or keeled. The only exceptions from freshwater in Africa are 1) *Congothrissa,* which lacks abdominal scutes entirely except for a pelvic scute; 2) *Laeviscutella,* with seven to eight keel-less prepelvic scutes and five to six keeled postpelvic scutes; and 3) *Gilchristella,* with six to nine unkeeled prepelvic scutes and no postpelvic scutes. The postpelvic scutes in *Laeviscutella* are unique in lacking lateral arms as adults (lateral arms are, however, absent in the postpelvic scutes of larval *Pellonula*). The lateral arms of the pelvic scutes are usually simple; they are bifurcate in *Congothrissa* (Poll, 1964, fig. 5 on p. 14).

All previously described clupeoids have one or two supramaxillary bones except *Congothrissa.* Pellonulinae characteristically have only one supramaxillary bone (Regan, 1917); its presence has been noted in alevins of *Poecilothrissa moeruensis, Stolothrissa tanganicae* and *Microthrissa stappersii* so small that the abdominal scutes are as yet unformed (Poll, 1964: 19). The supramaxillary is reduced in size in some Pellonulinae. The maxillary bone bears teeth in all other African freshwater clupeoids except *Congothrissa* and *Potamothrissa.* Most African freshwater clupeids have 6,6 or more branchiostegal rays; *Poecilothrissa, Microthrissa* and *Potamothrissa* have as few as five; *Congothrissa* has 3,4 (here as elsewhere in this paper, the count on the left side is given first). All other African clupeoids have 16 or more gill rakers on the first gill arch, excepting *Congothrissa,* which has only seven on the lower limb and four on the upper limb of the first arch.

All other African Pellonulinae have 23 or fewer anal rays, except *Microthrissa,* which has up to 25. *Congothrissa* has only 15. In *Congothrissa* the dorsal fin origin is distinctly anterior to a vertical through origin of pelvic fins. In almost all African freshwater clupeids the anal fin origin is far behind a vertical through base of last ray of anal fin, the exceptions being larval *Pellonula,* in the metamorphosis of which the dorsal fin migrates forward, and *Microthrissa* and *Gilchristella,* in which the anal fin origin is on or only slightly posterior to a vertical through the last ray or two of the dorsal fin. In larval *Pellonula* the anal fin origin may be as far forward as posterior third of dorsal fin. All other African freshwater clupeoids have 11 or more pectoral rays.

In all other African clupeoids the body is completely scaled in adults; the highest vertebral count previously recorded is 44, with abdominal vertebrae usually more numerous than caudal (Poll, 1964, table 1). *Congothrissa* has 21+20 vertebrae. The number of epurals is unrecorded for most Pellonulinae; *Congothrissa* and larval *Pellonula* have two epurals.

Etymology. Thrattidion, Greek, neuter diminutive of Thrassa (Thratta), feminine, a small, herringlike fish.

Thrattidion noctivagus, new species

Figures 1 and 2; Table 1

Holotype. MCZ 48161, 21.4 mm, Sanaga River at Edea, Cameroon, 4 May 1971.

Paratypes. MCZ 48162, 175 specimens, 9.8–20.7 mm (of which 11 specimens 10.4–20.7 mm cleared and stained), Sanaga River at Edea, 17 April and 4 May 1971.

The specimens are in excellent condition. They were fixed in formalin immediately after capture and placed in Nalgene plastic bottles containing only small specimens and filled to the brim to prevent damage by shaking. Consequently, the fins are in perfect condition on almost all specimens, and the squamation completely intact. After three months in formalin they were soaked in water for two days, in 40 percent ethyl alcohol for two more days, then transferred to 70 percent ethyl alcohol for permanent preservation.

General characteristics. Snout short and rounded. Jaws equal. Body relatively compressed, depth 3.55–5.0, increasing with size.

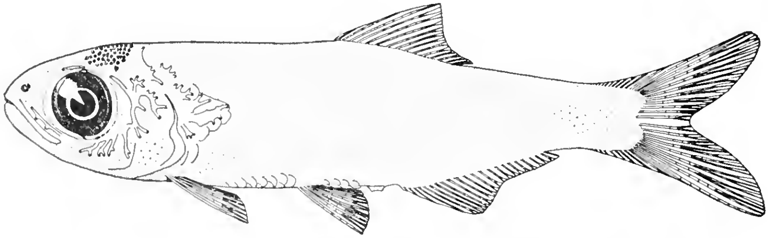

Figure 1. *Thrattidion noctivagus,* 19.4-mm paratype. MCZ 48162.

Eye large, 8.5–9.9, its center on or only slightly above longitudinal midline of body (center of eye distinctly above midline in most Pellonulinae, markedly so in *Odaxothrissa* and *Cynothrissa*). Adipose eyelid well developed. Dorsal fin origin distinctly posterior to a vertical through pelvic origin, slightly closer to end of hypural fin than to snout tip. Anal fin long, its origin on a vertical through base of eighth or ninth dorsal fin ray.

Pelvic, dorsal, and anal origins on verticals through 15th, 19th, and 25th vertebrae. Pelvic fin relatively large, only slightly smaller than pectoral, its origin closer to pectoral fin origin than to anal fin origin. Dorsal and anal fin margins gently falcate, dorsal height about 1.5 times anal height. Caudal fin deeply forked, upper and lower caudal lobes identical in size and shape.

For proportional measurements see Table 1.

Fin counts (Table 1). Dorsal fin with 14–16 rays, first three or four simple, last divided to base. Anal fin with 23–25 rays, first four or five simple, last divided to base. Length of first dorsal and anal rays variable, minute in some specimens. Pectoral fins usually with ten rays. Pelvic fins with either seven or eight rays. Principal caudal rays invariably 10+9, upper procurrent rays 12–13 and lower procurrent rays eight to ten.

Squamation (Fig. 1). Scales largely absent, restricted to a double row of four to nine scales superficial to lateral arms on each side of prepelvic scutes, a single row of four or five scales superficial to lateral arms on either side of postpelvic scutes, and about a dozen scales in four or five short rows immediately behind head. The latter scales are deeply embedded in tough tissue in which the trunk portion of the cephalic laterosensory system ramifies, and can only be fully discerned in cleared and stained specimens. A 20.7-mm specimen has 12 scales in four rows (three in the uppermost row, five in the second row, one in the third row, and three in the lowermost row); a 19.1-mm specimen 11 scales in five rows (2–4–1–3–1); and an 18.6-mm specimen 11 scales in five rows (1–2–4–2–2). Most of the scales in the longest row are perforated by laterosensory canals. Larval *Pellonula* of 36–38 mm have the body naked except for two or three scales immediately behind the head and complete squamation on the caudal peduncle.

Standard length	Holotype 21.4 mm	[illegible]	[illegible]	Specimen in Fig. 1 19.4 mm	19.1 mm	Specimen in Fig. 13 18.6 mm	17.[illegible] mm	17.1 mm	15.[illegible] mm	14.3 mm	12.1 mm	11.0 mm	10.4 mm	Range, Frequency, or Comment
Head	3.6	3.7	3.9	3.6	3.7	3.65	3.56	3.6	3.6	3.6	3.7	3.55	3.7	3.55-3.9
Eye	9.7	9.9	9.5	9.0	9.1	8.9	9.4	9.5	9.0	9.5	9.3	[illegible]	9.0	8.5-9.9
Snout	13.4	16.0	16.6	13.6	17.4	14.3	14.2	12.2	14.4	13.0	15.2	12.2	13.0	12.2-17.4
Depth	3.55	4.1	4.0	4.1	3.9	4.15	4.35	4.3	4.3	4.3	4.65	5.0	4.7	3.55-5.0
Snout-dorsal origin	1.66	1.90	1.65	1.86	1.87	1.86	1.87	1.88	1.88	1.90	1.86	1.82	1.79	1.79-1.90
Snout-anal origin	1.60	1.55	1.66	1.58	1.54	1.54	1.60	1.56	1.56	1.55	1.60	1.60	1.55	1.54-1.90
Snout-pelvic origin	2.04	2.10	2.08	2.06	2.03	2.10	2.06	2.08	2.05	2.07	2.09	2.04	1.98	1.98-2.10
Depth caud. ped.	8.9	9.0	9.1	9.5	9.1	9.3	9.1	9.0	9.3	8.9	9.7	10.0	9.0	8.9-10.0
Length caud. ped.	6.5	7.1	6.9	6.8	7.35	7.45	7.1	7.4	7.0	7.15	6.05	6.5	6.9	6.05-7.45
Pect. length	5.5	5.8	5.6	5.4	5.5	5.3	5.4	5.5	5.45	6.0	-	5.7	-	5.3-6.0
Pelvic length	6.9	7.1	6.4	6.7	7.6	7.15	7.7	6.8	6.9	7.15		6.5		6.5-7.6
Anal base	3.7	3.8	4.0	4.05	4.0	3.9	3.6	4.0	3.6	3.8	4.7	5.65	4.6	3.6-5.65
Prepelvic scutes	-	5	7	-	7	4	6	6	4	6	4		4	4-7
Postpelvic scutes		4	5	-	4	4	3	4	4	4	4		2	2-5
Branchiostegal rays	-	5,5	5,4	-	5,5	5,5	5,5	5,4	5,5	5,5	5,5		1,4	5,5(7), 5,4(2), 1,4(1)
Gill rakers		5+11	-	-	-	5+11				-				5+11
Supraneurals	-	10	12	-	12	11	11	11	10	12	[illegible]		[illegible]	10-12
Epurals	-	3	3	-	3	3	3	3	3	3	3		-	3
Vertebrae	-	47 (24+23)	45 (23+22)	-	46 (23+23)	45 (23+22)	47 (23+24)	45 (22+23)	45 (23+22)	47 (23+24)	46 (23+23)	-	46 (23+23)	45(1), 46([illegible]), 47(3)
Dorsal fin	iv 11	iii 12	iii 12	iv 12	iv 11	iii 12	iii 11	iii 11	iv 10	iv 11				14(3), 15(6), 16(1)
Anal	v 18	v 19	[illegible] 18	v 18	[illegible] 18	iv 19	iv 21	iv 19	iv 20	v 19			-	23(6), 24(3), 25(1)
Pectoral	10,10	10,10	10,10	10,10	10,10	11,11	10,10	9,10	10,10	10,10	10,9			[illegible], 10,10
Pelvic	8,8	8,8	7,7	8,8	7,7	8,8	8,8	8,8	7,7	7,7	7,7	-	-	7,7(5), 8,8(6)
Caudal	12X-IX10	12X-IX9	12X-IX10	12X-IX9	12X-I[illegible]	12X-IX9	12X-IX10	12X-IX10	12X-IX10	13X-IX10	9X-I[illegible]		[illegible]X-IX[illegible]	[illegible] 12X-IX10

TABLE 1. *Thrattidion noctivagus.* Proportions expressed as times in standard length, fin ray counts, and other counts. In counts of branchiostegal rays and pectoral and pelvic fin rays, first numeral is for left side, second numeral for right side.

Cephalic laterosensory system (Fig. 2). Cephalic laterosensory system with supraorbital, infraorbital, mandibulo-preopercular, pterotic, opercular, occipital and lateral canals (cf. Wohlfahrt, 1937). A supratemporal branch arises from the supraorbital; in some specimens it appears to enter the occipital canal, but in others it definitely stops short of reaching the occipital canal. Figure 2 is based on a 15.1-mm specimen that had a drop or two of Ehrlich's hematoxylin placed on its head. Of several specimens thus treated, its canals showed up the best. The mandibular portion of the mandibulo-preopercular canal could not be distinguished on this specimen, but it appeared in others. The main canals appear to join in the manner illustrated, but the figure should be used with caution. The canals did not take up stain evenly, and comparisons with less well-stained specimens did not eliminate my reservations about the interpretation. I could find no connections between the laterosensory systems of the two sides of the head. In particular the ethmoidal commissure is absent.

Dentition. Premaxillary with four to seven small conical teeth solidly implanted, and two to four replacement teeth in the gum.

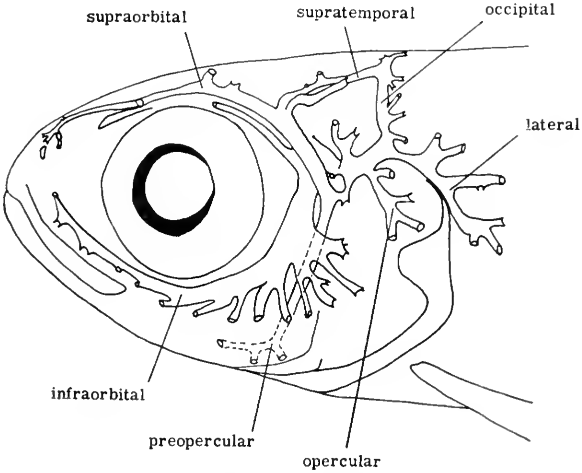

Figure 2. *Thrattidion noctivagus,* cephalic laterosensory canals of 15.1-mm paratype.

Maxillary edentulous. Dentary with a dozen to 15 small conical teeth solidly implanted and several teeth in stages of replacement. Palatine with one to three teeth, roof of mouth otherwise edentulous. Fifth ceratobranchial and upper pharyngeal with numerous small teeth, gill arches otherwise edentulous.

Abdominal scutes. Four to seven prepelvic scutes, unkeeled, with well-developed lateral arms. Pelvic scute keel-less, with bifurcate or trifurcate lateral arms in largest specimens. Postpelvic scutes three to five, usually four, with well-developed keels and lateral arms. Specimens as small as 12–14 mm with full complement of scutes (Table 1).

Coloration of preserved specimens. Body opaque white, without melanophores, or with only a few melanophores in some specimens at base of anal fin rays and on caudal peduncle. No lineum argenteum. Peritoneum probably opaque white and body otherwise translucent in living specimens. A dense cluster of large melanophores over brain. Specimens were collected only at dusk or at dawn and immediately preserved, so observations were not made on their appearance in life.

Additional characteristics. See generic diagnosis and osteological account.

OSTEOLOGY

Neurocranium (Figs. 3–5). Anterior and posterior frontal fontanelles very large. Anterior margin of anterior frontal fontanelle formed by diverging posterior arms of mesethmoid. Posterior frontal fontanelle incompletely divided into right and left halves, the median extension of supraoccipital failing to reach posteromedial border of frontal bones. Of the types of clupeoid posterior frontal fontanelles figured by Whitehead, those of *Spratelloides* and *Ehirava* (Whitehead, 1963a, fig. 1) resemble most closely that of *Thrattidion.* As in *Ehirava,* a median extension of the frontals forms a distinct wedge in the posterior frontal fontanelle. Frontals slightly separated at midline of skull. Anterior fontanelle about half as wide as posterior fontanelle.

Mesethmoid solidly ossified, with well-developed anterolateral and descending processes, and diverging posterior processes firmly united to anterior ends of frontal bones. Lateral ethmoid with a large cartilaginous portion ventrally.

Pre-epiotic fossa large, an anteroventrally directed process of parietal bone only partially separating it from temporal foramen. Pre-epiotic fossa bordered mainly by frontal and parietal; temporal foramen bordered by parietal, epiotic and pterotic (Fig. 3).

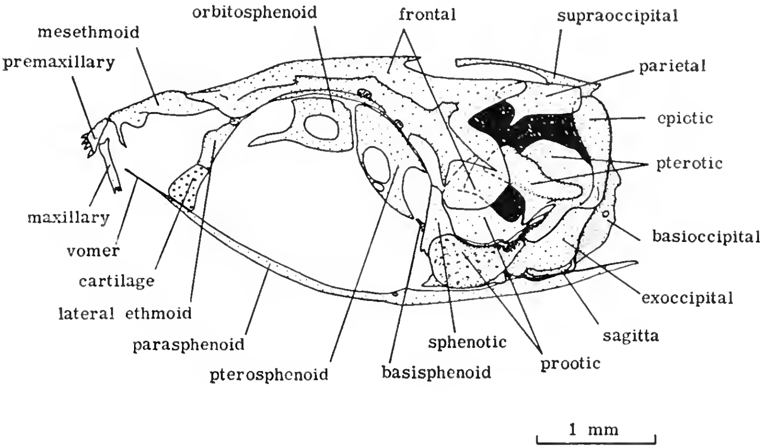

Figure 3. Cranium of 18.6-mm *Thrattidion noctivagus*, lateral view.

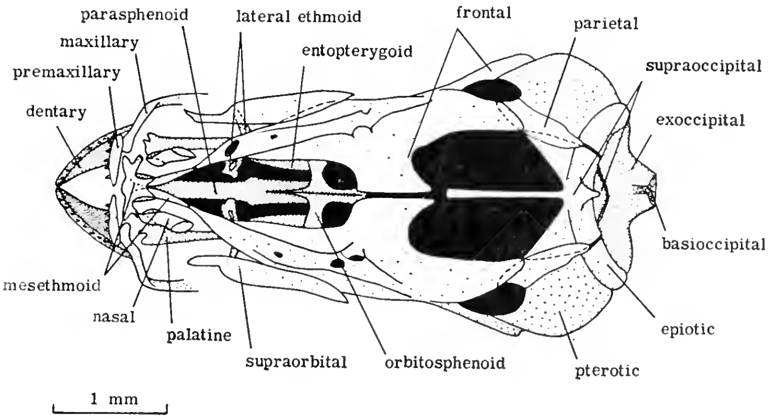

Figure 4. Cranium of 20.0-mm *Thrattidion noctivagus*, dorsal view.

A large foramen bordered by the frontal, pterotic, and prootic opens into the recessus lateralis (Fig. 3). It seems likely that all of the main branches of the cephalic laterosensory system enter the recessus through this one large opening. A laterally directed ridge on prootic extending onto anteroventral portion of pterotic, both bones apparently contributing to this ridge posteriorly.

Intercalar bone present, a small, oval bone lying in the interosseous membrane between exoccipital, pterotic, and prootic, its edges touching each of these bones (Fig. 5). When the pectoral girdle is removed from the skull, the intercalar is invariably carried away with the lower limb of the posttemporal bone.

I am unable to find a passageway through which anterior extensions of the swim bladder might gain the prootic bulla. A small oval opening in the exoccipital bone opens into a passageway directed dorsoposteriorly, away from the prootic. This opening and its passageway do not have counterparts in the prootic. The opening is flush with the exoccipital, not funnel-shaped as one would expect of an opening for the swim bladder; it probably serves for passage of cranial nerves. A large dorsal foramen of the prootic is readily visible.

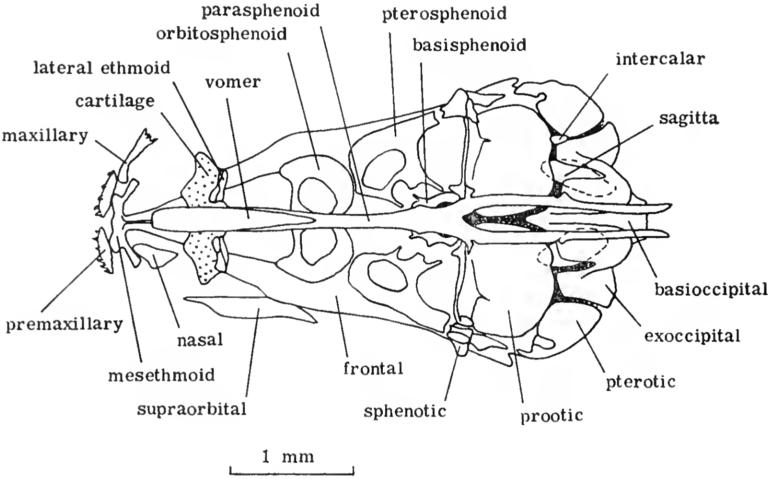

Figure 5. Cranium of 18.6-mm *Thrattidion noctivagus,* ventral view.

Orbitosphenoid, pterosphenoids, and basisphenoid well developed, with large lateral foramina. Orbitosphenoid with an anteriorly directed process.

Vomer edentulous, elongate, and flattened. Parasphenoid uniformly slender, dividing where it meets base of neurocranium into a pair of posterior processes, the tips of which extend beyond occiput to immediately below second or third vertebral centrum (Fig. 5).

Jaws (Figs. 6–7). Premaxillaries separated at midline, each bearing four to seven conical teeth. Maxillary relatively slender, extending to below anterior third of eye, toothless. Supramaxillaries absent. Dentary with a low coronoid process and a single row of about a dozen to 15 conical teeth. Articular with a posteriorly directed process posterior to quadrate socket.

Suspensorium (Fig. 7). Palatine bifid at its tip, bearing one to three conical teeth. Suspensorium otherwise edentulous. Ectopterygoid slender anteriorly, moderately expanded where it

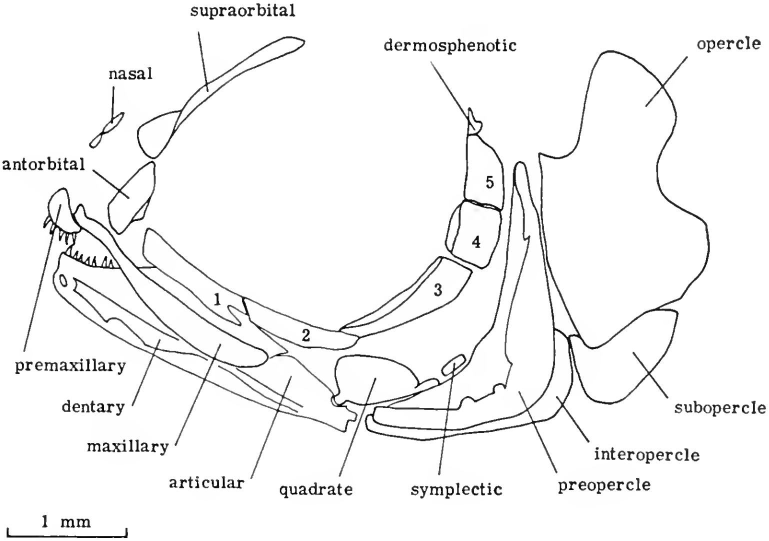

Figure 6. Jaws and facial bones of 20.7-mm *Thrattidion noctivagus,* lateral view (1–5 = circumorbital bones).

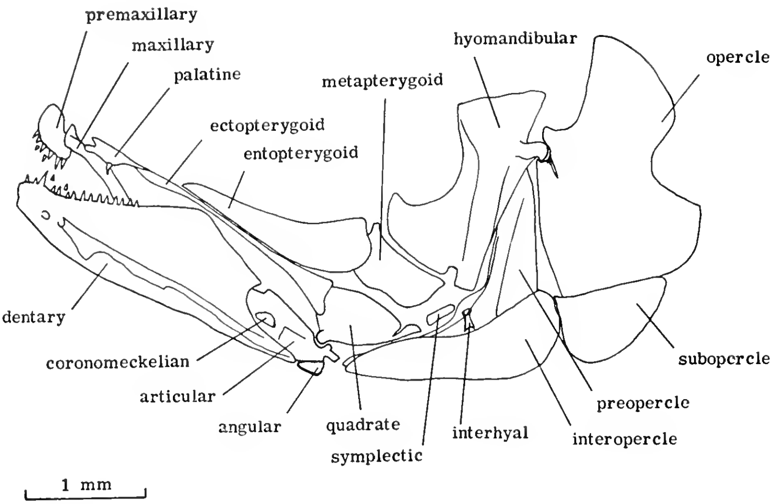

Figure 7. Jaws, suspensorium, and opercular bones of 20.7-mm *Thrattidion noctivagus,* medial view.

attaches to dorsoanterior portion of quadrate bone. Entopterygoid and metapterygoid well developed. Sphenotic and pterotic articular surfaces of hyomandibular not strongly differentiated from its main body. Hyomandibular with a distinctively shaped lamella dorsoanterior to its symplectic process, the ventral margin of this lamina separated from symplectic process of hyomandibular by a notch. Symplectic bone relatively small, lying midway between hyomandibular and quadrate but in contact with neither. Quadrate with a posterior process directed towards anterior end of symplectic.

Facial bones (Fig. 6). Circumorbital series with an antorbital followed by six infraorbitals, a pattern found in generalized members of many teleostean groups, including Clupeomorpha (Nelson, 1969). Dermosphenotic greatly reduced. Infraorbitals shallow, without extensive ventral laminae. Supraorbital bone large and elongate.

Nasal bones widely separated, moderate in size, bearing a tube for laterosensory canal.

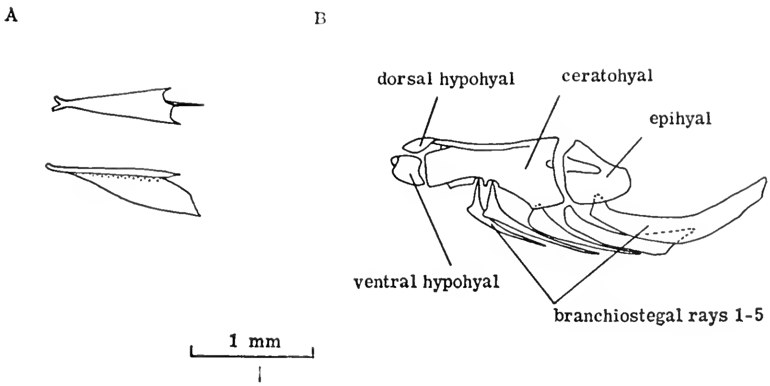

Figure 8. A. Urohyal bone (upper: dorsal view; lower: left lateral view); and B. hyoid arch (basihyal and interhyal removed), lateral view, of 20.7-mm *Thrattidion noctivagus.*

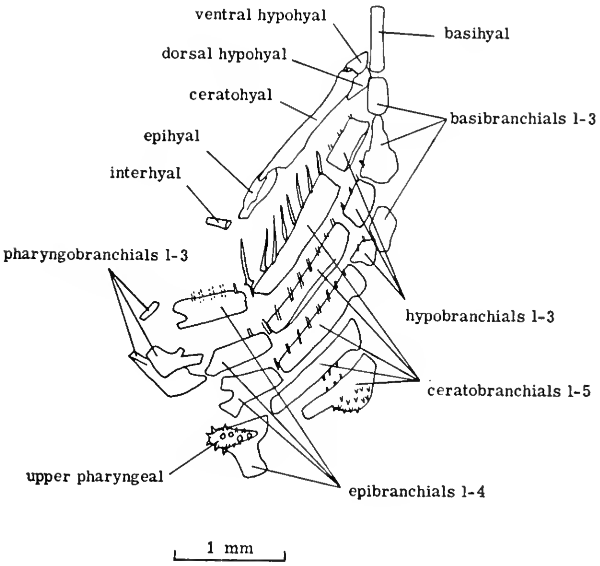

Figure 9. Hyoid arch (branchiostegal rays removed) and branchial arches of left side, of 20.7-mm *Thrattidion noctivagus.* Dorsal view, upper limb of gill arches unfolded and pinned to the side.

Opercular series complete; dorsoanterior corner and posterior margin of opercle deeply incised.

Hyoid and branchial arches (Figs. 8–9). The branchial skeleton of *Thrattidion* differs from that in most clupeids in several respects; this is perhaps mainly due to its reduced size. Gill rakers and pharyngeal dentition reduced. Branchial skeleton lacking elongation of individual parts typical of most living clupeoids (and which is at least partly correlated with increased numbers of gill rakers and branchiostegal rays). Basihyal well ossified and toothless (usually cartilaginous and tooth-bearing in Pellonulinae, Nelson, 1967: 393). Pharyngeal teeth restricted to upper pharyngeal and ceratobranchial 5. Gill rakers few in number, widely spaced, and relatively short. The 20.7-mm specimen represented in Figure 9 has 15 rakers on the first gill arch, including a few that are rudimentary or unossified. Gill rakers progressively reduced in size and number on arches 2–5.

The hyoid arch has paired ventral and dorsal hypohyals, ceratohyal, epihyal and interhyal, and a median basihyal. Branchiostegal rays 5,5 in eight specimens, 5,4 in two; generally one branchiostegal ray attached to epihyal, three to ceratohyal, and one branchiostegal ray in between, not attached to either bone.

Individual ossified parts of the branchial arches are median basibranchials 1–3, and paired hypobranchials 1–3, ceratobranchials 1–5, epibranchials 1–3, suspensory pharyngeals or infrapharyngeals 1–3, and upper pharyngeals.

Pectoral girdle (Fig. 10). Two slender postcleithra, distal end of second postcleithrum attached by ligament to distal end of first rib. Four proximal radials and about six distal radials (distal radials absent in clupeoids other than Chirocentridae, according to Whitehead, 1963a and Greenwood, 1968). Other bones in pectoral girdle: extrascapular, posttemporal, cleithrum, coracoid, scapula, mesocoracoid.

Pelvic girdle (Fig. 11). Pelvic bones relatively elongate and slender. Articular portion of pelvic bone with a deep, elongate notch. Three pelvic radials. Pelvic splint present (pelvic splint absent in clupeoids, according to Whitehead, 1963a and Greenwood, 1968).

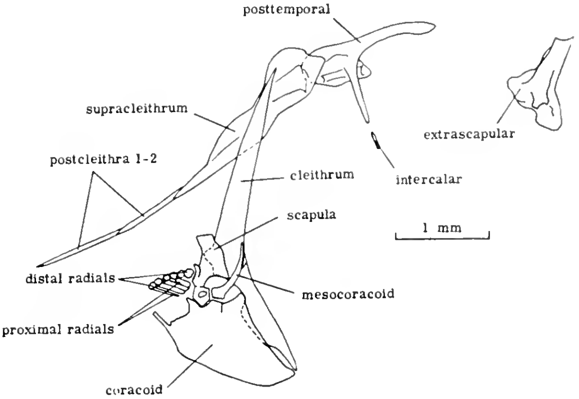

Figure 10. Pectoral girdle of 20.7-mm *Thrattidion noctivagus*, medial view. Inset, upper right hand corner: extrascapular bone of same specimen, lateral view.

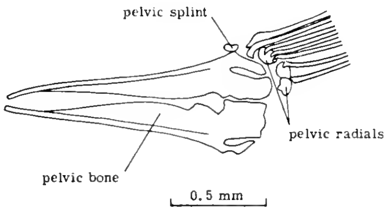

Figure 11. Pelvic girdle of 18.6-mm *Thrattidion noctivagus*, dorsal view.

Abdominal scutes (Fig. 12). Prepelvic scutes four to seven, keel-less, with slender lateral arms. Pelvic scute enlarged, with bifurcate or trifurcate lateral arms in larger specimens (specimen figured has two branches on one side, three on the other). Postpelvic scutes usually four, invariably with well-developed keels. Specimens only 12.1 and 14.3 mm have a full complement of pelvic scutes (Table 1). In a 10.4-mm specimen only the pelvic scute is visible. In a 12.1-mm specimen the scutes are represented only by the lateral arms, which ossify separately. With growth they fuse to form a median scute. In the middle of the scutes in larger specimens is sometimes a foramen or gap in the ossification where the two halves are incompletely fused, as in the second three prepelvic scutes in the 20.7-mm specimen figured.

Vertebral column and associated bones (Fig. 13). In a series of ten specimens the vertebral count ranges from 45 to 47; abdominal and caudal vertebrae about equal in number. The counts and their frequencies are 22+23 (1); 23+22 (3); 23+23 (3); 23+24 (2); and 24+23 (1). The third vertebra is the first to bear ribs. The tips of ribs 4–7 to 2–9 are bound by connective tissue to the lateral arms of the prepelvic scutes; rib 9 or 10 to the pelvic scute, and ribs 10 or 11 through 15 to the postpelvic scutes.

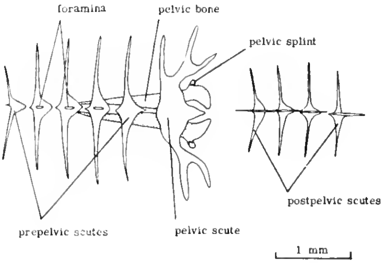

Figure 12. Abdominal scutes of 20.7-mm *Thrattidion noctivagus,* ventral view.

There are four distinct sets of intermuscular bones: 1) epaxials or epineurals, 2) epicentrals, 3) anterior hypaxials or epipleurals, and 4) posterior hypaxials. The epaxials begin at about the eighth vertebra and continue to the second preural centrum. The epicentrals begin at the first vertebra and continue to the second preural centrum. The epicentrals begin at the first vertebra and extend to about the first caudal vertebra. The anterior hypaxials or epipleurals begin at the second vertebra and extend to the last abdominal vertebra. The posterior hypaxials begin at about the fourth or fifth caudal vertebra and extend to about the second preural centrum. All of the intermuscular bones are relatively simple; in particular the epicentrals, epaxials, and posterior

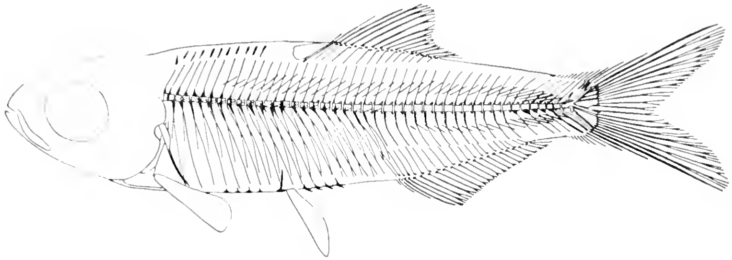

Figure 13. Axial skeleton of 18.6-mm *Thrattidion noctivagus*, lateral view.

hypaxials are unbranched. The anterior hypaxials are almost as long as the ribs and are expanded near their proximal ends into a triangular lamella.

There are ten to twelve supraneural bones. The first supraneural lies just dorsal to the first neural spine; the last lies over the tenth to twelfth neural spine.

Caudal skeleton (Fig. 14). Caudal skeleton with six hypurals, hypural 1 separated from ural centrum 1 by a distinct gap. Preural centrum 1, ural centrum 1 and ural centrum 2 fused.

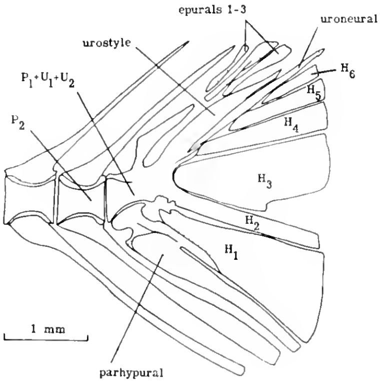

Figure 14. Caudal skeleton of 20.7-mm *Thrattidion noctivagus*, lateral view (H_1 - H_6 = hypurals; $P_1 + U_1 + U_2$ = fused preural centrum 1, ural centrum 1 and ural centrum 2; P_2 = preural centrum 2).

Hypural 2 fused with ural centrum 1. Parhypural (= hemal spine of preural centrum 1) closely articulated with centrum of preural centrum 1, its dorsal margin with a very large, laterally directed flange or hypurapophysis. The single uroneural lies free against the ural spine and does not extend anteriorly to the ural centrum 1. Epurals three.

Caudal fin lobes almost perfectly symmetrical. Principal caudal rays invariably ten in upper lobe and nine in lower lobe. Specimens 14 mm upwards have 12 or 13 upper and eight to ten lower procurrent rays, all of which take up alizarin stain. Hypurals 1 and 3 expanded, hypural 2 slender. Hypural 1 articulating with six principal rays, hypural 2 with two, and hypural 3 with five.

DISCUSSION

Ecology of African Pellonulinae. Relatively little has been published on the ecology of African Pellonulinae. Poll (1953) and Coulter (1962) gave some information about *Limnothrissa* and *Stolothrissa*, the two genera endemic to Lake Tanganyika (Tanganyika is the only East African lake with endemic clupeids). Reynolds (1970; 1971) reported on feeding habits and schooling and migration of *Pellonula* and *Cynothrissa* in man-made Volta Lake in Ghana. The ecology of Pellonulinae in the Congo basin is unknown, excepting brief remarks on food or general habitat by Gosse (1963) and Matthes (1964).

Stolothrissa feeds on zooplankton. Juvenile *Limnothrissa* feed on zooplankton, but adults are macrophagous and evidently feed to some extent on larval *Stolothrissa*. *Stolothrissa* are apparently the only food of the endemic centropomid *Luciolates* (Poll, 1953). Some riverine Pellonulinae are insectivorous to a greater or lesser extent. Mature *Povilla* (Ephemeroptera) nymphs were the dominant item in the food of *Pellonula* in Volta Lake, with terrestrial insects and aquatic stages of Diptera contributing significantly to the rest of the food taken by them (Reynolds, 1970, table 1 on p. 578). Of the Congo species, *Potamothrissa obtusirostris* feeds largely on aquatic insects, *Nannothrissa parva* on phytoplankton (unicellular algae, diatoms) and zooplankton (entomostracans), and *Odaxothrissa losera* on shrimps, *Povilla* nymphs, and small fish (mainly other clupeids) (Matthes, 1964).

The West African *Cynothrissa* (which superficially resembles *Odaxothrissa*) is piscivorous, feeding largely on *Pellonula* in Volta Lake (Reynolds, 1970).

Reynolds (1971) found that *Pellonula* was among several small species in Volta Lake that migrate upwards [and shorewards?] at night in mixed aggregations, and compared this migration to that of *Stolothrissa* and *Limnothrissa* in Lake Tanganyika. It should be noted that a similar phenomenon occurs in the Pellonulinae of the Congo basin. *Poecilothrissa, Microthrissa royauxi, Potamothrissa,* and *Odaxothrissa* evidently migrate upwards or shorewards at dusk in aggregation with other small fishes, principally the cyprinids *Chelaethiops, Engraulicypris* and *Leptocypris,* and the schilbeids *Parailia* and *Pareutropius.* These aggregations apparently do not remain close to the shore all night long, but reform there for another short period around dawn. Reynolds (1971) discusses the selective advantages of such diel migrations, which are evidently primarily improved feeding opportunities, coupled with predator avoidance and possibly a metabolic advantage in living at lower temperatures and feeding at higher ones.

Thrattidion was collected only at dusk and dawn, by dipnetting in water two to three feet deep flowing swiftly along the low retaining wall that extends for about a mile above the hydroelectric dam on the Sanaga River at Edea. The only other fishes caught with it were small characids, tentatively identified as juvenile *Alestes* and *Virilia.* Its stomach contents included much unidentified material and some terrestrial insects (either Diptera or Hymenoptera) (kindly identified by Dr. David Rentz).

The larval stage of Pellonula. The only other species of Clupeidae known or likely to occur in the Sanaga River much above its mouth are *Pellonula* and *Cynothrissa.* Although adults of these genera can be distinguished, they evidently are closely related. Distinguishing characters for the juveniles have not been reported. Svensson (1933) described larvae of *Pellonula* from the Gambia River. I have collected similar juveniles in the Tano River and in the Sanaga River along with adults of *Pellonula,* and am inclined to believe that they are the same species. They are radically different from *Thrattidion.* The larvae and juveniles of *Cynothrissa* are yet to be described; presumably they are similar to those of *Pellonula.* There can be little doubt that *Sierrathrissa*

(Audenaerde, 1969), from Sierra Leone, is based on the larvae of either *Pellonula* or *Cynothrissa*. My specimens of larvae from the Tano and Sanaga rivers agree in almost all respects with the figure and description of *Sierrathrissa* except that they have more vertebrae (24+17 instead of 19+17) and are incompletely scaled (scales present only immediately behind head and on caudal peduncle). Audenaerde reported "approximately 37–38 scales in a longitudinal line, about one scale row for each body segment, scales hardly visible on posterior part of body in largest specimens." Svensson (1933: 47–48, fig. 16) describes the larva of *Pellonula* (identified as *P. vorax*) and its metamorphosis. His description of the larva agrees very well with that of *Sierrathrissa*. Concerning the metamorphosis, we may quote Svensson:

> When the fry is about 30 mm. long, an obvious and rapid change takes place in its appearance. The transparency disappears, and pigment commences to develop on the back; the head and the anterior part of the body grows thicker and higher, and the dorsal fin advances forwards so that its front part becomes situated above, or slightly behind, the vertical of the origin of the ventral fins. The gill-rakers increase in number to 25 (they are 25–30 in the adult fish, according to Boulenger) and the number of rays in the pectoral and ventral fins, as well as in the branchiostegal membrane, increases to that in the adult. It may be presumed that those changes represent a kind of metamorphosis, corresponding to that in other *Clupeids*, and in *Elopids*, and *Albulids*.

Svensson found that larval *Pellonula* have nine to ten pectoral rays, seven pelvic rays, rudimentary abdominal scutes, about 14 gill rakers on lower part of first arch, and only three branchiostegal rays visible (in specimens stained with alizarin). He did not mention the presence of scales. Adult *Pellonula* have 14 pectoral rays, eight pelvic rays, 12–14 prepelvic and eight to nine postpelvic abdominal scutes, all strongly serrate and with lateral arms, 27–32 gill rakers on the first gill arch, and six branchiostegal rays. Despite statements to the contrary (Ridewood, 1904; Poll, 1964, table 1 opp. p. 29), adult as well as larval *Pellonula* bear numerous fine teeth on the maxillary bone (Regan, 1917; personal observation). The supramaxillary bone is well developed in both adults and larvae.

Concerning other African Pellonulinae, *Limnothrissa* and *Stolothrissa* undergo profound changes in morphology from eight or ten to 25 mm, including considerable forward migration of the dorsal fin (Poll, 1953). *Microthrissa miri*, from the Niger and Chad basins, has a slender larva in the metamorphosis of which the dorsal fin position changes relatively little (Daget, 1954: 66–67, fig. 12; Blache, 1964: 58–59, fig. 21 on p. 418). Development is direct or nearly direct in at least some riverine Pellonulinae of the Congo basin. *Thrattidion* has direct development: specimens as small as 12 and 14 mm have the main features of the larger specimens, including full or nearly full complements of abdominal scutes, scales, fin rays, branchiostegal rays, gill rakers, and teeth. Fin placement remains unchanged. The most notable change is a regular increase in depth of body from 4.7–5.0 in 10–11-mm specimens to 3.55–4.1 in 19–21-mm specimens (Table 1), at which size *Thrattidion* is deeper bodied than any other African freshwater clupeid.

Systematic status of Congothrissa. In erecting a new family for *Congothrissa*, Poll (1964) stressed its 1) lack of prepelvic and postpelvic abdominal scutes; 2) unkeeled pelvic scute [with branched lateral arms]; 3) terminal mouth; 4) lack of supramaxillary; 5) short lateral [medial?] branch of supraorbital canal; 6) relatively large scales; and 7) low branchiostegal ray count. Characters 1, 4, 6, and 7 are loss or reduction characters such as one commonly finds in teleosts of greatly reduced size. Reliance on such characters leads to classifications in which the smallest representatives of a group are placed in either monotypic or polyphyletic taxonomic categories. Reduction of scutes has occurred in many lines of clupeoids. *Thrattidion* has also lost the supramaxillary. The branchiostegal ray count of *Thrattidion* (5,5 or 5,4) is intermediate between that of *Congothrissa* (3,4) and other Pellonulinae. *Congothrissa* has about 24 scales in a lateral series (Poll, 1964, table 1; fig. 1 opp. p. 8). Judging from the figure of *Congothrissa,* it may have 25 scales in a lateral series, since there are usually deeply embedded scales immediately behind the head that are not externally visible in Pellonulinae. Some specimens of *Poecilothrissa* have as few as 28 scales in a lateral series (personal observation). An unkeeled pelvic scute with branched lateral arms similar to that in *Congothrissa* is found in *Thrattidion.* I find nothing in the nature of the supraorbital canal of *Congothrissa* to distinguish it from other Pellonulinae. A terminal mouth occurs in *Thrattidion* and in some of the Congo Pellonulinae.

In conclusion, *Congothrissa* does not merit placement in a family by itself. It may either be placed in a separate subfamily, Congothrissinae, or preferably in the Pellonulinae. Its closest relatives are to be sought among the Pellonulinae in the Congo basin.

Systematic status of Thrattidion. Several of the distinguishing characteristics of *Thrattidion* — absence of supramaxillary, toothless maxillary, reduced squamation and scutellation, and low branchiostegal and gill raker counts — are loss or reduction characters more or less shared with *Congothrissa.* On the other hand, *Thrattidion* has more vertebrae (45–47), anal rays (23–25), and epurals (three) than are recorded for almost any other African Pellonulinae (*Microthrissa royauxi* has as many as 24 or 25 anal rays), and is relatively deeper bodied than any of the others at comparable size. If Congothrissinae is recognized, then a separate subfamily might also be justified for *Thrattidion.* It is preferable to place them both in the Pellonulinae.

Relationships of Dussumieriidae. Whitehead (1963b) advanced a theory with important implications for clupeoid phylogeny, namely, that Dussumieriidae are modern representatives of a primitive group of scuteless clupeoid. This theory is strongly contraindicated by the following considerations:

1) All Dussumieriidae have at least a pelvic scute that is apparently homologous with the prepelvic and postpelvic scutes in other clupeoids.

2) Several dussumieriids have either prepelvic or postpelvic scutes or both: *Etrumeus* (subfamily Dussumieriinae) has a postpelvic scute immediately behind, and partially overlapping, the pelvic scute (Chapman, 1948, fig. 17 of *E. micropus* on p. 38; personal observation); *Gilchristella* and *Ehirava malabaricus* (subfamily Spratelloidinae) have prepelvic scutes, unkeeled but with lateral arms, and no postpelvic scutes (Whitehead, 1963b; and Poll, Whitehead, and Hopson, 1965: 286); and *Laeviscutella,* which Poll, Whitehead, and Hopson placed in the same tribe with *Gilchristella* and *Ehirava,* has both prepelvic and postpelvic scutes. In *Laeviscutella* the prepelvic scutes have lateral arms but are unkeeled, whereas the postpelvic scutes are keeled but lack lateral arms, a condition unlike that in any other clupeoid.

If the absence of prepelvic and postpelvic scutes is a primitive character in those Dussumieriidae lacking them, then such scutes must have originated independently in several lines of clupeoids, including Indo-Pacific Engraulidae and two subfamilies of Dussumieriidae. It seems more likely that the ancestors of living clupeoids had a more or less full complement of scutes, and that they have been reduced or lost to varying degrees many times. A strong trend to reduce scutellation is evident in Pellonulinae. So far as known, the pelvic scute is retained in all living clupeoids. Whitehead (1963b) suggested that the pelvic scute of Dussumieriidae originated from pelvic splint bones, independently of prepelvic and postpelvic scutes. Greenwood (1968: 256) rejected a pelvic splint origin for the pelvic scute, largely on the ground that the pelvic scute is morphologically so similar to the other abdominal scutes. In *Thrattidion* the ontogeny of the pelvic scute is similar to that of the others, and the pelvic splint bone (usually absent in clupeoids) is quite separate.

While placing *Laeviscutella* in the dussumieriid tribe Ehiravini on account of its reduced scutellation, Poll, Whitehead, and Hopson (1965: 286–288) also cited reasons why it might be placed in the Clupeidae, and specifically in Pellonulinae. Daget and Iltis (1965: 45) placed it in the Clupeidae because "the only known species of *Laeviscutella* is in reality very close to the forms of *Pellonula* with which it is easily confused." In my opinion *Laeviscutella* should be placed in the Pellonulinae. Other genera currently placed in the Ehiravini also may have close relatives in the Pellonulinae. Thus the scuted *Pellonulops,* from Madagascar and South Africa (cf. Smith, 1954: 90–91, fig. 110), looks as if it might belong to the Pellonulinae and at the same time be closely related to *Gilchristella* and *Sauvagella.*

Whitehead's main reason for considering the Dussumieriidae a primitive type of clupeoid, apart from their lack of scutes, is the high number of branchiostegal rays in the subfamily Dussumieriinae, and a belief that reduction in number of branchiostegal rays is a major trend in clupeoid evolution. The notion that the number of branchiostegal rays can be reduced but not increased in teleostean phylogeny is one that had some currency formerly but has lost ground in recent years. Rosen (1964) mentions several phyletic lines in Acanthopterygii in which the number of branchiostegal rays has increased. Increases — some quite striking — surely have occurred in various highly specialized lines of catfishes in South America and India (personal observation), as well as in eels. Reduction of branchiostegal rays, of course, is the more usual trend, very frequently associated with reduction in body size, as it surely is in *Congothrissa* and *Thrattidion.* The high number of branchiostegal rays in Dussumeriinae is probably due to specialization rather than retention of a primitive character. The more pellonulin-like Spratelloidinae have only six or seven branchiostegal rays.

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B R E V I O R A

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TWO NEW GENERA OF BEMBIDIINE CARABID BEETLES FROM AUSTRALIA AND SOUTH AMERICA WITH NOTES ON THEIR PHYLOGENETIC AND ZOOGEOGRAPHIC SIGNIFICANCE (COLEOPTERA)[1]

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ABSTRACT. Two genera and two species are described as new. A key to related species is given and morphological structures are discussed in a phylogenetic perspective with other bembidiine groups. An "elytral chaetotaxy map," which is based on a broad study of tachyine beetles, is included. The distribution of each species is presented by locality records. Illustrations of important morphological characters are given as well as habitus drawings of two species, each representing the new genera described.

INTRODUCTION

Darlington (1962) pointed out that the members of the *hobarti* group "are certainly *Tachys* rather than *Bembidion* by current classification, [although] the species of this group are anomalous (primitive?) in some ways and should be specially considered by students of bembidiine phylogeny." During the course of my current study of tachyine beetles, I examined several specimens of the *hobarti* group and found some remarkable characteristics, as well as representatives of two new species. In the analysis of these characteristics and their distribution throughout the carabid beetles, another species with unusual characteristics was uncovered; Jeannel (1962) redescribed and illustrated

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[1] The types located in the British Museum (Natural History), London, were examined with the support of a grant from the American Philosophical Society, Penrose Fund #5795.

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this species, *"Plataphus" reicheellum* Csiki, and assigned it to a "phylogenetic series" of the Tribe Bembidiini *s. str.* On the basis of these newly discovered and newly interpreted characteristics, and information from my general tachyine study, I here propose two new genera to contain the groups of species discussed above, and discuss the phylogenetic implications and relict distribution pattern exhibited by the extant species of each group. I have included in this paper an "elytral chaetotaxy map," which is the result of the examination of all described and many undescribed groups of tachyine beetles. This was done now to facilitate the descriptions and discussions of these groups.

METHODS

The methods used here are essentially the same as those I employed elsewhere (Erwin, 1970) with a few exceptions. Measurements were made with a micrometer eyepiece in a Wild M5 stereoscopic microscope at a magnification of 50 diameters. The scale interval was 0.015 mm. Total length given here is in the sense of Lindroth (1961–69), that is, one overall "habitus" measurement of the specimen in a near normal pose, rather than the summation of head, pronotum, and elytron measurements used commonly for variation studies.

Illustrations are of two types. Most are India Ink on bristol board, but those with half-tone qualities were made with an "F softness" pencil on bristol board.

ACKNOWLEDGEMENTS

I wish to thank P. J. Darlington, Jr. and H. B. Leech for the loan of beetles in their charge and C. H. Lindroth for critically reading the manuscript and offering many valuable suggestions.

TAXONOMY

Tasmanitachoides new genus

(Figures 1, 5, 6, 8, 10, 11, 12, 13, 15, 16, 19, 21, 22)

Type Species. Bembidion hobarti Blackburn 1901: 123, present designation. This genus includes those species Darlington (1962) recognized as the *hobarti* group of *Tachys*, as well as two new species described below.

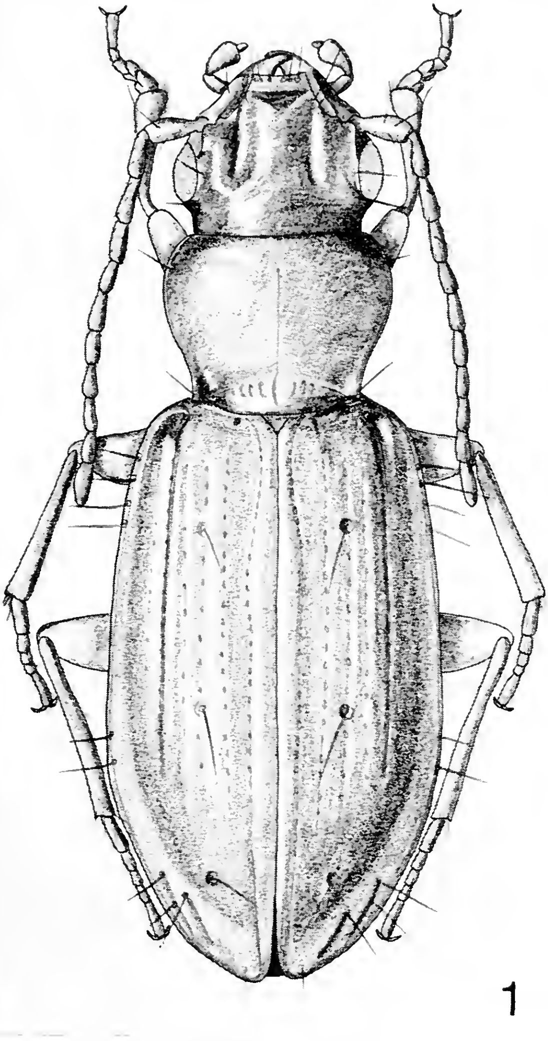

Figure 1. *Tasmanitachoides hobarti* (Blackburn), dorsal aspect, male. Queenstown, Tasmania.

Diagnosis. Head with two parallel and sulcate frontal furrows continuous on clypeus; apical palpal article subulate; ligula 6-setose; anterior coxal cavity uniperforate; anterior tibia with apex truncate to suboblique; scutellar stria absent externally; sutural stria entire, but not strictly recurrent (see below); male aedeagus with symmetrical basal lobes.

Description. Size: small beetles, 1.6–2.8 mm (upper limit from Darlington). Color: piceous to testaceous, appendages rufous to testaceous, or piceous. Microsculpture: wide, irregularly isodiametric meshes almost longitudinally arranged on elytra, more transverse on head and pronotum, very finely impressed. Head: broad and moderately depressed, with small but protruding eyes; frontal furrows sulciform and long, continuous on clypeus; clypeus with two setae at each anterior angle; ligula 6-setose (Fig. 10); mentum not foveate, anterior margin acutely and strongly toothed; mouthparts (Figs. 5, 10, 16). Antennal article 2:3 ratio more than 1.0; flagellar articles longer than wide, filiform (Fig. 15). Eyes and head with very short and sparsely spaced setae. Prothorax: pronotum narrowly cordiform with sharp hind angles and broadly lobed base, sides barely reflexed, carina medial to hind angles; two pairs of lateral setae present, the anterior pair far forward even before anterior third, the posterior pair just before hind angles; margins not serrate or setulose; anterior transverse impression obsolete, the posterior impression deeply engraved, interrupted at middle, basal foveae deeply impressed. Prosternum with short, sparsely spaced setae. Coxal cavities uniperforate-separate-closed. Tibia very shallowly oblique apically with outer spine lateral to subapical transverse comb. Male with two dilated basal tarsal articles each with sparse setae beneath. Claws simple. Pterothorax: elytra narrow and elongate, more or less parallel-sided with prominent humeri; sides barely reflexed, without subapical plica; margins setulose-serrate or not; dorsal surface with deeply impressed punctulate striae, at least sutural and base of 5 always present, others various, but 8 absent except at seta Eo8a (Fig. 3); recurrent groove appearing double because of two elongate and foveate punctures (Fig. 1) that are not continuous with sutural stria. Elytral chaetotaxy as in Figure 1. Mesonotum fully winged. Mesocoxae conjunct-confluent. Middle tibia of male with lateroapical brush. Claws simple. Abdomen: segments II, III, IV, and V with a single pair of ambulatory setae; segment VI with one pair in male and two pairs in female specimens, those in female parallel to hind margin of segment; venter with many scattered setae as described for eyes and head. Genitalia: female stylus (Figs. 8, 11, 12). Male parameres and median lobe (Figs. 19, 21, 22), the latter with symmetrical basal lobes.

Habitat. According to Darlington (1962) these beetles occur "in sand or gravel or under stones by rivers or brooks."

Distribution. The known range extends from Tasmania and temperate southeastern Australia north to Katherine in the Northern Territory, but no specimens are known from the area between Rockhampton and Katherine, a distance of more than 1500 miles.

Etymology. From Tasmania, the type locality of the type species; from genus *Tachys* (another group of carabid beetles), to which this group was originally assigned; and from Latin, *oides,* meaning similar to.

Key to species of *Tasmanitachoides* new genus (modified from Darlington's 1962 key to the *hobarti* group)

1. Dorsal elytral striae, except sutural, obliterated... *lutus* Darlington
1′. Dorsal striae, at least 5, and usually some others, present on disc 2
2(1′). Clypeus distinctly impressed at middle 3
2′. Clypeus not distinctly impressed at middle 5
3(2). Color piceous, length *ca.* 1.75 mm ......*murrumbidgensis* Sloane
3′. Color: forebody darker, rufo-piceous to rufo-testaceous, than elytra, rufous to testaceous; length *ca.* 1.95 mm or longer 4
4(3′). Small narrow beetles, *ca.* 1.95–2.0 mm long, 0.65 mm wide across elytra; forebody rufo-piceous, elytra testaceous *arnhemensis* n. sp.
4′. Larger and broader beetles, *ca.* 2.5–2.8 mm long and 0.9–1.1 mm wide; forebody rufo-testaceous, elytra testaceous at apex; male genitalia (Figs. 6, 19) .... *fitzroyi* Darlington
5(2′). Larger (2.3–2.7 mm long), almost black beetles with more or less well-defined elytral striae 6
5′. Small (1.8 mm or less), pale beetles with weakly impressed elytral striae 7
6(5). Head across eyes subequal to distance across pronotum at widest part; elytral striae well impressed (may include *leai* Sloane) *hobarti* Blackburn

6′. Head narrower than pronotum; striae, especially 5, shallower *wattsense* Blackburn

7(5′). Elytral stria 5 well defined to at least middle of elytron; pronotum convex, broad anteriorly, and wider than head across eyes; male genitalia (Fig. 22) .... *kingi* Darlington

7′. Elytral stria 5 hardly visible, barely impressed except just behind humerus; pronotum subconvex, narrower than head across eyes .... *katherinei* n. sp.

Tasmanitachoides arnhemensis n. sp.

(Figure 11)

Type specimens. The holotype female and one female paratype, labelled "Australia, N.T., Edith Falls nr. Katherine, 110 m, X–25–62," and "Collectors E. S. Ross, D. Q. Cavagnaro" are in CAS (California Academy of Sciences, San Francisco).

Type locality. Edith Falls on the north branch of the Daly River, near Katherine, Northern Territory, Australia.

Diagnosis. Medium-sized beetles, broad, subconvex with rufopiceous forebody and testaceous elytra; clypeus well impressed medially; striae 1, 2, and 5 well marked beyond middle.

Description. Size: 1.95–2.0 mm total length; 0.6–0.7 mm wide (2 specimens measured). Microsculpture: almost perfectly isodiametric on elytra, moderately impressed, surface shiny. Head: broadly transverse, slightly wider across eyes than pronotum; antennae with middle articles slightly longer than wide; clypeus well impressed medially; frontal furrows deeply sulcate from anterior margin of clypeus to just behind mid-eye level, roughly parallel throughout. Prothorax: subcordate, sides sinuate just before acute hind angles; base broadly lobed, sinuate laterally inside hind angles; side margins moderately beaded, strongly rounded at apical third; anterior margin truncate; surface micropunctulate; basal transverse impression deep and coarse laterally, interrupted medially by extended median groove. Pterothorax: wings long; elytra elongate and narrow, sides subparallel; humerus about square, margins subserrate and microsetulose; stria 1 (sutural) deep and entire from base to apex, broadly recurrent at apex to foveate puncture Eo8b; stria 2 moderately impressed from near base to Ed6c; striae 3 and 4 short, weakly impressed from Ed3 to Ed5a; stria 5 sulcate behind recurrent humeral margin to level of Ed3, less impressed from Ed3 to mid-elytron; Ed7b foveate, forming inner pseudo-recurrent groove. Abdomen: as described under generic description. Male genitalia unknown. Female stylus (Fig. 11).

Notes. This species is most closely related to the more southern *T. fitzroyi* Darlington, but it has members that are considerably smaller, both in length and width.

Habitat notes. Exact habitat unrecorded, but taken near Edith Falls, so probably as Darlington (1962) and Sloane (1921) recorded for other species, that is, near water's edge.

Distribution. Known only from the type locality.

Etymology. From Arnhem Land, the northernmost projection of land in Australia; in reference to the general area where the types were collected.

Tasmanitachoides katherinei n. sp.

(Figure 12)

Type specimen. The holotype female labelled "Australia, N.T., Edith Falls nr. Katherine, 110m, X–25–62," and "Collectors E. S. Ross, D. Q. Cavagnaro" is in CAS.

Type locality. Edith Falls on the north branch of the Daly River, near Katherine, Northern Territory, Australia.

Diagnosis. Small beetles, narrow, fragile, depressed, with rufotestaceous forebody and testaceous elytra; clypeus not impressed; striae 2–5 almost obliterated; micropunctulae and microsculpture well marked.

Description. Size: 1.6 mm total length; 0.5 mm wide (type). Microsculpture: almost perfectly isodiametric on elytra, moderately impressed, surface shiny. Head: broadly transverse, slightly wider across eyes than pronotum and elytra; antennae with middle articles about twice as long as wide; clypeus not impressed medially; frontal furrows shallowly sulcate, poorly defined behind level of anterior edge of eye, slightly convergent posteriorly. Prothorax: subcordate; sides sinuate just before slightly obtuse hind angles; base broadly lobed, abruptly sinuate laterally inside hind angles; side margins weakly beaded, moderately rounded at apical third; anterior margin truncate; pronotum barely convex, micropunctulate; basal transverse impression deep and short, laterally interrupted well inside hind angle and at middle by extended median groove. Pterothorax: wings long; elytra elongate and narrow, sides parallel; humerus almost square; side margins subserrate and microsetulose; stria 1 deep and entire from base to apex, broadly recurrent at apex to foveate puncture Eo8b; outer striae nearly obliterated; Ed7b shallowly foveate, forming an inner pseudo-recurrent groove. Abdomen: as described for genus. Male genitalia unknown. Female stylus (Fig. 12).

Notes. This species is most closely related to the more southern *T. kingi* Darlington, but it has members with much less impressed striae and a pronotum that is narrower than the head across the eyes.

Habitat notes. See preceding species.

Distribution. Known only from the type locality.

Etymology. From Katherine, the name of the town near which the type was discovered.

NOTES ON OTHER SPECIES OF *TASMANITACHOIDES*

Darlington (1962) thought that *Bembidion wattsense* Blackburn might be a synonym of *T. hobarti.* I have examined the type in the British Museum and believe that *B. wattsense* is a valid species and should be included in *Tasmanitachoides.* I have not seen specimens of *T. leai* Sloane and prefer to follow Darlington's ideas at this time. I have seen the types of all other species listed in the key; those described by Darlington are in the Museum of Comparative Zoology, Cambridge, Massachusetts, and those of Sloane and Blackburn are in the British Museum (Natural History).

Bembidarenas new genus

(Figures 2, 4, 7, 9, 14, 17, 18, 20, 23)

Type Species. Bembidion reicheellum Csiki 1929: 162, present designation. This species was originally described as *Bembidium reichei* Germain (1906: 617). Since *reichei* was preoccupied (Putzeys, 1846), Csiki (1929: 162) proposed *reicheellum.* Jeannel (1962: 653) placed the species in *Plataphus* because of the structure of the basal lobes of the aedeagus. However, his drawings (Jeannel 1941: 533) are not accurate, and, as Lindroth (1963) points out, "The structure of the basal orifice of penis, used by Jea. (1941, p. 533) for characterizing his 'genus' *Plataphus,* is not different from that of related groups."

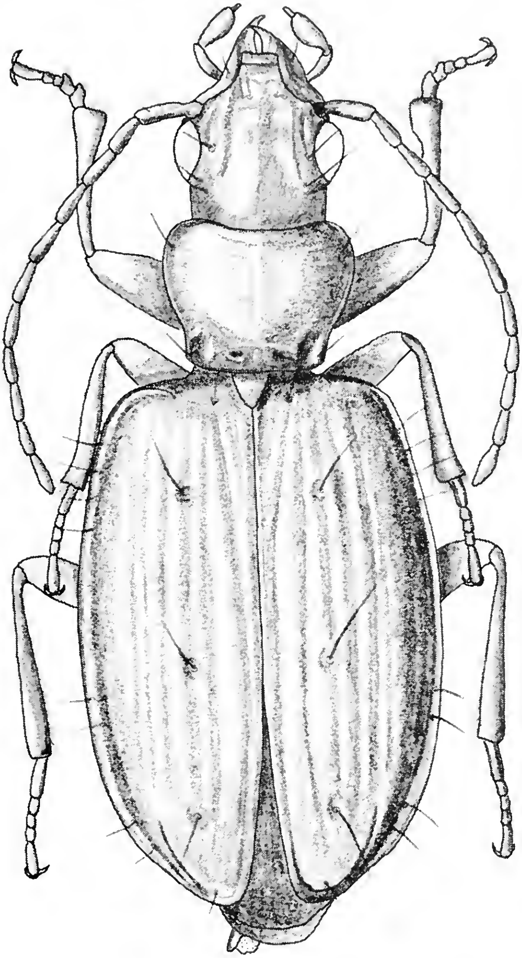

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Figure 2. *Bembidarenas reicheellum* (Csiki), dorsal aspect, male, vicinity Punta Arenas, Chile.

Diagnosis. Apical palpal article subulate, scutellar stria present, anterior coxal cavity uniperforate, anterior tibia with apex truncate, but with transverse subapical comb, clypeus 4-setose, apex of stria 5 deepened, abdomen pubescent and male aedeagus with symmetrical basal lobes.

Description. Size: 3.6 to 4.2 mm. Color: piceous with rufescent tibiae. Microsculpture: moderately wide on elytra, almost regularly isodiametric meshes with slight tendency toward transverse arrangement throughout. Head: broad and moderately depressed, with moderate but prominent eyes; frontal furrows double, the inner pair linear, deep and wide from clypeus to just behind eyes at posterior edge, and with a slightly raised tubercle at middle of each furrow, the outer pair short and deep, enclosing the anterior supraorbital setae but not continued on clypeus; clypeus with two setae at end of each frontal furrow; ligula 6-setose (Fig. 9); mentum not foveate, anterior margin with strong, truncated tooth; mouth parts (Figs. 4, 9, 17). Antennal articles 1, 3–5 of subequal length, 1 more robust; flagellar articles and 2 only slightly shorter (Fig. 18). Eyes and gena beneath eyes with short and scattered setae. Prothorax: pronotum narrowly cordiform with sharp but slightly obtuse hind angles and truncate base, sides slightly reflexed, with deep basal foveae; two pairs of lateral setae present, the anterior pair far forward, even before anterior third, the posterior pair just anterior to hind angles; margin not setulose, anterior transverse impression obsolete, the basal impression deep and wide. Prosternum glabrous. Coxal cavities uniperforate-separate-open. Tibia truncate apically but with subapical transverse comb terminated with two spine-like setae. Male with two dilated basal tarsal articles each with parallel rows of sparse modified setae beneath. Claws simple. Pterothorax: elytra moderately narrow, depressed and elongate, with slightly arcuate sides and prominent humeri; sides reflexed, with small subapical plica; margins not setulose; dorsal surface with 5 well-impressed striae, the sixth feebly impressed, seventh obsolete, and eighth well impressed behind middle only, absent before middle; scutellar striae well developed; apex of stria 5 deeply impressed and connected with sutural stria (forming "recurrent groove"). Elytral chaetotaxy as in Figure 2. Mesonotum fully winged. Mesocoxae conjunct-confluent. Metasternum and metacoxae with scattered pubescence. Abdomen: segments II, III, IV, V with a single pair of ambulatory setae; segment VI with one pair in male and two pairs in female specimens, those of female arranged in a row transversely across segment; all segments with short, sparse pubescence. Genitalia: female stylus (Fig. 20). Male parameres and median lobe (Fig. 23), the latter with symmetrical basal lobes, but no "brush sclerite" in the internal sac as in *Bembidion* members.

Notes. I have also seen specimens of a second species of this genus from southern South America in the collection of J. Négre. Négre plans to describe and figure this species in a paper he is preparing on *Bembidion* of southern South America.

The presence of short sparse setae covering the venter of all segments of the abdomen is also found in the subgenus *Trichoplataphus* Netolitzky of *Bembidion.* Setae are also found along only the apical margin of each segment in members of the subgenus *Blepharoplataphus* Netolitzky. This character state must be regarded as convergent in these otherwise quite different groups of beetles.

Habitat. According to Darlington (*in litt.*) this beetle "live(d) in gravel by brooks."

Distribution. The known range of this group is southern Chile (Prov. Magellanes) in the vicinity of Punta Arenas (53°40′ S Lat.).

Etymology. From *Bembidion,* another group of closely related beetles, and Punta Arenas, the area in which these beetles are found.

DISCUSSION

The unexpected discovery of symmetrical basal lobes on the male genitalia of the *hobarti* group and *Bembidarenas* led me to investigate this and many other characteristics, as well as their distribution throughout the trechine-bembidiine complex. Some of this investigation has been done on actual specimens, but I have also consulted articles by Jeannel (1926, 1932, 1936, 1941, 1946, 1962), Lindroth (1961, 1963, 1966, 1969), Darlington (1962), Ball (1960), Bell (1967), Valentine (1932), and benefited through correspondence with T. C. Barr and his unpublished "Key to Tribes of Subfamily Bembidiinae."

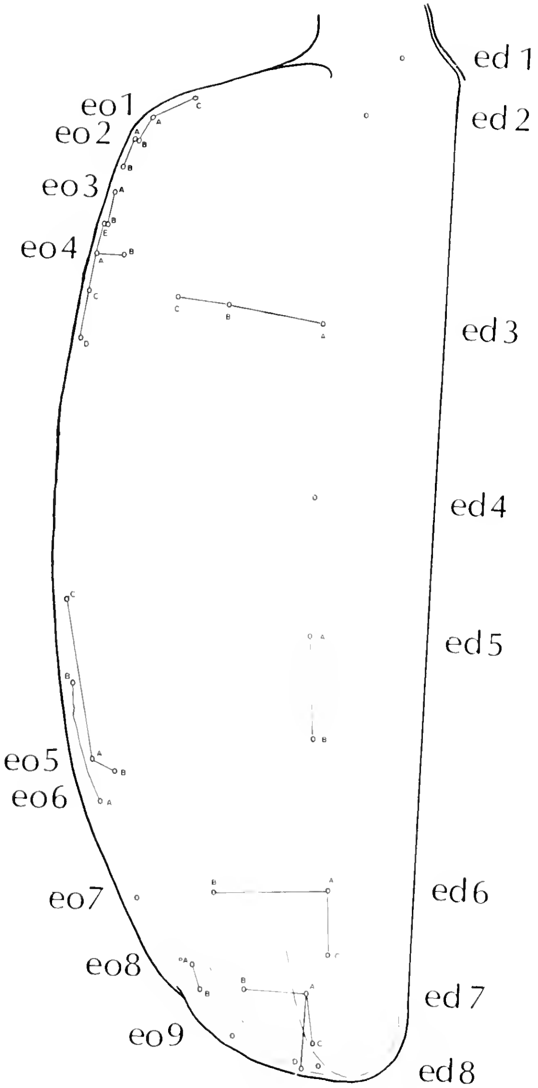

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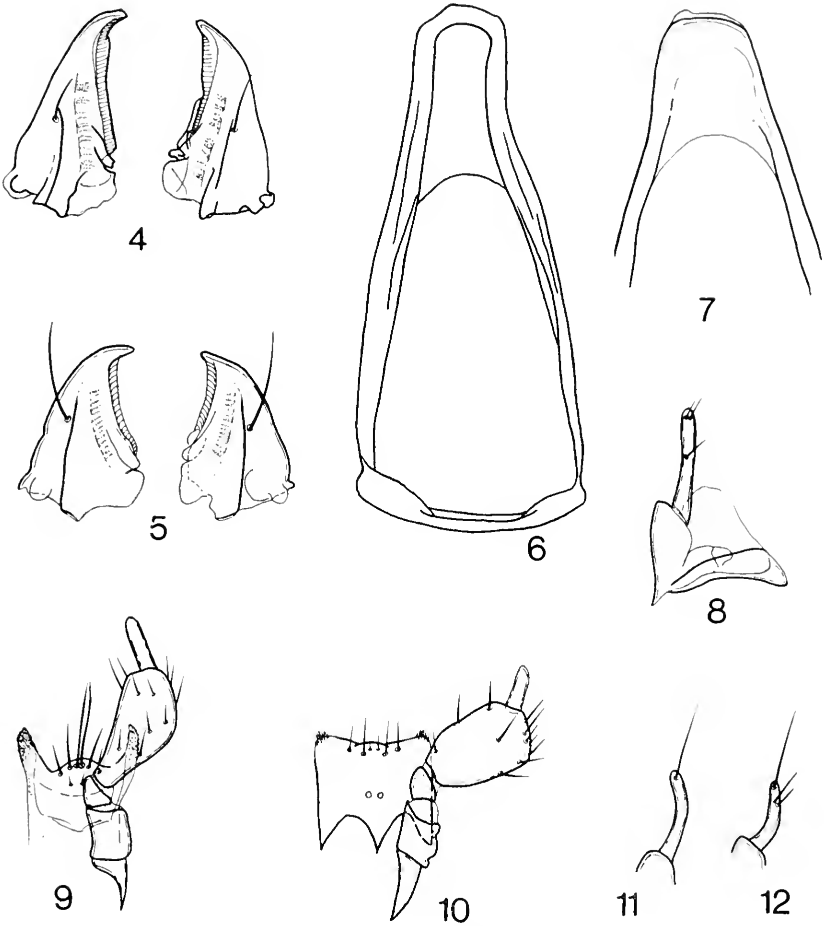
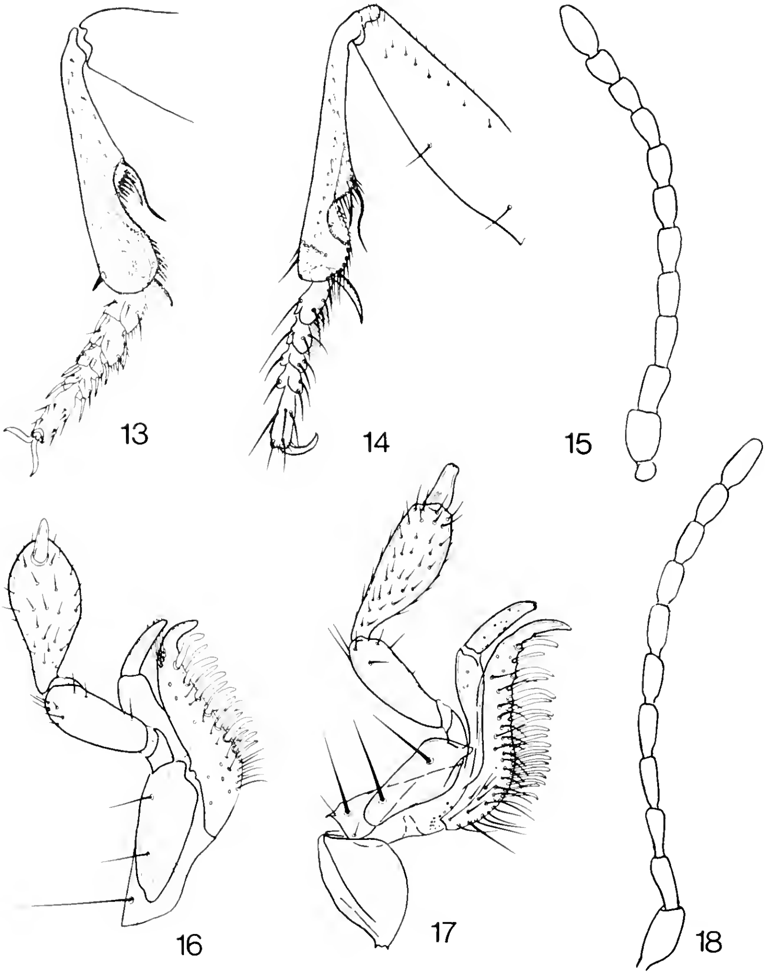
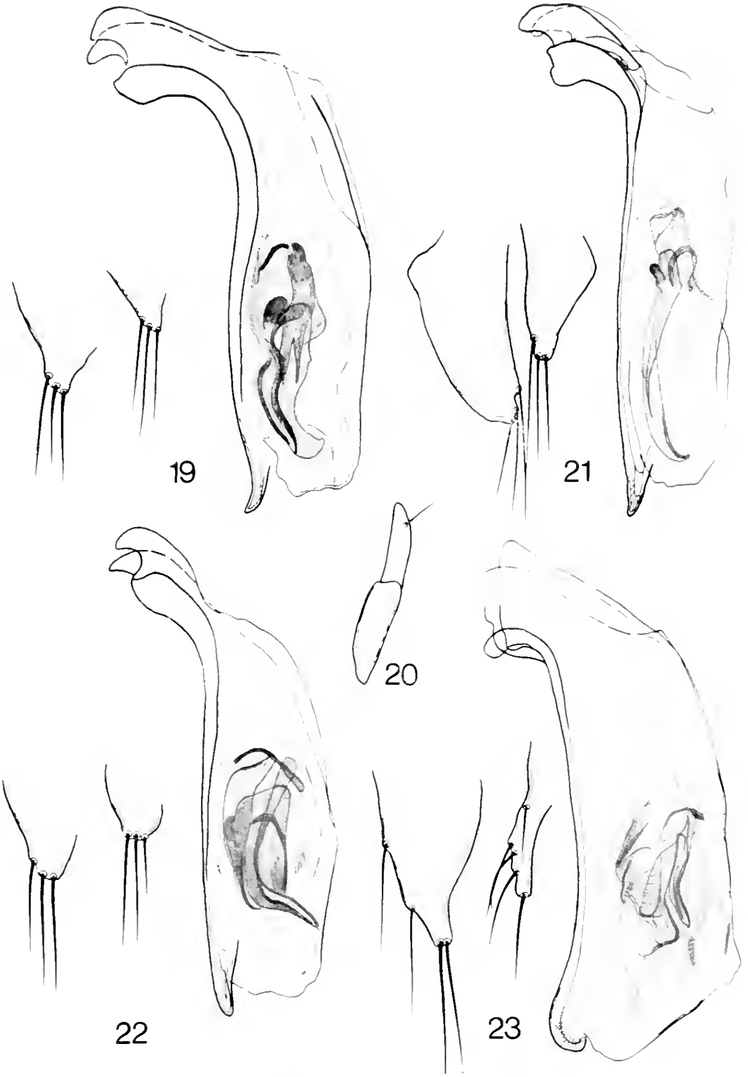
Figure 3. Diagrammatic elytron showing all known positions of setae (O) in tachyine beetles. The Eo series is the elytral "umbilicate" series. The Ed series is the elytral disc series. The letters represent the various positions in which these setae are found in different groups, while the short connecting lines are the hypothetical directions of movement from the ancestral condition (A). This drawing is to be used as a map to accompany the descriptions.



Figures 4-12. Fig. 4. Mandibles of *Bembidarenas reicheellum* (Csiki), dorsal aspect, male, vicinity Punta Arenas, Chile. Fig. 5. Same of *Tasmanitachoides hobarti* (Blackburn), male, Queenstown, Tasmania. Fig. 6. Genitalic ring sclerite of *Tasmanitachoides fitzroyi* (Darlington), dorsal aspect, male, Fitzroy River, North Rockhampton, Queensland, Australia. Fig. 7. Base of genitalic ring sclerite of *Bembidarenas reicheellum* (Csiki), dorsal aspect, male, vicinity Punta Arenas, Chile. Fig. 8. Genital sclerites of *Tasmanitachoides hobarti* (Blackburn), ventral aspect, female, Queenstown, Tasmania. Fig. 9. Labium and left palpus of *Bembidarenas reicheellum* (Csiki), ventral aspect, male, vicinity Punta Arenas, Chile. Fig. 10. Same of *Tasmanitachoides hobarti* (Blackburn), male, Queenstown, Tasmania. Fig. 11. Right stylus of female genitalia of *Tasmanitachoides arnhemensis* n. sp., ventral aspect, Edith Falls, Northern Territory, Australia. Fig. 12. Same of *Tasmanitachoides katherinei* n. sp., same locality.



Figures 13–18. Fig. 13. Left anterior leg of *Tasmanitachoides hobarti* (Blackburn), lateral aspect, male, Queenstown, Tasmania. Fig. 14. Same of *Bembidarenas reicheellum* (Csiki), vicinity Punta Arenas, Chile. Fig. 15. Right antenna of *Tasmanitachoides hobarti* (Blackburn), lateral aspect, male, Queenstown, Tasmania; pubescence and setae not shown. Fig. 16. Left maxilla and palpus of *Tasmanitachoides hobarti* (Blackburn), dorsal aspect, male, Queenstown, Tasmania. Fig. 17. Same of *Bembidarenas reicheellum* (Csiki), vicinity Punta Arenas, Chile. Fig. 18. Same of *Bembidarenas reicheellum* (Csiki), vicinity Punta Arenas, Chile; see Fig. 15.



Figures 19–23. Fig. 19. Male genitalia and apicies of parameres of *Tasmanitachoides fitzroyi* (Darlington). Fitzroy River, North Rockhampton, Queensland, Australia. Fig. 20. Female stylus of *Bembidarenas reicheellum* (Csiki), ventral aspect, vicinity Punta Arenas, Chile. Fig. 21. Male genitalia and apicies of parameres of *Tasmanitachoides hobarti* (Blackburn), Queenstown, Tasmania. Fig. 22. Same of *Tasmanitachoides kingi* (Darlington), Queenstown, Tasmania. Fig. 23. Same of *Bembidarenas reicheellum* (Csiki), vicinity Punta Arenas, Chile.

Traditionally, the trechine-bembidiine complex has been considered as two closely related groups, each at the tribal level (higher levels in the Jeannelian "French School"). Trechini, Bembidiini, and other more loosely associated groups were considered by Jeannel (1941) to constitute the "Stylifera," a "groupement naturel" of the "Caraboidea Limbata" or higher Carabidae. Jeannel's contention that this "groupement naturel, sans cependant avoir eté exactement defini" still holds today. It seems no authors before Ball (1960) and Lindroth (1961–69) worried much that their classifications were based on one or two major character states, as well as one or two minor characteristics, or less. Also these character states were investigated on only one or two specimens of one or two local species in what were in reality unknowingly diverse groups. Even so, the general classification of Carabidae has been in relatively good shape for the last 30 years and many small studies have contributed much to our knowledge at all levels; some of these studies were based on new and novel techniques and approaches. It is hoped that this paper will stimulate just such studies in the "Stylifera" to determine its inner and outer limits and its place among the diversity of the entire Family.

DISCUSSION OF *BEMBIDARENAS*

Members of *Bembidarenas reicheellum* differ from *Bembidion* at least to the extent that *Phrypeus ricksecker*i Hayward does, and under certain analysis considerably more. Superficially, though, *B. reicheellum* is more conservative than *P. rickseckeri* and thus has not undergone close scrutiny by students of carabid phylogeny. The symmetrical basal lobes of the male genitalia in *B. reicheellum* do not occur anywhere in the true *Bembidion,* but are characteristic of many trechines, all patrobines, Anillina, apotomines, psydrines, *Horologion,* deltomerines, and *Tasmanitachoides.* Nearly symmetrical lobes occur in *Phrypeus* and the subgenus *Pseudolimnaeum* of *Bembidion,* but the reduction of the right lobe is easily observable after dissection. The distribution of symmetrical basal lobes in the Stylifera and other carabid groups indicates to me that this condition is primitive (plesiomorphic). If so, then reduced right basal lobes and the "basal bulb" have arisen several times in diverse groups, and hence must be used with caution in phylogenetic analyses.

B. reicheellum has another major difference in the male genitalia. All known *Bembidion* species possess a "brush-sclerite" in the internal sac, or remnants of one; in some groups there are species without the structure but it is clearly a secondary loss (Lindroth, personal communication). *B. reicheellum* does not have this structure at all. The brush sclerite does not occur in *Phrypeus* either, but is found in *Asaphidion*. This structure and many others clearly illustrate the sister group relationship of *Bembidion* and *Asaphidion,* regardless of the one extra umbilicate seta (Eo9) in the latter.

B. reicheellum has a plurisetose ligula with remnants of paraglossal lobes. The plurisetose ligula is found in all trechines, *Asaphidion,* and *Tasmanitachoides,* each with six to eight setae. All other bembidiines, pogonines, patrobines, etc., of the Stylifera have four or less setae, usually two. The long narrow lateral lobes, probably remnants of the paraglossae, are characteristic of all trechines, but also occur in some Anillina, patrobines, and *Horologion*. Other members of the Stylifera have small rounded lobes or no lobes. The distribution of these character states indicates to me that the multisetiferous ligula is derived (apomorphic), while the produced lateral lobes are primitive (remnants of the paraglossae). At present, any attempt to interpret these two character states into overall phylogenetic analysis leads to utter confusion; new data must be accumulated before further attempts are made.

The last characteristic that is now known to be peculiar in *B. reicheellum* is the presence of two pairs of setae on the clypeus. This character state also is now known in *Tasmanitachoides* and a few primitive trechines, e.g., *Amblystogenium pacificum* Putzeys.

On the basis of gross overall form (e.g., subulate terminal palpal articles, short sutural stria, elytral chaetotaxy, pubescent penultimate palpal articles, etc.) and the analysis of character states above, I think that *B. reicheellum* is an early off-shoot of the Bembidion lineage which retained some characteristics of the mutual "trechine-bembidiine" stock. It seems more primitive in several characteristics than *Phrypeus* and probably separated from the main line of evolution before *Phrypeus*. The habitat of gravel by brooks is considered by Darlington (*in litt.*) to "be a very old, stable habitat, and that the running water acts as a buffer against climatic changes. I think insects in this habitat may persist for very long periods."

DISCUSSION OF *TASMANITACHOIDES*

In addition to some of the points discussed above, *Tasmanitachoides* members have other peculiar characteristics not generally found in the Bembidiini. Deeply sulcate frontal furrows, extending to about mid-eye level, are elsewhere found only in *Phrypeus*. The small group of lateral papillae of the lacinia are unique, but some Anillina and *Lymnastis* have a single spine near this same location. Whether the structures are truly homologous is doubtful, however, because of their orientation.

On the basis of gross overall form (e.g., subulate terminal palpal articles, complete sutural stria, elytral chaetotaxy, uniperforate anterior coxal cavity, pubescent penultimate palpal articles, etc.) and the analysis of character states above, I think the *hobarti* group is best placed as an early off-shoot of the tachyine lineage which gave rise to the Anillina. All true tachyines (and *Lymnastis-Micratopus,* which I regard as true tachyines on the basis of many characteristics) have biperforate anterior coxal cavities, and are the only Stylifera that do (aside from *Apotomus* if this group really belongs to the Stylifera). The distribution of biperforate coxal cavities indicates that this character state is derived (apomorphic), but convergent in distantly related groups, perhaps in strengthening the prothorax under greater demands for digging in partial subterranean life (but see also Erwin, 1970: 168).

The characteristics of members of the *hobarti* group show similarities to the trechines, but as in *B. reicheellum* I think these characteristics indicate an old lineage surviving in an old but stable habitat, and maintaining certain characteristics of an early "trechine-bembidiine" stock.

The relationships within the Stylifera and particularly within the trechine-bembidiine complex will be thoroughly discussed along with the supporting evidence in my current revision of the Tachyina (Erwin, MS) and need not be dealt with at length here.

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AN ATTEMPT TO DETERMINE THE SYSTEMATIC POSITION OF *ELLOPOSTOMA MEGALOMYCTER*, AN ENIGMATIC FRESHWATER FISH FROM BORNEO

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Abstract. The types and only known specimens of *Ellopostoma megalomycter* (Vaillant) are figured and redescribed. This highly distinctive fish may have a Weberian apparatus with osseous swimbladder capsules similar to those in Cobitidae, but it differs from all Cobitidae in several important respects. Resemblance between *Ellopostoma* and Kneriidae evidently is mainly superficial. *Ellopostoma* cannot be classified with assurance because fundamental osteological information about it is lacking, owing to the present condition of the specimens. Its relationships, when worked out on the basis of fresh material, are likely to be of phyletic significance. The present account will permit the identification of new material of *Ellopostoma* with greater facility than the older accounts, because some errors are now corrected and more descriptive details are given.

INTRODUCTION

The rich fish collections obtained by the Netherlands Borneo Expedition of 1893–97 included specimens of a peculiar little fish that Vaillant (1902: 141–149, figs. 42–45) described as *Aperioptus megalomycter* and assigned to the Cobitidae. He also proposed a provisional new genus, *Ellopostoma,* for it. Vaillant's figures depict a moderately elongate, small-scaled fish with very large nostrils and eyes, and a most peculiar inferior mouth with a single pair of barbels. No modern ichthyologist has found it possible to assign a firm systematic position to this strange fish. Despite

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Vaillant's placement with the cobitids, later accounts of that family have neglected the species. Its appearance calls to mind the Kneriidae, a family of gonorynchiform fishes known only from fresh water in Africa. Weber and de Beaufort (1916: 237–239, fig. 97) examined the type specimens and doubted that they belong to the Cobitidae. They reproduced Vaillant's figures and pointed out that the species is not an *Aperioptus* and should be known as *Ellopostoma megalomycter* (Vaillant) (see below). No additional specimens have been found and nothing further about it has appeared in print.

Dr. M. Boeseman, Curator of Fishes of the Rijksmuseum van Natuurlijke Historie in Leiden, kindly lent his institution's type specimens of *Ellopostoma* so that I might try to classify it. The following account gives an emended description of *Ellopostoma* and points out the difficulties in trying to place it on the basis of the available material. There remains a major question as to whether the structures interpreted as a Weberian apparatus by Vaillant are really such. If they are, *Ellopostoma's* closest relationship probably is with Cobitidae. If its postcranial bony capsules have some other origin the relationships are more problematic and might lie with Kneriidae. In the description given below its characteristics are compared with those of both Cobitidae and Kneriidae.

I wish to thank Mr. Andrew Konnerth for preparing radiographs and Professor George S. Myers for reading the manuscript, and Dr. M. L. Bauchot for information about the Paris specimen of *Ellopostoma.*

ELLOPOSTOMA Vaillant 1902

Type species. Aperioptus megalomycter Vaillant 1902, by monotypy.

Note. In describing *Aperioptus megalomycter,* Vaillant proposed for it the new generic name *Ellopostoma* in a footnote in case it should prove not congeneric with *Aperioptus. Aperioptus* Richardson 1848 (type species *Aperioptus pictorius* Richardson 1848, by monotypy) was based on a rather unsatisfactory drawing and notes made before the only two specimens were inadvertently thrown away, and its identity may never be resolved. The only locality information for the specimens is that they came from Borneo. If they were freshwater they may have been cobitids, as implied by Günther (1868: 371). In any event, Richardson's description and figure (reproduced on pp. 238–239 in Weber and de Beaufort, 1916) indicate a fish differing in several major respects from Vaillant's fish, the proper designation for which is thus *Ellopostoma megalomycter,* as pointed out by Weber and de Beaufort.

Ellopostoma megalomycter (Vaillant)
Figure 1

Material. The type series of *Ellopostoma* consists of four specimens. No holotype was designated and thus they are equivalent syntypes. Three specimens, 24.3, 39.5 and 41.4 mm in standard length, were retained by the Rijksmuseum in Leiden (RMNH 7777) and one specimen, 40.5 mm in standard length, was presented to the Museum National d'Histoire Naturelle in Paris (MNHN 03–202). I have examined all four and find them very soft and poorly preserved. The 24.3-mm specimen belongs to the genus *Noemacheilus.* It has the characteristic three pairs of barbels and 11 dorsal fin rays. Its eye is relatively smaller than that of *Ellopostoma,* but unusually large for a *Noemacheilus.* The Paris specimen has the mouth, snout, orbit on one side and possibly some gill arches badly damaged. The 41.4-mm specimen, badly damaged to begin with, was dissected by Vaillant; the posterior gill arches are missing and structures in the anterior region of the vertebral column are missing or badly damaged. The 39.5-mm specimen (RMNH 7777) is intact and is hereby designated lectotype. The following description is based primarily on the lectotype and 41.4-mm paralectotype. Vaillant reported that the 41.4-mm specimen contained eggs which seemed ripe or nearly so. It is now completely eviscerated.

The specimens arrived in the Netherlands along with other unlabelled material collected by Dr. J. Büttikofer in the vicinity of Sintang, near the middle portion of the Kapuas River (Vaillant, 1902: 149).

Coloration. The specimens are now discolored and their original color pattern has largely disappeared. Vaillant (p. 147, fig. 42) gave a rather good color description, to which I can add but little: "La coloration est identique sur les trois grands exemplaires [i. e., in all but the 24.3-mm specimen, which is a *Noemacheilus*] et doit se rapporter sans doute à une livrée fondamentale, plus ou moins masquée peut-être sur le vivant, mais qui se rétablit lorsque les animaux sont plongés dans la liqueur. Dans l'état actuel la teinte générale est roux très pâle, devenant blanchâtre argenté en descendant vers le ventre, tout à fait argentée à la région operculaire, ainsi que sur les côtés et le dessous de la tête. Une série de taches plus ou moins en quadrilatères, occupant de 3 à 5 rangées d'écailles, ornent le dos et les flancs. Sur le premier on en compte 7, les deux antérieures, les plus petites, sont l'une à la région nuchale, l'autre à mî-distance de la dorsale, les trois suivantes, respectivement sous l'origine de cette dorsale, en son milieu, enfin juste en arrière d'elle; les deux dernières l'une à distance égale de cette tache métépiptérique et de la septième tache, celle-ci placée un peu en avant de l'insertion de la caudale. Sur la ligne latérale se voient 7 ou 8 taches, les antérieures peu distinctes; la dernière est au milieu du pédoncule caudal à l'insertion même de l'uroptère, les deux précédentes répondent aux intervalles clairs des trois dernières taches dorsales, disposées par rapport à celles-ci en damier; la quatrième en procédant toujours d'arrière en avant est sous la partie antérieure de la tache dorsale métépiptèrique, les 3 ou 4 taches antérieures

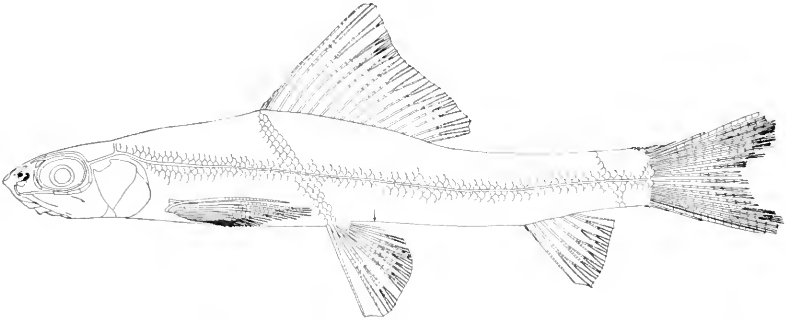

Figure 1. *Ellopostoma megalomycter*, 39.5-mm lectotype, RMNH 7777 (camera lucida). First elongate ray of anal and one or two rays of dorsal fin that are broken off restored on basis of 41.4-mm paralectotype. Arrow indicates position of vent. Base of pectoral fin should be slightly more anterior than figured.

moins développées, moins distinctes, sont plutôt placées au-dessous de la ligne latérale, la plus avancée serait juste en avant de l'origine de la dorsale; dans l'espace compris entre ces taches latéroantérieures et les taches dorsales se voient 4 macules, nuageuses, répondant aux intervalles des cinq taches dorsales antérieures. Enfin il ne faut pas négliger d'attirer l'attention sur une petite tache de forme demi-circulaire, d'un noire bleuâtre accentué, qui pourrait bien être cerclée de blanc, c'est-à-dire ocellée, laquelle orne la caudale dans sa partie inférieure au point d'insertion avec la pédoncule. L'iris paraît sombre; un cercle pupillaire argenté." The silvery white coloration on the opercle and lower side of the head is still evident, as is the small black spot on the ventral half of the caudal peduncle. A similar spot is present on the caudal peduncle in many Cobitidae and in some Kneriidae.

Proportional measurements. Proportional measurements expressed as times in standard length, those of 39.5-mm lectotype followed in parentheses by those of 41.4-mm paralectotype: head 4.4 (4.8); eye 14.9 (13.8); snout 16.5 (17.6); bony interorbital 27.3 (26.7); depth 6.5 (5.9); depth of caudal peduncle 11.5 (10.6); snout-tip to dorsal origin 2.5 (2.45); snout-tip to pelvic origin 2.08 (1.91); snout-tip to vent 1.80 (1.72); snout-tip to anal origin 1.23 (1.20); length of dorsal base 3.9 (3.75); length of anal base 12.4 (14.3); length of caudal peduncle 8.0 (8.6); length of pectoral fin 5.1 (4.9); length of longest dorsal ray 4.5 (broken); length of anal fin 6.7 (6.2).

Fins (Fig. 1). Dorsal iii 16, last ray divided to base. Anal iii 5 or iii 6, last branched ray divided to base. Pectoral i 11 or i 12. Pelvic i 7 (pelvic splint present). Caudal with nine principal rays in both lobes, about seven procurrent rays in upper lobe and four in lower lobe.

Dorsal fin origin slightly posterior to a vertical midway between insertions of pectoral and pelvic fins. Pelvic insertion slightly anterior to a vertical through base of seventh segmented ray of dorsal fin. Anal fin set far back, its origin somewhat anterior to a vertical midway between base of last dorsal fin ray and end of hypural fan. Origin of dorsal on a vertical through ninth vertebra. Pelvic insertion on a vertical through 13th or 14th vertebra. Anal origin on a vertical through 25th vertebra.

Pectoral fin somewhat larger than pelvic fin, none of its rays hypertrophied or otherwise modified, its longest ray reaching almost to insertion of pelvic fin. Height of dorsal fin almost twice that of anal fin. Dorsal fin base about three and one half times longer than anal fin base. Dorsal fin margin slightly falcate, the first three branched rays slightly longer than the rest. Anal fin margin more or less straight. Caudal deeply forked (damaged in both specimens). Membranes between rays in all fins uniformly thin.

Anal fin position variable in Kneriidae, several of them having the anal fin as far posterior as in *Ellopostoma.* In Kneriidae dorsal fin short-based, never with more than 10 rays. Fin counts and placements highly variable in Cobitidae. Relatively few cobitids have the anal fin as far posterior as *Ellopostoma.* Some (e.g., *Noemacheilus pavonaceus*) have fin placements and number of fin rays near those of *Ellopostoma.* Number of principal caudal rays variable in both Cobitidae (from 17 to 19) and Kneriidae (16 in *Grasseichthys,* 18–20 in *Parakneria*).

Position of vent (Fig. 1). Vent located between pelvic fins, somewhat closer to insertion of outermost pelvic ray than to tip of longest pelvic ray. In cobitids the vent position varies from midway between pelvic insertion and anal origin (in some Noemacheilinae) to immediately anterior to anal fin origin (in some Cobitinae and Botiinae). In at least some (all?) kneriids vent slightly or immediately anterior to anal fin origin.

Squamation (Fig. 1). Head scaleless. Body entirely scaled except for a small area in front of pectoral base. Isthmus scaled up to attachment of gill membranes. Fin bases scaleless. Approximately 75 scales in a lateral series from upper angle of gill opening to base of caudal fin, 20 scales between supraoccipital spine and dorsal fin origin, 20 scales between dorsal fin origin and pelvic fin insertion (11 rows above and eight rows below lateral line), and 17 scales around caudal peduncle.

Scales cycloid, height about 1.25 times width. A scale from side of body above pectoral fin has 12 radii and 22 circuli on its anterior field and 14 radii and 16 circuli on its posterior field. Focus well within anterior half of scale.

Vaillant regarded the scales of *Ellopostoma* as belonging to the type (multiradiate) characteristic of Cobitidae, and quite distinct from the type (pauciradiate) characteristic of Cyprinidae.

Mouth (Figs. 1–4). Mouth inferior. No teeth on jaws or roof of mouth. Upper jaw apparently bordered exclusively by premaxillaries, which have broad-based ascending processes and are well separated from each other at midline. Approximate shape of premaxillaries and of portion of dentaries bordering mouth as in Figure 4. Preoral and oral barbels absent. A median fleshy thickening or mentum on lower lip behind symphysis of mandibles (Figs. 2, 3). The name *Ellopostoma* was given because the mouth resembles that of a sturgeon (Vaillant, 1902: 145).

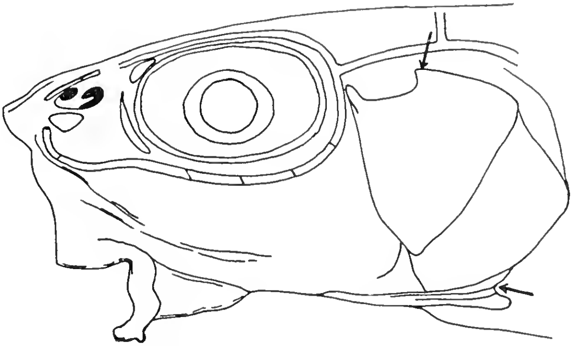

Figure 2. Close-up of head with mouth almost fully open, 39.5-mm lectotype (camera lucida). Arrows indicate extent of gill opening.

Vaillant recorded a pair of barbels, one at each side of the mouth, at the junction of the upper and lower jaws, which he supposed were located at the ends of the maxillary bones (I am unable to ascertain the presence of maxillaries, although they may be present). He was able to view the barbels only with difficulty. There is a fold or flap of skin in the lip at or near the rictus of the jaws, but this can hardly be described as a barbel. Certainly there are no structures corresponding to the elongate pair of barbels depicted in Vaillant's figure 43 in either the lectotype or the 40.5 and 41.4-mm paralectotypes. As noted above, the 24.3-mm paralectotype is actually a specimen of *Noemacheilus,* and has three pairs of barbels.

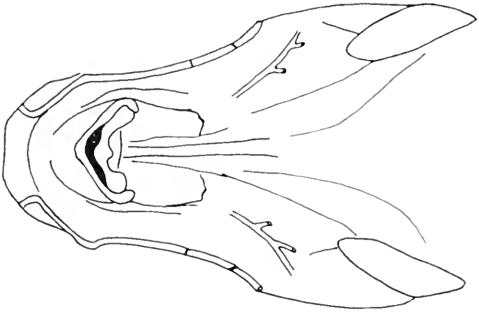

Figure 3. Ventral view of head, 39.5-mm lectotype (camera lucida).

Snout (Figs. 1–3, 5). Snout obliquely truncate and very rigid. Mesethmoid immovably articulated to frontals. Nasal organs occupying a large cavity, its diameter about one-third that of eye. Nostrils separated by a membraneous strip with a small, posteriorly directed flap (vestigial nasal barbel?). Dorsal to nostril a slender nasal bone, ventral to nostril a small, broad-based triangular shaped bone (antorbital?) with its apex directly ventrally, and posterior to nostril a supraorbital bone and the lateral margin of the lateral ethmoid bone. Lateral ethmoid forming part of anterior rim of orbit, not extending ventrally to orbit, of generalized morphology. The snout is unlike that in any other teleost I have seen.

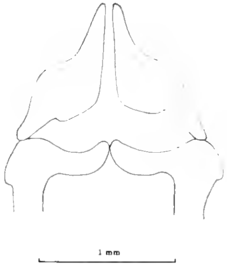

Figure 4. Ventral view of jawbones bordering mouth, 39.5-mm lectotype (freehand).

Eye (Figs. 1, 2, 5). The eye is misshapen in all three specimens of *Ellopostoma.* Figures 1, 2 and 5 depict its approximate shape. It presumably is oblong in live specimens, not perfectly round as in Vaillant's figures. Orbital rim free. Adipose eyelid absent. The combination of large eye and exceptionally large nostrils found in *Ellopostoma* is unusual. The eye is relatively much smaller in Cobitidae and Kneriidae (in both of which orbital rim usually attached) with the exception of the minute kneriid *Grasseichthys,* which has relatively small olfactory organs.

Laterosensory canals (Figs. 1–3, 5). Laterosensory system with supraorbital, infraorbital, preopercular, temporal, occipital and lateral canals. Supraorbital canal enclosed in a superficial bony tube on frontal bone until anterior margin of eye, then continued unenclosed for a short distance before it is again enclosed by the tubular nasal bone, without ethmoidal commissure or medially-directed branches. Infraorbital canal enclosed in a superficial, segmented bony tube (the infraorbital series?), continued anteriorly onto snout, where it turns upwards abruptly and terminates immediately anterior to nostrils. The appearance of the infraorbital canal is similar to that in Cobitidae (and Kneriidae?). Preopercular canal with two or three short lateral branches terminating in a small pore (Fig. 3). Occipital canal

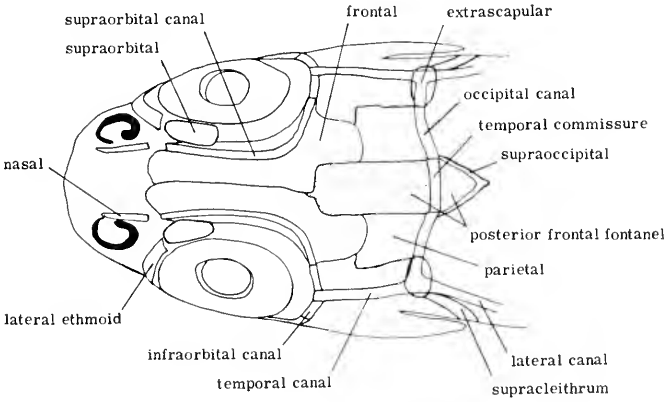

Figure 5. Dorsal view of head, based mainly on 39.5-mm lectotype (camera lucida).

with a temporal commissure, the lateral portions enclosed in a superficial bony tube, the median portion unenclosed, traversing the posterior frontal fontanel distinctly anterior to supraoccipital bone (Fig. 5). The temporal commissure is usually (always?) present in Cobitidae and Kneriidae but usually it lies flush with the anterior margin of the supraoccipital bone, sometimes entirely enclosed in a bony tube well within the supraoccipital bone (cf. Ramaswami, 1953; Greenwood *et al.*, 1966). Lateral canal of *Ellopostoma* extending along middle of body to base of caudal fin, as in Cobitidae and Kneriidae.

Roof of cranium (Fig. 5). Cranial roof exposed, with only a thin cover of skin, unlike most Cobitidae in which dorsum of head is usually rather fleshy or at least covered with moderately thick skin. No anterior frontal fontanel. Posterior frontal fontanel slightly longer than eye, bordered by frontals, parietals, and supraoccipital, very similar to posterior frontal fontanel in Cobitidae (cf. Ramaswami, 1953). In adults of the larger kneriids (cf. Greenwood *et al.*, 1966; Giltay, 1934) the cranial roof is complete. *Cromeria* (cf. Swinnerton, 1903) and *Grasseichthys* have a frontal fontanel extending to the snout, quite unlike that in either Cobitidae or *Ellopostoma*.

Posterior region of basicranium (Fig. 6). Parasphenoid extending posteriorly to anterior margin of supraoccipital, with which it is firmly sutured. Parasphenoid with a median sutural process. In Cobitidae and Kneriidae (cf. Ramaswami, 1953; Greenwood *et al.*, 1966, fig. 6 on p. 376) posterior portion of

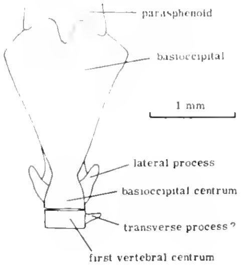

Figure 6. Ventral view of part of basicranium and first vertebral centrum, 41.4-mm paralectotype (freehand).

parasphenoid divided, the two divisions extending distinctly posterior to anterior margin of basioccipital; parasphenoid without median sutural process. Basioccipital centrum of *Ellopostoma* with anteriorly directed lateral processes, otherwise devoid of processes that might be identical with pharyngopophyses of Cobitidae. Pharyngopophyses of Cobitidae frequently poorly developed or absent; if present, they are posteriorly directed. Pharyngopophyses absent in Kneriidae.

Gill cover (Figs. 1, 2). Subopercle relatively large. Shape of opercle and subopercle generalized compared to cobitids in which they are often highly modified. Gill opening wide; gill membranes broadly united to isthmus at a point below middle of subopercle (Fig. 2). Branchiostegal rays apparently three, as Vaillant reported. Cobitidae invariably have three branchiostegal rays as do other cyprinoids. The number of branchiostegal rays is also reduced in Kneriidae, *Kneria* and *Cromeria* with three (Giltay, 1934; Swinnerton, 1903), *Grasseichthys* with only two (Géry, 1965). The extent of the gill opening, variable in Cobitidae, is always very narrow in Kneriidae.

Gill arches (Fig. 7) The following notes on the gill arches are based on the damaged 41.4-mm paralectotype in which only the first three arches of the left side and the first arch of the right side are present. Suspensory pharyngeals large. First arch of right side with about ten gill rakers on leading edge (none on suspensory pharyngeal) and 15 gill rakers on trailing edge (including a few on suspensory pharyngeal). First arch of left side with about 12 rakers on leading edge (none on suspensory pharyngeal) and 18 on trailing edge (of which five are on suspensory pharyngeal). The rakers on the first arch are all on the

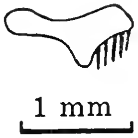

Figure 7. Dorsal view of left suspensory pharyngeal 1 with gill rakers, 41.4-mm paralectotype (camera lucida).

uppermost third of the arch. Perhaps the rakers from the lowermost two-thirds have been stripped away. Second and third gill arches with a full complement of gill rakers, at least 25 on both leading and trailing edges. Teeth absent on first three gill arches.

Vaillant did not mention the gill arches or rakers; he was unsuccessful in an attempt to remove the pharyngeals intact from the 41.4-mm specimen, and they are now missing.

Pectoral skeleton. Extrascapular bone present, bearing junction of temporal, occipital, and lateral branches of laterosensory canal system on its dorsal surface (Fig. 5). Pectoral arch of left side of 41.4-mm specimen detached from cranium and with supracleithrum exposed; posttemporal missing (normally absent?), postcleithrum evidently absent.

In Cobitidae the posttemporal is reduced, sometimes absent, and there are no postcleithra (Rendahl, 1930, 1933a; Băcescu-Meșter, 1970). The pectoral skeleton of the more typical kneriids, *Kneria* and *Parakneria,* is undescribed. Swinnerton (1903: 67, fig. N) described the pectoral skeleton of *Cromeria,* which has a posttemporal with a very elongate upper limb articulated directly to the supraoccipital (quite unlike the posttemporal of Cobitidae) and a slender postcleithrum.

Anterior region of vertebral column, postcranial bony capsules, swimbladder. Radiographs of the lectotype and 41.4-mm paralectotype and examination of the latter reveal a pair of large, rounded, bony capsules, one on either side of the vertebral column almost immediately posterior to the cranium. The capsules of the 41.4-mm specimen are broken (their ventral portions missing) and detached from the vertebral column. Their transverse diameter is about three-fourths of the eye diameter. Portions of a tough membrane, presumably that of the swimbladder, remain inside the capsules. Vaillant interpreted these structures as homologues of the swimbladder capsules in Cobitidae. As the anterior portion of the vertebral column itself is also damaged and detached, and some parts possibly missing, it is impossible to tell precisely what structures contribute to form the capsules. The appearance of the capsules in radiographs of various Cobitidae is at least superficially similar to that of the capsules of *Ellopostoma.* The first centrum of *Ellopostoma* is free and relatively short, and bears a small lateral projection on one side (a transverse process?) which is absent (broken off?) on the other side (Fig. 6).

Either *Ellopostoma* has a Weberian apparatus with swimbladder capsules like Cobitidae or else it has complicated bony structures superficially similar and perhaps comparable in function to the swimbladder capsules of Cobitidae. I am inclined toward the first possibility. I am unable to make a detailed comparison of the capsules of Cobitidae with *Ellopostoma* on the basis of the present material. Nothing comparable to the capsules of Cobitidae or *Ellopostoma* has been reported in Kneriidae.

Vaillant (1902) was unable to find a swimbladder in *Ellopostoma* and stated (p. 142): "Pour la vessie natatoire je n'ai pu en trouver trace, pas plus que d'enveloppe osseuse pouvant la contenir, l'état de l'exemplaire [41.4-mm] paraissait cependant devoir permettre d'en constater l'existence." The development of the swim bladder is variable in Cobitidae. Frequently it is reduced to only the left and right halves of the anterior portion enclosed in the bony capsules, but some forms also have a nonenclosed posterior portion, the genus *Noemacheilus* with several species in which it is particularly large (Rendahl, 1933b). The swimbladders of Kneriidae have not been described in detail; Rosen and Greenwood (1970: 11) indicated that Kneriidae possess a swimbladder divided by a distinct constriction into a small anterior and a much larger posterior chamber, as in *Chanos* and in ostariophysans generalized with respect to their swimbladders.

Vertebral counts. Radiographs reveal about 32 vertebrae (excluding hypural centrum) in the lectotype of *Ellopostoma* and about 31 in the 41.4-mm paralectotype.

The following vertebral counts have been recorded for Kneriidae: *Grasseichthys* 36–37 (Géry, 1965); *Parakneria* 41–42 (Poll, 1965); and *Cromeria* 42 and 45 (Swinnerton, 1903). Vertebral counts of Cobitidae range very widely.

Caudal skeleton (Fig. 8). Figure 8 is based on a radiograph of the 41.4-mm specimen in which some elements are relatively well defined but others are indistinct, so that it is somewhat interpretive and should be used with caution. Hypurals apparently five. Proximal ends of hypurals 1–4 indistinct; impossible to determine from radiographs whether hypural 2 separate or fused with ural centrum. Parhypural evidently united to ural

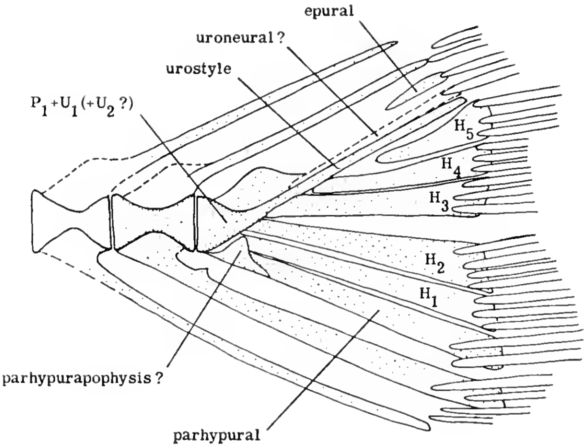

Figure 8. Caudal skeleton, 41.4-mm paralectotype (camera lucida of radiograph).

centrum by a saddlelike joint, and bearing a well-developed parhypurapophysis. A single epural. Urostyle slender. What appears to be a slender separate ossification (uroneural?) dorsal to urostyle may actually be part of it. Bases of neural and hemal spines of vertebrae 1 and 2 indistinct.

The caudal skeleton of *Ellopostoma,* so far as can be determined, agrees in almost all respects with the caudal skeletons of both Cobitidae (undetermined cobitid; *Botia macracanthus*) and Kneriidae (*Cromeria, Grasseichthys*) described and figured by Monod (1968). The cobitids and kneriids lack uroneurals; it is possible that one is present in *Ellopostoma.* The cobitids have hypural 2 fused to the ural centrum, whereas it is evidently free in the kneriids; the condition of hypural 2 in *Ellopostoma* is undetermined. All agree in having a single epural and five hypurals, except *Botia macracanthus,* which has six hypurals. Rosen and Greenwood (1970: 13, fig. 10) found six hypurals and two epurals in *Kneria wittei* and in *Parakneria* sp. In *K. wittei* the first epural is very reduced, but in *Parakneria* sp. both epurals are large.

DISCUSSION

Ellopostoma differs from all Cobitidae and Kneriidae in the relatively large size of its nostrils and eyes and in the morphology of its snout, mouth, and (so far as known) parasphenoid bone. It also differs from all Cobitidae in lacking barbels, and from all Kneriidae in its possession of postcranial bony capsules, a long-based dorsal fin with relatively numerous rays, and an extensive gill opening, and in the morphology of its posterior frontal fontanel.

Ellopostoma cannot be classified with reasonable assurance because important information about the structure of its snout, mouth, pharyngeal bones, and postcranial bony capsules is lacking. If the postcranial bony capsules are part of a Weberian apparatus (as seems likely), then it is probably closer to Cobitidae than to any other living group. It does not show the specialized traits (mesethmoid movably articulated to frontals, lateral ethmoid highly modified as an erectile suborbital spine) of the subfamilies Botiinae and Cobitinae, and differs greatly from them in general appearance. It shares many characters with the Noemacheilinae and is somewhat like them in general appearance, but the resemblances may be due to convergence and retention of generalized characters. Cobitidae, Kneriidae, and *Ellopostoma* are similar in many respects, and this is of particular interest in view of evidence that gonorynchiforms and ostariophysans are closely related (Greenwood *et al.*, 1966; Rosen and Greenwood, 1970). Whatever the relationships of *Ellopostoma,* it is likely to be of major phyletic significance.

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B R E V I O R A

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THE CHAÑARES (ARGENTINA) TRIASSIC REPTILE FAUNA. XII. THE POSTCRANIAL SKELETON OF THE THECODONT *CHANARESUCHUS*.

Alfred Sherwood Romer

Abstract. A description is given, with a reconstruction, of the postcranial skeleton of the long-snouted thecodont *Chanaresuchus bonapartei* from the early Middle Triassic Chañares Formation of Argentina. The general proportions are comparable to those of crocodilians, and life habits may have been similar. However, there is no positive indication of relationship to either later Crocodilia or Phytosauria, and *Chanaresuchus* and its relatives (Proterochampsidae) appear to be a sterile offshoot of the primitive proterosuchian stock. Dermal armor is little developed; the pelvis, although somewhat advanced in build, shows no trend toward the crocodilian elimination of the pubis from the acetabulum; the pes is of a specialized nature, with emphasis on the inner digits.

INTRODUCTION

In a recent paper in this series (Romer, 1971), I described the cranial anatomy of two long-snouted thecodonts, *Chanaresuchus bonapartei* and *Gualosuchus reigi,* from the (? Anisian) Triassic Chañares Formation of Argentina. Few postcranial remains of *Gualosuchus* are available to me. For *Chanaresuchus,* however, a number of specimens from our 1964–65 expedition are at hand, and Sr. Bonaparte allowed me to study several further specimens in the Instituto Lillo of Tucumán collections. Below, I give a description, with restoration, of the postcranial skeleton of *Chanaresuchus*.

Materials. The following specimens from the La Plata-Harvard expedition include postcranial remains:

The holotype: (La Plata Museum 1964–XI–14–12) Skull, partial column, a few limb bones.

MCZ 4035. Part of the contents of a large nodule, including a column articulated to caudal 3, and considerable girdle and limb material.

MCZ 4036. The remainder of material in this nodule, including incomplete and in part poorly preserved remains of skulls and postcranial materials of two further individuals.

MCZ 4037. A skull and presacral column.

MCZ 4038. A slab containing a mélange of materials; most, however, appear to belong to a nearly completely disarticulated *Chanaresuchus* skeleton.

There is considerable variation in the size of the individuals concerned. Largest is MCZ 4037, in which skull length to the quadrate is 260 mm. In the type skull this measurement is 211 mm. My figures of postcranial material (including restoration) are based mainly on MCZ 4035, in which postcranial vertebrae and limb bone measurements indicate a size approximately that of the type. The two skulls somewhat imperfectly preserved in MCZ 4036 measure about 230 and 220 mm. The imperfect skull with which the array of postcranial material on MCZ 4038 appears to be associated had a length of approximately 165 mm.

Several specimens in the Instituto Lillo collections were studied. Best was a specimen with articulated column extending to the proximal part of the tail, and much of the appendicular skeleton; the skull measured, to quadrate, 175 mm, and the individual was thus considerably smaller than the type. A second specimen included much of the postcranial skeleton of a moderately large individual; the skull is missing, but comparison of limb bone measurements indicate a size slightly larger than MCZ 4035. A third Tucumán specimen is an immature individual, in which postcranial measurements are about half those of the type; preserved is a hind foot exactly duplicating the peculiar structure, and a nearly complete tail.

Vertebral column. The atlas-axis complex, best seen in MCZ 4037 (Fig. 1, *a, b*), is of a type readily derivable from that of primitive reptiles. The atlas neural arches are paired. Dorsally a posterior extension was applied to the lateral surface of the axis arch; an anterior extension is flattened ventrally, presumably for articulation with the exoccipital (no pro-atlas has been found). A slight rugosity seen on one specimen indicates a rib attachment. Ventrally the stem of the arch extends stoutly downward to

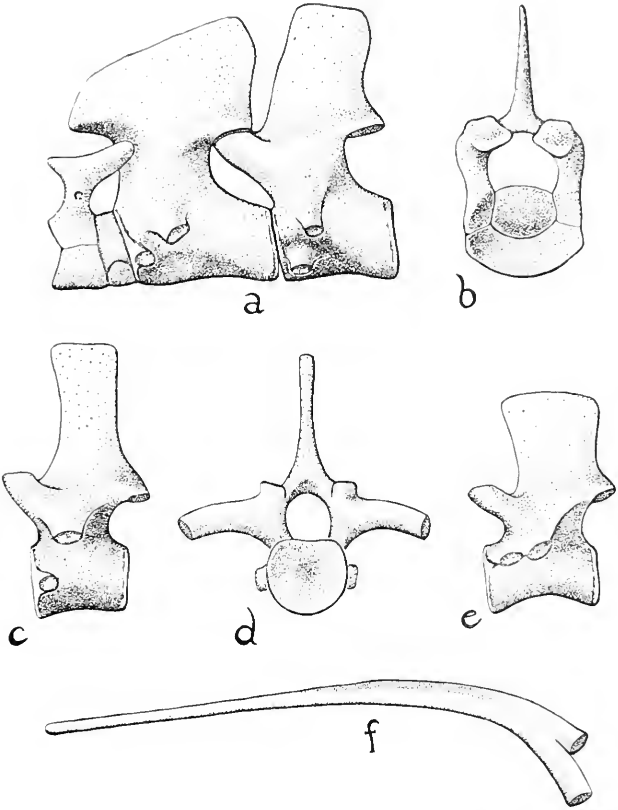

Figure 1. Vertebrae and rib of *Chanaresuchus bonapartei.* Composite, mainly from MCZ 4036. *a,* lateral view of vertebrae 1–3; *b,* anterior view of atlas-axis; *c, d,* lateral and anterior views of an anterior dorsal vertebra; *e,* lateral view of a posterior dorsal; *f,* an anterior dorsal rib, in posteroventral view. × 1.

articulate with the atlas intercentrum; internally it is excavated to form the dorsolateral segment of the socket for reception of the skull condyle. The lower part of this socket is formed by the atlas intercentrum, a stoutly developed crescent that articulates broadly on either side with the neural arches and is bevelled anteriorly for condyle articulation. Behind the atlas intercentrum lies the axis intercentrum, a thin crescent connecting ventrally the atlas intercentrum and the axis centrum. The atlas centrum is a stout element, which forms the deeper part of the condylar socket (slightly indented centrally by a notochordal pit); dorsally it forms the anterior end of the floor of the neural canal; posteriorly it is firmly apposed to the axis centrum. It is partially obscured in lateral view by the atlas arch and intercentrum and ventrally by the axis intercentrum.

The axis neural arch is relatively low but long. As noted, the articulation of the atlas arch is simply a flattened area on the lateral surface of the arch, anteriorly; posteriorly, normal postzygapophyses are present. A slight lateroventrally directed process, rugose at its tip, is an incipient transverse process for the tubercular articulation of the rib. The parapophysial articulation of the rib capitulum is indicated by a pronounced rugosity far down the side of the centrum and close to its anterior border. In contrast to the intercentrum anterior to it, the axis centrum (like the cervical vertebrae that follow it) is keeled ventrally.

Presacral column (Fig. 1, *c–e*). MCZ 4035 includes a presacral column and sacrum, showing definitely the presence of 23 presacral vertebrae; MCZ 4037 includes, in two segments, the 23 presacral vertebrae, the column having presumably broken off at the sacrum. Most of the description that follows is drawn from these two specimens; unfortunately, in much of both columns the transverse processes are broken and incomplete.

The column is, for the most part, of a typical thecodont character. In MCZ 4037 the length of typical dorsal segments, measured along the centra, averages 16 mm; in MCZ 4035, a somewhat smaller individual, this measurement averages 14 mm. The neural spines are centered somewhat to the back of the midlength of the centrum; they are broadened anteroposteriorly, expanding in width above the region of the zygapophyses. The anterior spines are relatively tall and narrow; posteriorly, in the lumbar region, they are lower and broader distally. They are narrow in transverse diameter, without noticeable expansion at the top. When the surface is well preserved, faint longitudinal striations are frequently seen. In the larger specimens there appears to have been a late continuation of growth (or rather ossification) of the spines, the neural spines in larger forms being taller in relation to other dimensions of the vertebrae. For example, in the large specimen, MCZ 4037, the total height of a posterior cervical (including both arch and centrum) is approximately three times the length of the centrum; in the smaller MCZ 4035, the height is barely above two and one-third times the central length.

The posterior zygapophyses are situated directly below the posterior margins of the neural spines; the prezygapophyses, on the contrary, lie well in advance of the anterior margins of the neural spines, on arch processes running upward and forward from the anterior margins of the transverse processes. The articular surfaces of the posterior zygapophyses face somewhat outward as well as downward; the anterior zygapophysial surfaces, in contrast, face inward as well as upward. Beginning with the axis, transverse processes are developed, their bases centering at a point well down on the side of the arch and toward the front. They are directed slightly posteriorly and ventrally rather than directly laterally. The axis process projects but 2 mm or so from the surface of the arch; posteriorly, the lengths increase so that, for example, by vertebra 7 in 4037, the length is close to 10 mm and there is obviously further increase more posteriorly, although, to my regret, the processes of the posterior dorsal and lumbar regions are mostly broken and imperfect. In MCZ 4035 the transverse processes as far back as vertebra 7 terminate in a narrow tip; posteriorly the transverse processes are broadened anteroposteriorly for their entire length, with oval distal facets for tubercular attachment.

The anterior margin of the arch curves almost directly downward from the process supporting the anterior zygapophysis to the anterior margin of the centrum; posteriorly the lateral margin of the arch is strongly concave in outline, allowing a large gap between arches here for passage of nerves and vessels.

The centra are smoothly oval in end contours, with a height considerably greater than the width. The centra are amphicoelous, with thickened rims at either end. Between the two ends of the centrum, the element pinches in somewhat laterally, and in side view the lower margin is somewhat concave in outline. The anterior centra are distinctly keeled ventrally; at about the beginning of the dorsal region the keel fades out, and posteriorly the ventral surface is smoothly rounded.

In the axis the parapophysis is merely a rugose area far down the anterior margin of the centrum. Posteriorly the parapophysis gradually moves upward along the anterior margin of the centrum and slowly comes to project distinctly from the surface of the bone so that, for example, by presacral 10 it has risen nearly to the top of the front margin of the centrum and projects outward for several millimeters. Posteriorly beyond this point the parapophysis continues movement upward and backward toward the transverse process and a thin ridge develops connecting the two (as in some primitive reptiles). Regrettably the processes are but imperfectly preserved in the "lumbar" region of materials available to me, but it appears that in the last four or so presacrals the two processes are united.

Sacral vertebrae. The two sacral vertebrae are present in MCZ 4035, and are present also in a Tucumán specimen. They differ mainly from the vertebrae anterior to them in the broad base from both centrum and arch from which the apophyses supporting the sacral ribs arise.

Caudal vertebrae. In the material available to me at Harvard, there is little identifiable caudal material; even in specimen MCZ 4035 articulated vertebrae cease at the third caudal. In the Instituto Lillo material, however, one specimen shows twelve caudal vertebrae in articulation with the sacrals and eleven are present in a second specimen. There is little decrease in vertebral length in these series of proximal caudals. Immediately behind the sacrum, however, the neural spines begin to show a backward slant and show a decrease in breadth distally; in the end members of these series, the neural spine is reduced to a small elevation lying above the postzygapophyses. Transverse processes are well developed; broad at their bases, they extend laterally and slightly ventrally to become pointed at their tips. In a Tucumán specimen of rather small size (skull length 175 mm), the lengths of the transverse processes of the anterior caudals, measured from the mid-line, are, in sequence, 29, 30, 28+, 33, 29, 25 and 20 mm. In this specimen the first chevron preserved lies between the fifth and sixth centra. That this is truly the first of the series is suggested by the fact that there is little space between the more anterior centra for insertion of a haemal arch, whereas more posteriorly a sufficient ventral gap is present. That the chevrons extended far down the tail is indicated by the fact that in the small specimen mentioned below, they are seen in the region of the 20–23rd caudals.

In an Instituto Lillo specimen considerably smaller than "adult" specimens of *Chanaresuchus* but definitely representing a young individual of this form, 35 articulated caudals are present, plus a few disarticulated elements beyond. In its present condition, little detail can be made out, but the last elements appear to be subterminal in nature, and a length of 40 or so caudals seems to be indicated.

Ribs. Regrettably, there is no available specimen with a good set of articulated ribs. In two instances a single rod-shaped structure that appears to be a single-headed atlantal rib, is present at the anterior end of a column. Back of the atlas, the ribs are distinctly double headed in typical archosaur fashion. In the anterior part of the presacral column, the two heads are widely separated; in correlation with the rapid development of transverse processes as we progress backward, the capitular branch is much longer than the tubercular, curving downward and inward from the line of the shaft. A short series of articulated vertebrae in MCZ 4038, representing an individual somewhat smaller than the "adults," bears a sequence of cervical ribs, presumably beginning with the atlas; the lengths are: 6, 12, 26, 32, 52, 60, ?, 75± and 85 mm. The more anterior, at least, of this series have pointed tips, indicating that they lay anterior to the point of rib connection with the (presumably cartilaginous) sternum. There is no indication in these cervical elements of an anterior "spur" from a point near the head of the rib that is found in crocodilians, and is highly developed in certain other thecodonts.

Of ribs in the dorsal region, remains are sparse. A number of rib heads show some variation in the amount of separation of tubercle and capitulum, those in which the two are less widely separated presumably coming from the posterior part of the region, in which transverse processes and parapophyses are approaching one another. In MCZ 4037 a complete rib (Fig. 1, *f*) is present close behind the eighth vertebra and may belong to that segment. Regrettably, no ribs are preserved in association with vertebrae of the "lumbar" region, in which shortened ribs were presumably present. For most of its extent the rib is slender; proximally, however, there is a slight expansion in the form of a thin flange posterior to the main proximal end of the shaft, which runs to the capitulum.

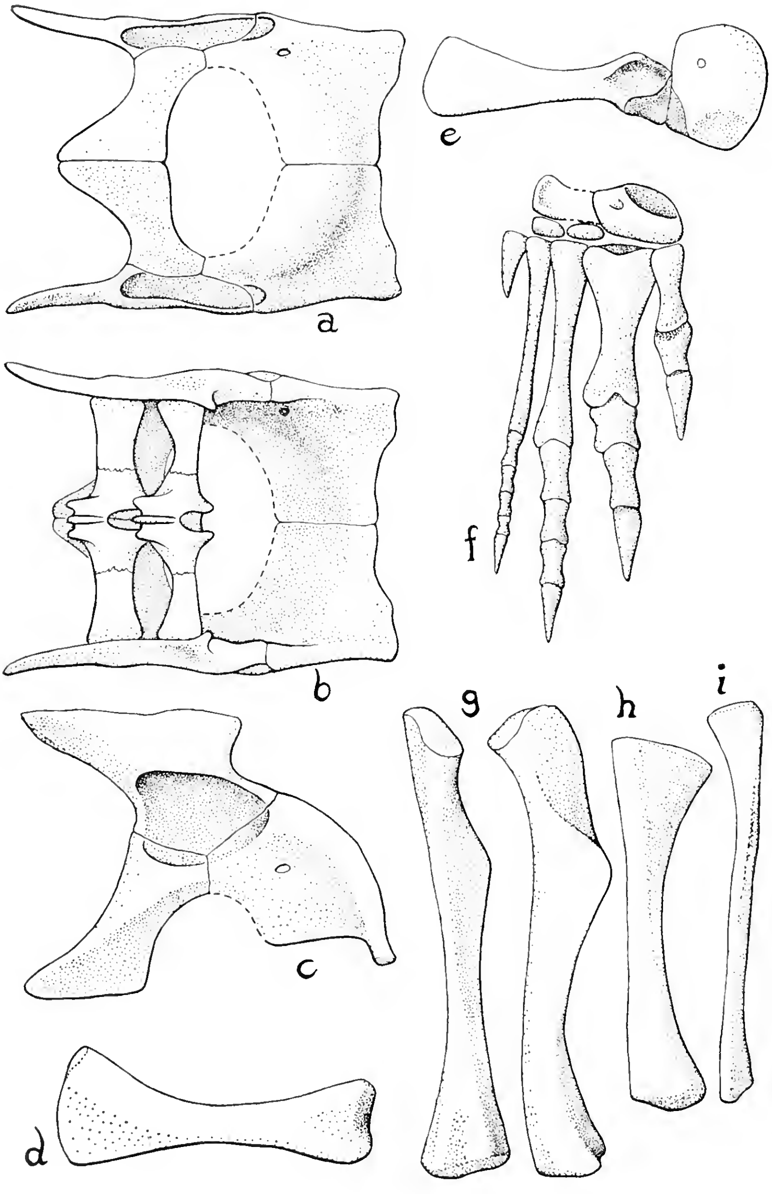
a
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Figure 2. *Chanaresuchus bonapartei,* girdle and limb bones. Composite, but mainly from MCZ 4035. *a,* ventral view of pelvic girdle; *b,* dorsal view of pelvic girdle and sacral ribs; *c,* pelvic girdle from right side; *d,* left humerus, dorsal surface; *e,* right scapulocoracoid (dorsal end of scapula at left); *f,* right hind foot, calcaneum incompletely preserved; *g,* dorsal and lateral views of left femur; *h,* extensor surface of left tibia; *i,* extensor surface of left fibula. × ½.

Two sacral ribs are present in MCZ 4035, although some details are obscured. They extend outward from a broad base, including much of the lateral surface of the centrum as well as the lower part of the neural arch. They expand somewhat distally and are blunt-ended; as indicated by several specimens of ilia, they were not too firmly attached to the articular areas for them on the internal iliac surface.

Girdles. Several examples of scapulae and coracoids are present in available material; that illustrated (Fig. 2, *e*) pertains to MCZ 4035. The two elements of the endochondral girdle are not tightly sutured to one another, and were found separated in two instances. The scapula is tall and slender, somewhat broadened at its upper margin, which is a "finished" one in the specimens studied. At its lower end the scapula is somewhat expanded anteriorly and its margin curved outward, presumably for clavicular attachment. The posteroventral portion of the bone is thickened and bears externally the well-defined upper margin of the glenoid cavity, which faces posterolaterally. Scapula and coracoid meet in a long horizontal suture. The latter bone is an oval plate, thickened posterodorsally to bear the lower part of the glenoid, and having the usual coracoid foramen. The remainder of the bone is relatively thin and convex in contour externally, the lower portion obviously turning medially across the chest. There is no trend toward posteroventral expansion, such as would be expected in a possible crocodile relative. Presumably clavicles and interclavicles were present, but I have not been able to identify such elements in the material available.

A number of specimens include pelvic girdle material, so that the nature of the ilium, ischium, and the anterodorsal portion of the pubis can be readily recognized. In no case, however, is there present a complete, well-preserved pelvis with the elements in proper relations with one another. Closest to this condition is that associated with MCZ 4035, and my figured restoration (Fig. 2, *a–c*) is based on this specimen. Here the proper position of the ilia can be determined by their relation to the preserved sacral vertebrae and ribs; the ischia are for the most part well preserved; the pubes, however, are imperfect.

The ilium is of the primitive type seen in many thecodonts — essentially a simple vertical blade, extending posteriorly in tapering fashion some distance beyond the region of the acetabulum, the front margin curving downward not far in advance of the acetabulum. On the inner surface are well-marked depressions for attachment of the two sacral ribs. On its outer surface the ilium forms the upper half of the acetabular cavity. This depression is most deeply incised posteriorly, where it reaches its most dorsal position, to be bordered dorsally by a sharp outwardly extending ridge on the ilium; thence the upper border, less sharply defined, slants forward and downward a considerable distance before reaching the pubis.

The pubis forms the anteroventral margin of the acetabulum; this cavity is here not as sharply incised into the bone as is true of its iliac and ischiadic margins, and the pubis is not greatly thickened here. The anterior surface of the ilium adjacent to the acetabular border is somewhat thickened; this surface continues downward to form a stout rounded ridge along the anterior margin of the pubis, the ridge turning ventrally in its distal portion. Medial to this ridge the pubis extends as a thin sheet to the midline of the body, where it meets its fellow in a long symphysis. Although the condition of the specimens makes the matter somewhat uncertain, it would seem that the anterior portion of this broad sheet of bone turns somewhat ventrally, while the posterior part of the symphysial region lies in a horizontal plane.

At the posterior end of this ventral expanse of bone, the pubic symphysis terminates and the posterior margins of the two pubes retreat upward and outward toward the acetabular region. The exact nature of the posterior margin of the bone and the distance it retreats dorsally before making contact with the ischium is uncertain. The usual obturator foramen penetrates the pubis not far below the acetabular border.

The ischium forms the posteroventral sector of the acetabular border. The dorsal portion of the bone is here greatly thickened, forming a horizontal shelf with a crescentic outer margin, to constitute a prominent segment of the acetabular cavity. Below this area the ischium rapidly decreases in thickness, but increases in anteroposterior breadth ventrally. The posterior margin of the bone, slanting medially, descends nearly straight downward for some distance, then curves posteriorly and, finally, ventrally to meet its fellow in symphysis. This symphysial union extends forward in a nearly horizontal plane to a point somewhat posterior to the level of the puboischiadic area of contact below the acetabulum. Here, the symphysis terminating, the anterior margin of the ischium ascends nearly straight upward and laterally toward the acetabular region. We thus have, in *Chanaresuchus,* a definite advance in pubic structure over the proterosuchian condition in the presence of a broad ventral "incision" in the primitive puboischiadic plate and a marked break in the primitively continuous ventral symphysis.

Pectoral limb. Little material of the pectoral limb is available. A humerus, 85 mm in length, was found with MCZ 4035 (Fig. 2, *d*), but is not too well preserved. It is expanded at both ends in primitive reptilian fashion, but shows little of the primitive "twist" of one end on the other. The posterior margin of the "head" segment curves medially to the proximomedial corner of the bone, whence the proximal articular surface, facing dorsomedially, curves laterally around the head of the bone. At the proximal end of the lateral margin a typical deltopectoral crest is present (in crushed condition). The distal end of the bone is distinctly divided, both dorsally and ventrally, into medial and lateral condyles, the medial the stouter, with distal articular surfaces for radius and ulna. Neither of the foramina often present distally in the humerus of early reptiles is present.

I cannot with confidence identify either radius or ulna in any of the adult *Chanaresuchus* specimens studied. They are present, however, in association with a humerus in the small specimen in Tucumán, mentioned above. As preserved in this obviously immature individual, they are merely elongate bony cylinders, with some expansion proximally of the element which I take to be the ulna, but without indication of an olecranon. These elements, measuring 32 and 33 mm in length, are associated with a humerus measuring 36 mm in length. If the same proportions were to hold in MCZ 4035, the radius and ulna would be expected to measure 74 and 76 mm in length respectively.

Pelvic limb. The series of three major elements of the hind legs — femur, tibia, and fibula — are preserved in articulation in three instances, and a number of isolated hind leg elements are present on MCZ 4038. In the three articulated specimens the lengths of these elements as preserved are 128 mm, 94 mm, and 95 mm in MCZ 4035; 151± mm, 129 mm, 91+ mm in the leg

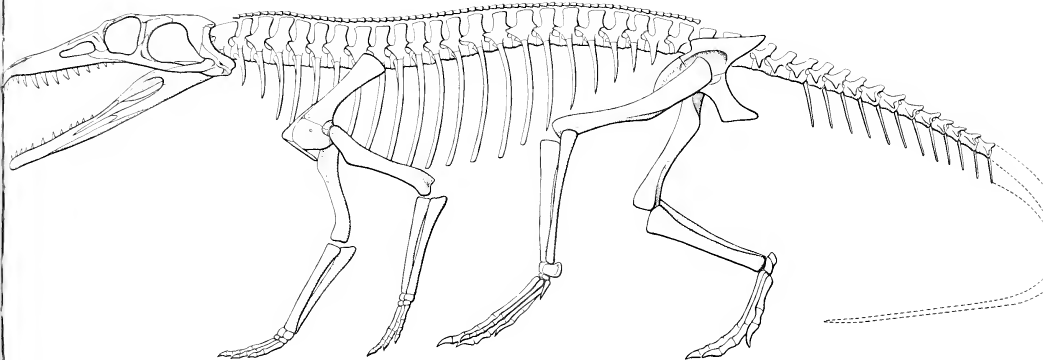

Plate 1. Skeletal restoration of *Chanaresuchus bonapartei.* Composite, but skull from the holotype, post-cranial skeleton mainly from MCZ 4035. Manus and dermal shoulder elements unknown; ribs imperfectly preserved and those of "lumbar" region unknown. About 1/3 size of type and MCZ 4035.

of MCZ 4036 with articulated foot, 150± mm, 135 mm and 117+ mm for another specimen in the same block. As noted elsewhere, the skeleton of MCZ 4035 is apparently somewhat immature; the limbs in MCZ 4036 appear to be those of essentially mature individuals. In all three articulated examples the femur is definitely longer than the tibia; there is, however, a very considerable difference between the examples, in MCZ 4036 where the femoral length is 111 percent and 117 percent of the tibia, and MCZ 4035, where the figure is 135 percent.

The femur (Fig. 2, *g*) is of a pattern seen in many thecodonts and preserved little changed in crocodilians. The bone is relatively long and slender, the ends little expanded. In side view, the shape is sigmoid, with the proximal end curved upward and somewhat medially, the distal end curved somewhat downward; the curvature, however, is less extreme than in more advanced thecodonts. The proximal end of the bone is much modified, so that the morphologically medial (or anterior) margin is turned upward, the lateral border downward. The curved head of the bone is thickened, the thickening increasing toward the medial (upper) border; preservation in available material, however, is not good enough to clearly outline the articular area. About two-fifths the distance down, the bone is extended ventrally, with, medially, a large oval area that probably (as in crocodilians) lodged the insertion of the long caudifemoral muscle; the projecting lower margin is a trochanter that presumably afforded insertion to the caudifemoralis brevis. The bone broadens somewhat distally, with a partial division into condyles, a shallow intercondylar fossa above, and a ventral popliteal depression. The distal end of the bone is unossified in MCZ 4035, so that details of areas of articulation cannot be made out.

Tibia and fibula, again, are of typical primitive archosaur construction (Fig. 2, *h, i*). The broad head of the tibia is essentially triangular in section; there is little development of a cnemial crest, which is represented merely by the top of a ridge that descends much of the length of the bone, separating a lateral-facing surface of the shaft from one facing anteromedially. Terminally, there is a broad oval surface, somewhat convex, for articulation with the astragalus. The fibula is, as expected, a relatively slender element, somewhat expanded proximally for apposition to the femur; distally (in contrast with the situation in many reptile groups) there is only a minor expansion in diameter of the bone to accommodate the oval terminal articulation with the calcaneum (and to a much lesser degree with the astragalus). Tarsal elements are present in MCZ 4035 and 4036. In 4035 the astragalus is well preserved (Fig. 2, *f*). Dorsally it bears a large articular area for the tibia, gently concave, elongate mediolaterally and facing somewhat anteriorly as well as dorsally, and dorsolateral to this a smaller facet for the fibula. No calcaneum was preserved with this specimen. MCZ 4036, on the other hand, lacks the astragalus, but has an incompletely preserved calcaneum. This shows a posterolateral tuber of "crocodilian" type, but the main body of the bone is imperfect. In both specimens mentioned distal tarsals 3 and 4 are present as flattened ovals lying over the heads of the lateral metapodials. There is no trace of more medial distal elements, although they may have been present in cartilage.

The structure of the pes is the most distinctive feature of *Chanaresuchus* (Fig. 2, *f*). Much of the right foot is present in MCZ 4035, but digit IV is represented only by a metatarsal splint; a right foot complete except for the ungual of toe IV is present in MCZ 4036, but the proximal ends of the inner toes are obscured by a refractory matrix. Two closely comparable specimens of the *Chanaresuchus* foot are present in the Tucumán material.

In archosaurs generally the trend in foot construction has been for a retention of the primitive phalangeal formula (except for frequent reduction of the fifth toe), but the development of a symmetrical pattern, with toe III the longest, toes II and IV somewhat shorter but subequal in length, and toe I short. This is true of the *Chanaresuchus* foot; but whereas in most archosaur toes II–IV are subequal in development, here there is very strong emphasis on the inner toes, and digit IV, on the contrary, is very slender. Digit I is somewhat shortened, but very stoutly built. Digit II is massive. Digit III is relatively slim. Digit IV is slender, almost splintlike in structure. Digit V is represented only by a metatarsal spur.

In some other archosaurs, such as certain crocodilians, *Ticinosuchus, Euparkeria* and *Stagonolepis,* there is a modest trend toward strength in the more medial digits, but never to an extent approaching the condition seen here. A similar trend (but usually a much less extreme one) towards a strengthening of the inner toes is found in mosasaurs and a number of chelonians. These are aquatic forms, and this specialization is apparently an "improvement" in paddle-action — a fact that gives strength to the assumption that *Chanaresuchus* was in great measure a water dweller. It has been assumed that *Chanaresuchus* and its relatives in the Proterochampsidae might be antecedent to the Crocodilia, but such strong emphasis on the inner toes is not to be expected in an ancestor of the group. As regards possible phytosaur relationship, foot material of that group is rare, and the pes, when restored, is generally based on poor material. I am indebted to Dr. Chatterjee, of the Geological Study Group of the Indian Statistical Institute, for a figure of a well-preserved foot of a phytosaur from the Maleri Formation. This shows almost no trace of emphasis on the inner toes, and relationship of the Proterochampsidae to the phytosaurs seems highly improbable.

Dermal armor. No gastralia are present in articulated fashion in any specimen. In contrast to a large fraction of the thecodont assemblage, other body armor appears to have been feebly developed, and consisted merely of a single row of thin scales lying over the neural spines. As preserved in several specimens, scales are definitely present from the axis to the last presacral; there is no evidence as to whether they extended onto the tail region, although this was probably the case. The scales are wedge-shaped as seen from above, narrow anteriorly, broader posteriorly, with a low longitudinal median keel. The anterior end of each scale underlies that anterior to it. There are approximately three scales the length of each vertebra, although there is no apparent relationship between vertebral segmentation and scale arrangement; in one specimen 57 scutes were present above the first 20 vertebrae. Their appearance and arrangement is very similar to that pictured in *Ticinosuchus* by Krebs (1965, fig. 8). This author restores the dorsal scales in the presacral region in a double row, in analogy, I suspect, with the pattern seen in various other thecodonts. I doubt if this was the case. The scales preserved in the presacral region number only about enough to make up a single median row. The presence of scales above the tail vertebrae in *Ticinosuchus* suggests that, were appropriate materials to be discovered, they would be found to continue along the tail in *Chanaresuchus* as well.

Restoration. In the accompanying plate I have attempted a skeletal restoration of *Chanaresuchus* at one third the natural size of a typical adult. Much of the skeleton is taken from MCZ 4035. The dermal shoulder elements, the manus, and the posterior ribs are restored, and the tail is imperfectly known. Despite these lacunae and the fact that in ribs and certain other elements the restoration is composite, I believe that the restoration gives a fairly accurate picture of the animal's skeleton.

In restoring an early archosaur, an important question is whether the pose was that of a biped or a quadruped. In all primitive reptiles the front legs are somewhat shorter and less massive than the hind. In most archosaurs this disproportion in limb lengths is usually much greater and led to a general (but not universal) belief (which I shared) that archosaurs *ab initio* were more or less bipedal in locomotor tendencies, and that most quadrupedal archosaurs, such as the sauropods and various ornithischians, had relapsed from a bipedal mode of progression back to progressing on all fours. Charig, Attridge and Crompton (1965) have, as a result of a study of probable sauropod history, come to the conclusion that quadrupedal pose was primitive for archosaurs, and that the development of powerful hind legs and a highly developed tail were, to begin with, adaptations for an amphibious life, and that bipedalism arose later.

It is not unreasonable to believe that, as these authors argue, the sauropods developed without passing through a bipedal stage. I think, however, that on present evidence, the primitive ornithischians were at least partially bipedal, although a majority of the ornithischian subgroups later became quadrupedal.

The possibility that the ancestral archosaurs were amphibious leads to speculation as to the general nature of early reptilian history. I have argued (although not without strenuous opposition) that the ancestral reptiles, although having acquired an amniote style of development, were still amphibious, and perhaps even mainly aquatic in habits. Of the great group of synapsids, which were dominant in the Permian and earlier Triassic, most became fully terrestrial, but the most primitive (and oldest) synapsids, the ophiacodont pelycosaurs of the Pennsylvanian and early Permian, were still essentially aquatic fish-eaters. Ancestral Permian archosaurs are almost unknown, but they may have followed a similar life pattern, but for a longer period of time. Further, we have no undisputed knowledge of the early ancestors of the euryapsid sauropterygians and placodonts or of the ichthyosaurs; at their earliest appearance these reptiles were aquatic — and perhaps primitively so. *Mesosaurus,* of the Permo-Carboniferous boundary, shows that if the primitive reptiles had become terrestrial, reversion to the water took place at a very early stage of reptilian history. And while I do not want to even suggest any close relationship between archosaurs and *Mesosaurus* (whose phylogenetic relationships are quite problematical), the similar adaptations in this genus and in the archosaurs in the powerful tail and highly developed hind limbs are strikingly suggestive.

But to return from this discussion to the question of limb disparity and body pose in archosaurs. Correlation between limb proportions and presumed posture is none too simple a matter. Such obviously amphibious and quadrupedal forms as crocodilians and phytosaurs have front legs nearly as well developed as hind; in a "sample" crocodilian, for example, the humerus plus radius are about 84 percent the length of femur plus tibia, and in a phytosaur described by McGregor (1906), the figure is 87 percent. But forms that seem quite surely quadrupedal may show a considerably greater disparity in length between front and hind legs. The heavily armored aetosaurs, for example, are universally considered to be quadrupeds, but in *Aetosaurus* and *Stagonolepis,* according to figures given by Walker (1961), the front legs are but 61 percent and 64 percent the length of the hind. *Proterosuchus* [*Chasmatosaurus*] is an early and surely primitive thecodont that is reasonably regarded as amphibious in habits although the available materials suggest that the front legs were but about 66 percent the length of the hind.

On the other hand, *Euparkeria, Hesperosuchus,* and *Ornithosuchus* are regarded by those who have studied them (Ewer 1965, Colbert 1952, and Walker 1964) as bipedal; and yet their limb ratios are as high or higher than some of the presumed quadrupeds, being 70 percent, 67 percent, and 70 to 75 percent, respectively. Obviously limb proportions in themselves are not sufficient to enable one to give a firm conclusion as to pose; body structure in general must be taken into consideration.

As regards *Chanaresuchus,* the limbs are very markedly disproportionate. If the radial length in MCZ 4037 was that estimated in relation to the humerus, the front leg would be but 53 percent that of the hind. However, the humerus of this specimen may be incomplete distally. If, instead, we take the small specimen from Tucumán in which all four bones conceived are present (with lengths of 39 mm for humerus, and 32, 59, and 59 for radius, femur, and tibia), we get a somewhat higher figure of 61 percent. These figures taken by themselves would seem to strongly suggest bipedality. But in other regards there is considerable reason to believe that *Chanaresuchus* was amphibious, spending much of its time in the water, where the body would be in a horizontal position; and while the animal could quite probably assume a semi-erect bipedal posture, this would only occur at such times when, ashore, speed seemed imperative. In consequence, I have restored the animal as a quadruped.

Relationships. In the preceding paper of this series, I have commented on possible relationships of *Chanaresuchus* and its relatives in the Proterochampsidae. Reig (1959) and Sill (1967) have argued for *Proterochampsa* as a pre-crocodile; Walker (1968), on the other hand, maintains that this genus is a pre-phytosaur rather than a pre-crocodilian, but maintains that its "cousin" *Cerritosaurus* is pre-crocodilian. Study of skull structure led me to believe that there was little in the cranial anatomy of *Chanaresuchus* to suggest relationships to either Crocodilia or Phytosauria, and that this group, the Proterochampsidae, was essentially a sterile one, representing a modest advance over the Proterosuchia, which in middle Triassic days occupied a position in the ecology similar to that of the phytosaurs of the late Triassic and the crocodilians of the later Mesozoic. Study of the postcranial anatomy does not lead me to change my previous conclusions.

The postcranial skeleton is for the most part of a primitive and generalized archosaurian type; the only advances over the proterosuchian condition lie in the fact that the pelvis has progressed to a more typical archosaurian condition in the "cleavage" between pubes and ischia for much of their height, with interruption of the primitively continuous ventral symphysis, and in the initiation of body armor not found in known proterosuchians. The armor is very lightly developed — much less than we would expect in an Anisian(?) predecessor of either crocodilians or phytosaurs. The pubis shows no indication of a trend toward exclusion from the acetabulum, as one might expect in a crocodile ancestor. The cervical ribs lack the specialization seen in crocodilians (and certain other thecodonts) of an anterior "spur" near the head.

Still further, the pes is of a highly specialized nature, not of a type antecedent to either crocodilians or phytosaurs.

Gualosuchus postcranial material. I may note that a small amount of postcranial material was found with the type skull of *Gualosuchus;* this included a scapulocoracoid, femur, parts of two tibiae, and a few bones of the pes. The elements preserved are in general comparable, except for larger size, to those of *Chanaresuchus.* The anterior border of the scapula is less everted than in *Chanaresuchus.* The height of the scapulocoracoid is 148 mm, the femoral length 158 mm. The femoral length is close to 50 percent the overall length of the skull, indicating that the *Gualosuchus* skull was rather shorter in proportion to body measurements than that of the relatively long-snouted *Chanaresuchus.* Further postcranial remains of *Gualosuchus,* which I trust will be described presently by Sr. Bonaparte, are present in the Instituto Lillo collections. In one specimen in that collection the humerus is somewhat less than two-thirds the length of the femur, thus indicating the same disproportion in limb length as in *Chanaresuchus.*

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A REVIEW OF THE AUSTRALIAN SPECIES OF *ELAPHROSYRON* AND *TELOSTEGUS*, WITH NOTES ON OTHER GENERA (HYMENOPTERA, POMPILIDAE)

Howard E. Evans

ABSTRACT. The genera *Elaphrosyron* and *Telostegus* are reported from Australia for the first time, and a brief review of the species is presented. The following new species are described: *E. socius*, *T. thomisivorus*, and *T. turneri*; *T. nigrocinerascens* (Turner) is also redescribed. Notes are presented on the genera *Pompilus*, *Ctenostegus*, and *Fabriogenia*, and the following new species described: *P. belardoo*, *C. warragai*, *F. canberra*, and *F. dilga*. Notes on the nesting behavior of these and other species will be presented separately.

During the summer of 1969–1970, Robert Matthews and I made a number of observations on the nesting behavior of Australian spider wasps (Pompilidae). Since the pompilid fauna of that continent has been little studied, we experienced much difficulty in identifying the species we worked on. Study of the types of Smith's and Turner's species in the British Museum has clarified many of our problems, but there remain several previously unnamed species for which we have field data that we consider worth publishing. Some of our most interesting data pertain to the related genera *Elaphrosyron* and *Telostegus* (neither previously reported from Australia), and I present here a review of the Australian members of those genera. Notes and descriptions relating to three other genera are also appended.

The material considered here will be deposited in the following museums, which are abbreviated in the text as follows:

AMS: The Australian Museum, Sydney
ANIC: Australian National Insect Collection, Canberra
BMNH: British Museum (Natural History), London
MCZ: Museum of Comparative Zoology, Cambridge
WAMP: Western Australian Museum, Perth

Genus *Elaphrosyron* Haupt

Elaphrosyron Haupt, 1929, Mitt. Zool. Mus. Berlin, 15: 120 (type-species: *E. heinrichi* Haupt).
—Arnold, 1937, Ann. Transvaal Mus., 19: 40–43 (African species).
Protelostegus Priesner, 1955, Bull. Soc. Ent. Egypt, 39: 167 (type-species: *P. arnoldi* Priesner). New synonymy.

Both Haupt and Arnold regarded this genus as closely related to *Episyron,* with which it shares several important features, most notably the bifid claws and the longitudinal folding of the wings along a vena spuria. However, the postnotum is shaped differently and there is no evidence of squamose pubescence on the body. The genus is poorly known but is apparently confined to warmer parts of the eastern hemisphere. The type species was described from the vicinity of the Caspian Sea, and Arnold recognized one species from central Africa and another from southern Africa. The genus has not previously been reported from Australia. There appears to be only one species on that continent, but it is widely distributed and locally common.

Arnold (1937) provided an accurate generic diagnosis, and there seems no need to present one here. The Australian species resembles the African *insidiosus* Smith closely.

Elaphrosyron socius new species

Holotype. ♀, Boundary Bend, Victoria, Australia, 25 Feb. 1970 (H. E. Evans and R. W. Matthews) [ANIC].

Description of type female. Length 10 mm; fore wing 9.7 mm. Body and appendages entirely black. Fore wings lightly infuscated except very narrowly darker at basal vein and broadly darker in marginal and outer two submarginal cells, also with a still darker band broadly margining the wing beyond the cells, but not quite reaching the extreme margin, which is whitish; hind wing very lightly infuscated, darker apically. Body clothed with conspicuous silvery pubescence over much of head, thorax, and leg-bases (but pubescence dark on much of mesoscutum and scutellum, metapleura, and anterior part of propodeum); abdomen with dark pubescence except most of first segment silvery, also posterior margins of sternite 2 and tergites 2–4. Head and thorax covered with pale erect hair which is especially long and dense on the temples, prothorax, mesopleura, and propodeum; coxae with short, pale hairs, femora weakly hairy; first abdominal tergite with pale hairs, apex of the abdomen with dark setae above and below.

Clypeus 2.4 × as wide as high, somewhat convex, the apical margin weakly concave. Front broad, middle interocular distance .65 × head width; inner eye margins subparallel below, strongly convergent above, upper interocular distance .77 × lower interocular distance; ocelli in a broad, flat triangle; postocellar line: ocello-ocular line = 5:4; third antennal segment equal to .70 × upper interocular distance. Pronotum short, broadly subangulate behind. Postnotum smooth, produced backward medially as an obtuse angle which is rounded at its apex. Front basitarsus with three long, weakly spatulate pecten spines, the apical basitarsal spine 1.6 × length of second segment; basitarsus also with two slender accessory spines nearly as long as the pecten spines, the accessory spines located on the inner margin and alternating with the pecten spines. Fore wing with the second submarginal cell 1.4 × as wide as the third, measured below, but of approximately the same width when measured on the radial vein; hind wing with the anal vein meeting media slightly basad of the cubital fork.

Allotype. ♂, same data as type [ANIC].

Description of allotype male. Length 7 mm; fore wing 5.8 mm. Coloration as in female; pubescence and erect hairs also as described for that sex. Fore wings subhyaline, with a brown band beyond the cells which does not quite reach the apex of wing; hind wings subhyaline, very slightly darkened apically.

Clypeus 2.2 × as wide as high, truncate apically. Middle interocular distance .64 × head width, 1.15 × lower interocular distance; upper interocular distance .95 × lower; ocelli rather large, in a flat triangle; postocellar line: ocello-ocular line = 4:3. First four antennal segments in a ratio of 10:4:8:9, segment three twice as long as thick, segments three and four together equal to .7 × upper interocular distance. Pronotum broadly angulate behind. Postnotum arcuately produced backward medially. Wing venation as described for female except second submarginal cell much larger than third, 1.6 × as wide measured below, 2.5 × as wide measured along the radial vein. Subgenital plate slender, tapering, its midline strongly elevated, surface with numerous strong setae and margin fringed with short, stiff setae. Genitalia as shown in Figure 1.

Paratypes. 13 ♀♀, 2 ♂♂, same data as type; 1 ♂, Yaapeet, Victoria, 18–22 Feb. 1970 (Evans & Matthews); 1 ♂, 5–15 miles south of Rainbow, Victoria, 21–22 Feb. 1970 (Evans & Matthews); 1 ♂, Wyperfeld Nat. Park, 25 miles north of Rainbow, Victoria, 18–23 Feb. 1970 (Evans & Matthews); 1 ♀, Near Adelaide, South Australia, 7 Jan. 1966 (O. W. Richards); 1 ♀, 1 ♂, Dedari, 40 miles west of Coolgardie, Western Australia, 11–21 Jan. 1936 (R. E. Turner); 1 ♀, 5 ♂♂, Merredin, Western Australia, 13 Dec. 1935 (Turner); 1 ♀, 2 ♂♂, Perth, Western Australia, Jan., Feb. 1914, 1936 (Turner); 1 ♀, 1 ♂, Yanchep, Western Australia, Nov., Dec. 1935 (Turner); 1 ♂, Mundaring Weir, Western Australia, 19–23 Feb. 1936 (Turner); 1 ♀, "New Holland" [ANIC, AMS, BMNH, MCZ, WAMP].

Variation. The females vary in length from 7.5 to 10.5 mm. In some specimens the apical margin of the clypeus is suffused with reddish brown, and the mandibles have a variable amount of this color. Otherwise there is little variation in color except that the female from Yanchep has slightly darker wings than usual and the silvery pubescent bands on the abdomen are reduced. This specimen also has the pecten spines unusually strongly spatulate.

The males vary in length from 5 to 9 mm. In several the second submarginal cell is only slightly larger than the third, and there is some variation in the patterning of silvery pubescence, but otherwise there is no noteworthy variation in this series.

Remarks. The females differ from those of the African species *insidiosus* Smith in the following particulars: clypeus slightly concave apically; third antennal segment considerably shorter; two strong accessory spines present on the front basitarsus in addition to the three pecten spines. I have seen no males of *insidiosus,* but I judge from Arnold's figures that the genitalia bear a close resemblance to those of *socius* but have somewhat differently shaped volsellae and parapenial lobes.

Genus *Telostegus* Costa

Telostegus Costa, 1887, Prospetto Imenotteri Italiani, II: 88 (type-species: *T. major* Costa). —Haupt, 1930, Mitt. Zool. Mus. Berlin, 16: 703–718 (Palaearctic spp.). —Arnold, 1937, Ann. Transvaal Mus., 19: 35 (African spp.). —Priesner, 1955, Bull. Soc. Ent. Egypt., 39: 168–183 (Egyptian spp.).

This genus is very closely related to *Elaphrosyron,* the major difference being that the second transverse cubital vein is absent. In all other respects, including the male genitalia, the two genera are scarcely separable. Our field notes suggest that the two genera are much alike ethologically.

Telostegus is widely distributed in warmer parts of the Eastern Hemisphere, but it has not previously been recorded from Australia. Although the specimens from that continent display little morphological diversity, I believe that they represent three species (one known only from males). The species may be separated by the following key:

Females

Vertex weakly arched above the eye tops; antennae elongate, third segment at least .75 × upper interocular distance; known specimens with a wing length of 7–8 mm. . . . . *nigrocinerascens* (Turner)

Vertex strongly arched above tops of eyes; antennae shorter, third segment .50 to .58 × upper interocular distance; known specimens with a wing length of 4.5 to 6 mm. *thomisivorus* new species

Males

1. Third antennal segment about 3 × as long as thick, third and fourth together subequal to upper interocular distance; postocellar line barely exceeding ocello-ocular line; vertex little arched above eye tops; genitalia as in Fig. 3. . . . . *nigrocinerascens* (Turner)

   Third antennal segment 2.0–2.7 × as long as thick, third and fourth together equal to from .65 to .80 × upper interocular distance; postocellar line: ocello-ocular line = 14:11; vertex strongly arched above eye tops. 2

2. Clypeus 2.5 × as wide as high; tibial spurs nearly as dark as the legs; volsellae slender, nearly parallel-sided (Fig. 4). . *turneri* new species

   Clypeus 2.8 × as wide as high; tibial spurs stramineous, much lighter than legs; volsellae much expanded, somewhat truncate apically (Fig. 2). . . . . *thomisivorus* new species

Telostegus nigrocinerascens (Turner) new combination

Aporus nigrocinerascens Turner, 1910, Proc. Zool. Soc. London, 1910: 334 (type: ♀, MacKay, Queensland, Australia, summer 1899, Turner Coll. [BMNH]).

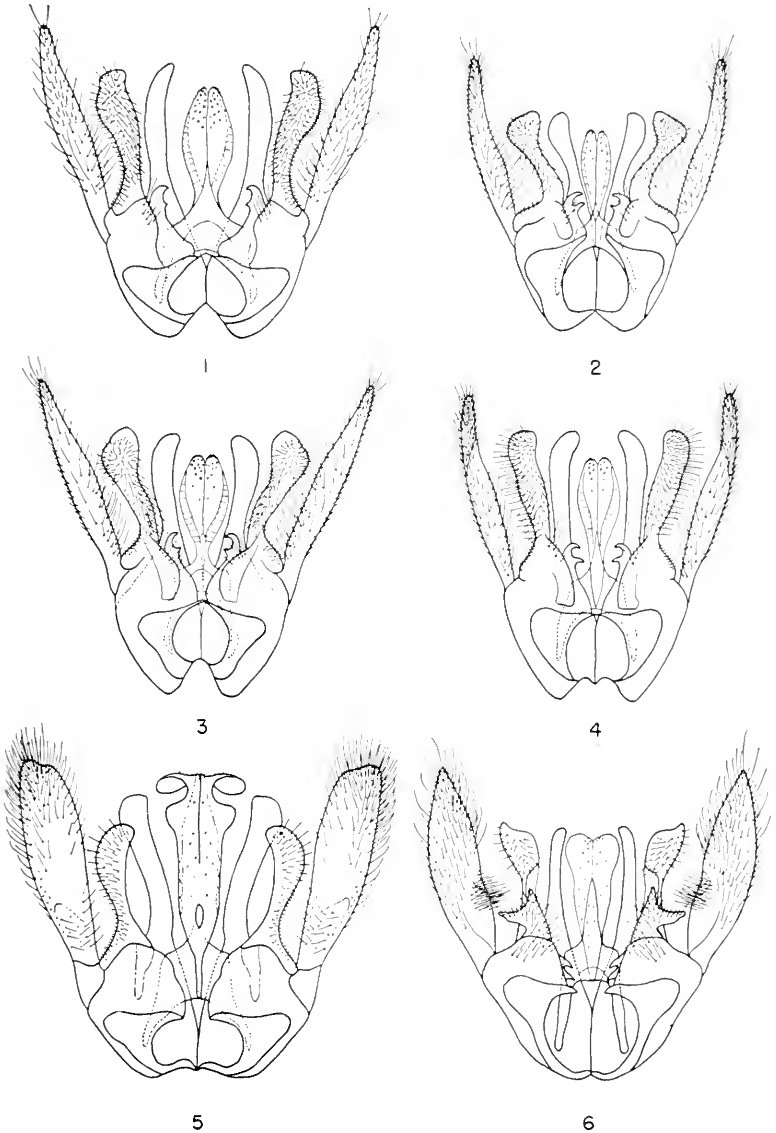
Description of type female. Length 8.6 mm; fore wing 7.5 mm. Black; antennae dark brown; legs black to dark brown, tibial spurs dusky testaceous. Fore wings subhyaline, with a brown cloud in the marginal and second submarginal cells that is partially separated from a brown band along the outer wing margin (not quite reaching the wingtip, which is hyaline); hind wings subhyaline, slightly darker apically. Body clothed with conspicuous silvery pubescence over much of head, thorax, and leg bases (but pubescence dark on much of mesoscutum, scutellum, and base of propodeum); abdomen silvery-pubescent over first segment and second sternite, also in a narrow posterior band on tergite 2, otherwise dark. Head and thorax covered with pale erect hair that is especially long and dense on the temples, prothorax, mesopleura, and propodeum; abdomen with sparse, dark setae ventrally and on the apical two segments dorsally.

Clypeus 2.7 × as wide as high, its apical margin truncate, polished and slightly elevated. Front broad, middle interocular distance .64 × head width; inner eye margins strongly convergent on the upper half, upper interocular distance .8 × lower; vertex passing nearly straight across between eye tops; ocelli in a flat triangle, postocellar line: ocello-ocular line = 7:6; third antennal segment equal to .8 × upper interocular distance. Pronotum short, broadly subangulate behind. Postnotum arcuately produced backward medially. Front basitarsus with three long pecten spines, the apical one 1.2 × the length of segment two; basitarsus also with two accessory spines ventrally, one quite short and the other nearly as long as the pecten spines. Fore wing with the second submarginal cell 2.5 × as wide as high; hind wing with the anal vein meeting media slightly basad of the cubital fork.

Plesiallotype. ♂, same data as type [BMNH].

Description of plesiallotype male. Length 6 mm; fore wing 5 mm. Black; antennae and legs, including tibial spurs, dark brown. Fore wings subhyaline, with a broad brown band along the outer margin; hind wings subhyaline. Body pubescence as described for the female. Head, thorax, and abdominal venter with sparse erect hair, including pale hairs on each side of the propodeum.

Clypeus 2.4 × as wide as high, its apical margin truncate. Front of moderate breadth, middle interocular distance .66 × head



Figures 1–6. Male genitalia of Pompilidae, ventral aspect (drawn to same scale). Fig. 1, *Elaphrosyron socius* n. sp. Fig. 2, *Telostegus thomisivorus* n. sp. Fig. 3, *T. nigrocinerascens* (Turner). Fig. 4, *T. turneri* n. sp. Fig. 5, *Pompilus belardoo* n. sp. Fig. 6, *Fabriogenia canberra* n. sp.

width; upper interocular distance .95 × lower; vertex weakly arched above eye tops; postocellar line: ocello-ocular line = 11:10. First four antennal segments in a ratio of 15:8:20:19, segment three 3 × as long as thick, segments three and four together equal to the upper interocular distance. Pronotum angulate behind. Postnotum arcuately produced backward medially. Venational features as in female. Subgenital plate elevated along the midline, pointed apically, the margin beset with strong spines. Genitalia as shown in Figure 3.

Other specimens examined. 4 ♀♀, 5 ♂♂, same data as type [BMNH]; 1 ♀, Yeppoon, Queensland, 3–6 Feb. 1970 (H. E. Evans) [ANIC]; 1 ♀, Ku-ring-gai Chase, 20 miles north of Sydney, New South Wales, 4–8 Jan. 1970 (H. E. Evans) [ANIC].

Variation. The females from Yeppoon and from Ku-ring-gai Chase resemble one another and differ from the MacKay series in the following respects: middle and hind tibial spurs white; abdominal tergites 3–6 with silvery pubescence apically; posterior margin of pronotum rather sharply angular; front basitarsus with both accessory spines rather long. These females resemble those from MacKay in all other particulars, and I feel it probable that all are conspecific.

Telostegus thomisivorus new species

Holotype. ♀, Nilemah Station, 50 miles south of Denham, Western Australia, 8–9 October 1969 (R. W. Matthews, note no. AM22) [ANIC].

Description of type female. Length 7 mm; fore wing 6 mm. Black, except anterior margin of clypeus and much of mandibles dull ferruginous, tibial spurs dusky testaceous. Fore wings lightly infuscated, more heavily clouded at the basal vein and in the marginal and second submarginal cells, also with a brown subapical band, the extreme outer wing margin hyaline; hind wings subhyaline, slightly darker apically. Body clothed with silvery pubescence over much of head, thorax, and leg-bases (but pubescence dark on mesoscutum, scutellum, and base of propodeum); abdomen with dark pubescence except silvery on first segment, second sternite, and apical margin of second tergite. Head and thorax covered with pale hair that is especially dense and long on the temples and propodeum; abdomen with sparse, dark setae ventrally and on the apical two segments dorsally.

Clypeus 2.8 × as wide as high, its apical margin truncate, polished and slightly elevated. Front broad, middle interocular distance .68 × head width; upper interocular distance .87 × lower; vertex forming a strong, even arc above tops of eyes; postocellar line: ocello-ocular line = 7:6; antennae rather short, third segment equal to only .55 × upper interocular distance. Pronotum broadly angulate behind. Postnotum arcuately produced backward medially. Front basitarsus with three slender pecten spines, the apical one 1.3 × the length of segment two; basitarsus also with two slender accessory spines, as described for *nigrocinerascens*. Fore wing with the second submarginal cell 2.5 × as wide as high; hind wing with the anal and cubital veins interstitial.

Allotype. ♂, same data as type except taken in a Malaise trap (H. E. Evans & R. W. Matthews) [ANIC].

Description of allotype male. Length 5.5 mm; fore wing 5 mm. Color of body and of tibial spurs as in female; pubescence as in that sex except abdominal dorsum with brownish pubescence beyond segment one. Fore wing lightly infuscated, slightly darker in marginal cell and in a subapical band; hind wing subhyaline, slightly darker apically. Sparse, pale hairs present on head, prothorax, pleura, and propodeum; abdominal venter with a few dark setae, especially toward the apex.

Clypeus 2.8 × as wide as high, its apical margin truncate. Front broad, middle interocular distance .7 × head width; upper interocular distance .9 × lower; vertex forming a strong, even arc above eye tops; postocellar line: ocello-ocular line = 14:11. First four antennal segments in a ratio of 8:3:7:7, segment three about twice as long as thick, segments three and four together equal to .66 × upper interocular distance. Pronotum angulate behind. Postnotum arcuately produced backward medially. Wing venation as in female except anal vein reaching media slightly before the cubital fork. Subgenital plate slender and tapering, its midline strongly elevated, surface with strong setae. Genitalia differing from those of *nigrocinerascens* chiefly in having the volsellae more abruptly truncate apically (Fig. 2).

Paratypes. 1 ♀, 1 ♂, same data as allotype; 1 ♀, 6 ♂♂, 2 miles west of Coorow, Western Australia, 12 Oct. 1969 (Evans & Matthews); 1 ♀, 1 ♂, 13 miles SW of Carnemah, Western

Australia, 12 Oct. 1969 (Evans & Matthews); 1 ♀, 1 ♂, 27 miles north of Northampton, Western Australia, 10 Oct. 1969 (Evans & Matthews); 1 ♀, Miaboolya Beach, 9 miles north of Carnarvon, Western Australia, 4 Oct. 1969 (Evans & Matthews) [AMS, ANIC, BMNH, MCZ, WAMP].

Variation. The females vary slightly in size but are consistently smaller than the known females of *nigrocinerascens* (length 4.5–7.0 mm). The fore wings vary from hyaline to moderately infuscated basally, and the abdomen often lacks silvery bands beyond the first segment. The middle interocular distance varies from .67 to .70 × the head width, the third antennal segment from .50 to .58 × the upper interocular distance.

The males vary in length from 4 to 6 mm. Some of the smaller specimens have more silvery pubescence on the abdomen than described for the allotype, and in some of these specimens the upper interocular distance exceeds the lower interocular distance slightly.

Telostegus turneri new species

Holotype. ♂, Yallingup, Western Australia, 1–12 Dec. 1913 (R. E. Turner) [BMNH].

Description of type male. Length 7 mm; fore wing 5.3 mm. Body black; antennae and legs dark brown except tibial spurs stramineous. Wings very lightly infuscated except fore wing with a darker band along the outer margin, hind wing slightly darker apically. Pubescence brownish except conspicuously silvery on front, temples, prothorax, coxae, lower pleura, posterior part of propodeum, first abdominal tergite, and first two sternites. Head, thorax, and abdominal venter sparsely setose, the temples, propleura, and propodeum with an abundance of pale hair.

Clypeus 2.5 × as wide as high, truncate apically. Front broad, middle interocular distance .69 × head width; upper interocular distance .95 × lower; vertex forming a strong, even arc above eye tops; postocellar line: ocello-ocular line = 14:11. First four antennal segments in a ratio of 16:7:19:17, segment three 2.7 × as long as thick, three and four together equal to .80 × the upper interocular distance. Pronotum angulate behind. Postnotum subangularly produced backward medially. Fore wing with the second submarginal cell 2.5 × as wide as high; hind wing with the anal and cubital veins interstitial. Subgenital plate strongly elevated medially, pointed apically, surface with several strong setae and margin with a row of stout spines. Genitalia very similar to those of *nigrocinerascens*, but the volsellae more slender and parallel-sided (Fig. 4).

Paratypes. 2 ♂♂, same data as type except one dated Nov. 1913 [ANIC, BMNH].

Variation. Both paratypes are smaller than the type (fore wing 3.8–4.3 mm). In the smaller specimen, the upper and lower interocular distances are subequal and antennal segments three and four only .65 × the upper interocular distance. In the larger male these measurements approximate those of the type.

Genus *Pompilus* Fabricius

Pompilus Fabricius, 1798, Suppl. Ent. Syst., p. 212 (type-species: *P. pulcher* Fabricius).

The precise limits of this large, cosmopolitan genus have never been defined. Many generic and subgeneric names are available, but for the most part these are difficult to apply when the genus is considered from a world point-of-view. *Pompilus*-like wasps are abundantly represented in Australia, and they are somewhat diverse morphologically, but there seems little hope of fitting them neatly into accepted subgenera or closely related genera at this time. Hence, I shall use the generic name in its broad sense and when discussing species simply attempt to point out the closest known relatives within the genus.

Pompilus cinereus (Fabricius)

Sphex cinerea Fabricius, 1775, System. Ent., p. 350.

Sphex plumbea Fabricius, 1787, Mant. Insect., I: 278. New synonymy.

Pompilus pulcher Fabricius, 1798, Suppl. Ent. Syst., p. 249. New synonymy.

This is a very common wasp in eastern Australia, its typical habitat being sea beaches and sand banks along streams. I have studied the Fabricius specimen in the Banks collection at the British Museum, probably the type, and my interpretation of the species is based on that specimen. Australian specimens compare very favorably with specimens of *plumbeus* and *pulcher* from India, Africa, and Europe, even to minor details of the male genitalia. Evidently this one species ranges in suitable habitats throughout the warmer parts of the eastern hemisphere. Arnold (1937, Ann. Transvaal Mus., 19: 47) recorded it from China, and one assumes that it also occurs in the East Indies.

There is an extensive literature on this species, mainly under the name *Pompilus plumbeus*. Our field observations, so far as they go, agree well with the accounts of various European authors. Arnold (1937) placed three additional species names in synonymy with *plumbeus*.

Pompilus belardoo new species

Holotype. ♀, Rottnest Island, Western Australia, 21–22 Oct. 1969 (H. E. Evans & R. W. Matthews) [ANIC].

Description of type female. Length 14 mm; fore wing 11 mm. Body and appendages entirely black; wings moderately infuscated, broadly darker along outer margins. Pubescence in large part dark, with a blue-green sheen in certain lights, but conspicuously silvery as follows: much of scape, clypeus, front, and temples; anterior third and posterior margin of pronotum; sides of scutellum and sides and central part of metanotum; much of upper surface of tibiae; narrow posterior margins of abdominal segments one to four, these bands narrowly interrupted mid-dorsally and broadly interrupted ventrally. Body clothed with rather long, dark hairs over much of the head and thorax, including the scape, propodeum, coxae, and to some extent the femora; abdomen with dark hairs ventrally and on the apical two tergites.

Clypeus 2.3 × as wide as high, truncate apically; malar space, at its minimum, about half the width of the anterior ocellus. Front rather narrow, middle interocular distance .56 × head width; upper interocular distance .82 × lower; vertex passing nearly straight across between eye tops; postocellar line: ocello-ocular line = 6:5; third antennal segment subequal in length to upper interocular distance. Pronotum broadly subangulate behind. Propodeum with a median sulcus anteriorly, posterior third with a flat declivity. Front basitarsus with a strong pecten consisting of five slender spines, the apical one 1.7 × as long as the second segment, the basitarsus also with two accessory spines nearly as long as the pecten spines. Fore wing with the marginal cell removed from the wing tip by approximately its own length, the radial vein somewhat angled at the third transverse cubital vein; third submarginal cell about as wide below as the second, but more strongly narrowed above.

Allotype. ♂, same data as type [ANIC].

Description of male allotype. Length 11 mm; fore wing 9.7 mm. Color of body and wings as in female, but silvery pubescence less extensive than in that sex, restricted to the base of the mandibles, sides of the clypeus and front, temples, and interrupted apical bands on abdominal tergites 1 and 2 and sternite 2. Head and thorax with an abundance of long, dark hairs, including some on the scape and on the coxae and to some extent the femora; abdomen sparsely setose ventrally.

Clypeus convex, twice as wide as high, its apical margin truncate; malar space rather long, nearly equal to width of anterior ocellus. Middle interocular distance .58 × head width; upper interocular distance .97 × lower; vertex passing nearly straight across between eye tops; postocellar line very slightly exceeding ocello-ocular line. Third antennal segment 2.4 × as long as thick, third and fourth together subequal to upper interocular distance. Pronotum subangulate behind. Propodeum rounded, abruptly declivous on posterior fourth. Apical segment of front tarsus symmetrical, unmodified, but the inner claw strongly curved, bifid. Venation as in female. Subgenital plate elevated along the midline, broadly rounded apically. Genitalia with the basal hooklets absent, the aedeagus with an abrupt apical expansion that is turned sharply downward (Fig. 5).

Paratypes. 6 ♀♀, 5 ♂♂, same data as type [AMC, ANIC, BMNH, MCZ, WAMP].

Variation. The females vary in length from 11 to 14 mm. In the majority the third antennal segment is very slightly shorter than the upper interocular distance (.93–1.00 × this distance) and in three the silvery pubescence on the posterior margin of the pronotum and on abdominal tergite 4 is weakly developed. The males vary in length from 8.5 to 11 mm. Three of them have slightly more silvery pubescence than the allotype, including some on the pronotum and sides of the scutellum; however, the banding of the abdomen is relatively constant.

Remarks. This species is closely related to several other Australian species, such as *semiluctuosus* Smith, but the patterning of silvery pubescence, the male genitalia, and the nature of the pecten spines of the female are distinctive. Belardoo is an aboriginal word from Western Australia referring to coastal sand dunes.

Genus *Ctenostegus* Haupt

Ctenostegus Haupt, 1930, Mitt. Zool. Mus. Berlin, 16: 685 (type-species: *Sphex cingulata* Fabricius).

This is a dominant genus of Pompilidae in Australia and on adjacent islands; in fact it may well be the largest genus of the family in that zoogeographic region. It is closely related to *Pompilus* and probably a derivative of that genus. Only a few of the species have been described. One of the commoner species, for which we have nesting data, is described below and compared with the type species.

Ctenostegus warragai new species

Holotype. ♀, 3 miles west of Wentworth, New South Wales, 27 Nov. 1969 (R. W. Matthews, note no. AM92) [ANIC].

Description of type female. Length 12 mm; fore wing 9.5 mm. Body and appendages entirely black. Wings rather heavily infuscated, broadly darker along outer margin. Pubescence wholly dark, on the abdomen with dark blue-green reflections in certain lights. Body with short, sparse, rather dark hairs as follows: front, vertex, temples, propleura, front coxae, propodeum, and tip of abdomen.

Clypeus 2.4 × as wide as high, apical margin narrowly polished, weakly concave; malar space well developed, at its minimum nearly as long as width of anterior ocellus. Front narrow, middle interocular distance .55 × head width; upper interocular distance .92 × lower; postocellar line: ocello-ocular line = 6:5; third antennal segment equal to .77 × upper interocular distance. Posterior margin of pronotum angulate. Propodeum rounded, with a flat, oblique declivity on the posterior third. Front basitarsus with four rather broad pecten spines, the apical one 1.7 × as long as the second segment. Second submarginal cell of approximately the same width as the marginal cell, measuring 2.2 × as wide as high, narrowed by two-thirds above.

Paratypes. 10 ♀♀, same data as type except collected by H. E. Evans & R. W. Matthews; 6 ♀♀, 4 miles east of Wilcannia, N.S.W., 1–2, 20–21 Nov. 1969 (Evans & Matthews); 1 ♀, 5 miles west of Wilcannia, N.S.W., 1 Nov. 1969 (Evans & Matthews); 4 ♀♀, Packsaddle, 111 miles north of Broken Hill, N.S.W., 31 Oct., 21–26 Nov. 1969 (Evans & Matthews); 1 ♀, Port Germein, South Australia, 28 Oct. 1969 (Evans & Matthews) [AMS, ANIC, BMNH, MCZ].

Variation. The paratypes vary in length from 8 to 14 mm; the middle interocular distance varies from .52 to .57 × the head width, the third antennal segment from .75 to .85 × the upper interocular distance. Several of the specimens have a small amount of silvery pubescence on the sides of the clypeus and/or lower front.

Remarks. This species is closely related to the type species, *cingulatus* Fabricius, but the pubescence is wholly or almost wholly dark, the propodeum more hairy, and the pecten spines longer. I have not been able to associate any males with these females with any certainty.

All specimens were collected in areas of extensive sand dunes or ridges. The species name *warragai* is an aboriginal word from New South Wales meaning "plenty of sand."

Genus *Fabriogenia* Banks

Fabriogenia Banks, 1941, Occ. Papers B.P. Bishop Mus., Honolulu, 16: 240 (type-species: *F. incompta* Banks).

This is the dominant genus of the tribe Auplopodini in Australia. Turner (1910, Proc. Zool. Soc. London, 1910: 310) presented a key to several of the species (under the name *Pseudagenia*), but there are many additional species. Both Banks (1941) and Townes (1957, Bull. U.S. Nat. Mus., 209: 141) pointed out the similarity of *Fabriogenia* to *Phanagenia,* but I regard them as generically distinct. Not all of the species have a well-developed malar space and lateral spines beneath the apical tarsal segments, as described by Banks for the type species, but they agree in having a central polished area on the apical tergite of the female (approaching the condition in *Auplopus*), as well as a group of stout bristles on the mentum. The generic classification of the Auplopodini is in a deplorable state, but for the present it seems sufficient to assign the majority of the Australian species to *Fabriogenia.*

Fabriogenia canberra new species

Holotype. ♀, Canberra, A.C.T., Feb. 1970 (R. W. Matthews, note no. AM191) [ANIC].

Description of type female. Length 9 mm; fore wing 8 mm. Body and legs black; antennae bright orange except scape and apical segment very weakly infuscated. Wings clear hyaline except fore wings with a narrow brown band at the basal and transverse median veins and a somewhat wider band through the base of the marginal cell, across the second submarginal and base of the third submarginal cell, and into the outer discoidal cell; tip of wing also darkened. Body covered with fine, silvery pubescence which is darker on the vertex and mesoscutum. Pale, erect hairs are present over much of the head, prothorax, front coxae, mesopleura, and propodeum; abdomen sparsely setose ventrally and densely so on the apical tergite.

Clypeus convex, weakly produced medioapically, measuring 1.9 × as wide as high. Middle interocular distance .64 × head width; upper interocular distance .95 × lower; postocellar line: ocello-ocular line = 7:9; vertex forming a low, even arc above eye tops. Antennae moderately thick, third segment 3.5 × as long as thick, exceeding the fourth segment as 10:9, equal to .70 × the upper interocular distance. Pronotum broadly subangulate behind. Postnotum, along the midline, about two-thirds the length of the metanotum. Propodeum evenly rounded in lateral view. Hind tibiae with numerous short spines laterally, smooth above. Second submarginal cell twice as wide as high, receiving the first recurrent vein slightly before the middle; third submarginal cell 1.7 × as wide as second, receiving the second recurrent vein .3 × the distance from the base.

Allotype. ♂, same data as type [ANIC].

Description of allotype male. Length 7.5 mm; fore wing 6.8 mm. Black, except as follows: mandibles with a cream band about halfway from the base, the tips rufous; clypeus cream laterally and apically; sides of lower front narrowly cream; front legs suffused with light brown on their inner sides; hind tibial spurs white, other spurs more or less infuscated; antennae orange except basal two segments weakly infuscated, apical four segments strongly infuscated. Wings clear hyaline, unbanded, fore wings slightly darkened at apex. Body clothed with fine, silvery pubescence. Head and thorax extensively covered with pale, erect hairs, including the propodeum and front coxae.

Clypeus 2.2 × as wide as high, truncate apically. Middle interocular distance .64 × head width; upper interocular distance 1.1 × lower; postocellar line: ocello-ocular line = 3:4; vertex forming a smooth arc above tops of eyes. Antennae elongate, third segment subequal to fourth, 3.4 × as long as thick, .67 × upper interocular distance. Pronotum broadly subangulate behind. Postnotum medially only slightly shorter than metanotum. Venation as in female. Abdominal sternite 6 with a pair of toothlike elevations bordering a median, flat area. Subgenital plate broad, outer apical margins rounded, extreme apex truncate; surface somewhat concave, margins fringed with setae. Genitalia as shown in Figure 6.

Paratypes. 4 ♀♀, same data as type [ANIC, BMNH, MCZ].

Variation. The four paratypes range in size from 7 to 9.5 mm and resemble the type closely in all details; the upper interocular distance varies from .93 to 1.0 × the lower, antennal segment three from .65 to .72 × the upper interocular distance.

Remarks. This species runs to the final couplet in the key to *Pseudagenia* provided by Turner (1910, Proc. Zool. Soc. London, 1910: 310). It is a smaller species than *australis* Cameron, and the male lacks banding on the fore wings and has the sixth sternite somewhat differently modified. The size is comparable to that of *fusiformis* Saussure, but the latter species is much less hairy and has a longer pronotum.

Fabriogenia dilga new species

Holotype. ♀, Canberra, A.C.T., 31 January 1970 (H. E. Evans, note no. A118) [ANIC].

Description of type female. Length 9.5 mm; fore wing 8.8 mm. Coloration of body appendages, wings, and pubescence exactly as described for *canberra*. Head and pronotum, including the front coxae, with numerous pale, erect hairs; propodeum with a few pale hairs on each side, but the pleura weakly hairy; abdomen sparsely setose ventrally and densely so on the apical tergite.

Clypeus convex, strongly and subangularly produced apically, measuring 1.6 × as wide as high. Middle interocular distance .61 × head width; upper and lower interocular distances subequal; postocellar line: ocello-ocular line = 2:3; vertex forming a low, even arc above eye tops. Antennae elongate, third segment 4 × as long as thick, exceeding the fourth segment as 10:8, equal to .82 × the upper interocular distance. Pronotum very broadly angulate behind. Postnotum along the midline about half the length of the metanotum. Propodeum evenly rounded, with a weak median sulcus. Hind tibiae weakly spinose laterally, almost without spines above. Second submarginal cell 1.7 × as wide as high, receiving the first recurrent vein slightly beyond the middle; third submarginal cell nearly twice as wide as the second, receiving the second recurrent vein .38 × the distance from the base.

Paratype. ♀, same data as type [ANIC].

Variation. The paratype is smaller (7.5 mm, fore wing 7 mm) and the third antennal segment equal to only .73 × the upper interocular distance. Otherwise it is very similar to the type.

Remarks. This species is exceedingly similar to the preceding, but differs in the shape of the clypeus, the more elongate antennae, the shorter postnotum, and minor details of wing venation. Only the female is known.

Dilga is an aboriginal word from New South Wales, meaning "a stick of wood." Two females were reared from a trap-nest, so I assume the species typically nests in hollow twigs or other cavities in wood.

B R E V I O R A

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GROWTH CHANGES IN *AMPHILIMNA OLIVACEA* (LYMAN) AND THE SYSTEMATIC STATUS OF *AMPHITARSUS SPINIFER* SCHOENER[1]

Lowell P. Thomas[2] and Amy Schoener[3]

Abstract. Analysis of the developmental sequence in the brittlestar *Amphilimna olivacea* (Lyman) has revealed the similarity between its young stages and those of adult *Amphitarsus spinifer* Schoener. Evidence is provided to justify synonymizing the latter species with the former.

INTRODUCTION

Two recent papers published almost simultaneously have dealt with the enigmatic brittlestar genus *Amphitarsus*. Schoener (1967a) described two new species of this previously monotypic genus and discussed its possible family affinities, while Thomas (1967: 126) pointed out the similarities between *Amphitarsus mirabilis* H. L. Clark 1941 and *Amphilimna olivacea* (Lyman, 1869). The information contained in these two papers has prompted a re-examination of *Amphitarsus spinifer* and a study of the growth stages of *Amphilimna olivacea*. As a result of our studies we synonymize *A. spinifer* as a junior synonym of *Amphilimna olivacea* and discuss changes that take place during the growth of this species.

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Amphilimna olivacea (Lyman, 1869)

Ophiocnida olivacea Lyman, 1869, Bull. Mus. Comp. Zool., 1(10): 340 (off Alligator Reef, Caribbean, 79 fms.).

Amphitarsus spinifer Schoener, 1967a, Breviora No. 267: 6, fig. 2 (NW Atlantic, 200 m). See Thomas (1967) for complete synonymy of *A. olivacea.*

Diagnosis. Adult specimens (see below for discussion of young animals). Jaws with two, occasionally three, infradental papillae at apex, two or three slender oral papillae bordering each adoral plate; two oral tentacle scales, resembling papillae, in each oral slit. Arms slender, six times disc diameter; tentacle pores large; eight to ten proximal ventral arm plates with two tentacle scales on each side, innermost attenuated; beyond tenth ventral arm plate a single tentacle scale on each side; seven to nine slender arm spines, ventralmost largest; arm spines of arm segments under disc greatly flattened, fused together to form peculiar flanges occupying genital slits; dorsal arm plates slightly wider than long. Disc scales studded with slender spines; primary plates present, often inconspicuous. Radial shields narrow, joined proximally, slightly separated distally; disc deeply notched at each pair of radial shields. Color variable, disc gray, tan, or brown, arms pink or orange.

SYSTEMATIC DISCUSSION

Although this species has been known for over a century, it has been only in the last nine years that the peculiar fused arm spines under the disc have been described. Early references to *A. olivacea,* in addition to omitting mention of this important character, are generally brief and often unillustrated. Lyman's only figures (1871, pl. 1, figs. 7, 8) show primitive plates, although only indistinctly, and a view of the ventral arm and disc surfaces, omitting the fused arm spines. The only other illustrations prior to 1962 are Verrill's (1899; pl. 42, figs. 1, 1a) stylized figures of the ventral disc surface and one row of arm spines. Again, the fused arm spines are omitted. Finally, Cherbonnier (1962) described and illustrated the fused arm spines, erroneously referring to them as "écailles genitales." They were described and properly identified by Thomas (1967), who also considered the similar "winglike flanges" of *Amphitarsus mirabilis* to be fused arm spines. If the latter observation is correct, it is almost certain, in view of the other similarities discussed by Schoener (1967a) and Thomas *(ibid.)*, that *Amphitarsus mirabilis* and *Amphilimna olivacea* are congeneric. External features and dissection of oral and dental plates indicate that *Amphilimna olivacea* belongs in the family Ophiacanthidae, but material of *Amphitarsus mirabilis* is not available for dissection.

GROWTH CHANGES

In the following section small (presumably young) and large (presumably adult) specimens of *Amphilimna olivacea* are figured in dorsal and ventral aspect (Figs. 1A, B & 2A, B). Synopses of the growth changes are given, purposely written so as to trace the growth sequence in reverse, going from the larger to the smaller individual. This was done so that specimens of the even smaller species, *Amphitarsus spinifer* (Figs. 1C, D & 2C, D), could be viewed as initial stages of a growth series terminating with large specimens of *A. olivacea.*

Growth changes on the dorsal surface

Amphilimna olivacea. In the larger specimen (9.7 mm disc diameter) important systematic characters of the dorsal surface (Figure 1A) appear as follows: (1) Only the central plate of the six primary plates is conspicuous. (2) The radial shields are contiguous for much of their length and are greatly attenuated. (3) Most of the disc is covered by fine overlapping scales, each of which frequently bears a spine. (4) The dorsal arm plates are rectangular or with a convex outer edge.

In a smaller specimen (4.5 mm disc diameter): (1) All six of the primary plates are conspicuous and occupy a greater proportion of the disk than in the larger specimen. (2) The radial shields, which are less attenuated, are not always contiguous. (3) The fine scale covering of the disc is comprised of fewer scales than in the larger specimen, and the scales less frequently bear spines. (4) The dorsal arm plates have convex distal edges and are concave laterally.

Amphitarsus spinifer. The holotype of this species (Fig. 1C) has a disc 3.8 mm in diameter, and is therefore comparable to the specimen of *A. olivacea* illustrated in Figure 1B. Here: (1) The six primary plates are conspicuous, although in this case they are

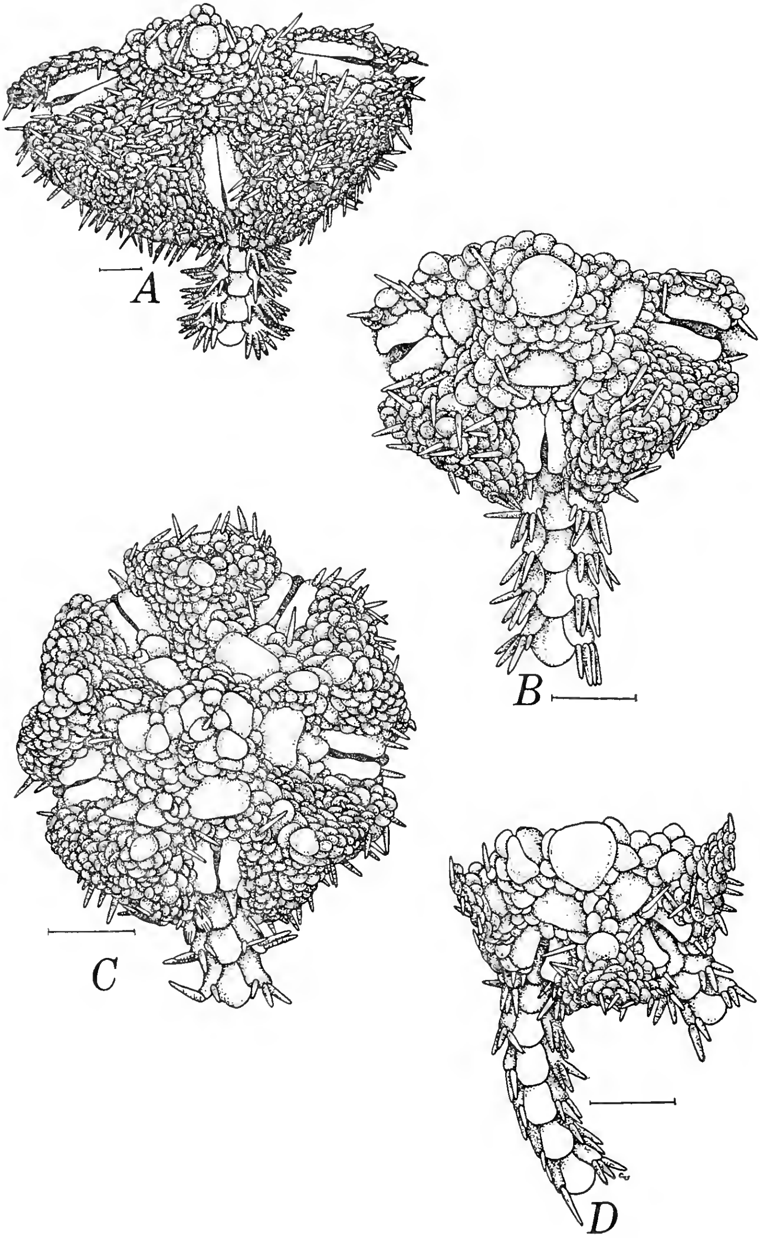

Figure 1. Dorsal views of specimens arranged in order of decreasing size. A. *Amphilimna olivacea* (9.7 mm); B. *A. olivacea* (4.5 mm); C. *Amphitarsus spinifer* (3.8 mm); D. *A. spinifer* (ca. 3 mm).

less perfectly arranged and other large irregular scales are present on the disc. (2) The radial shields are separated for their entire length and, although longer than wide, do not appear greatly attenuated. (3) The fine disc scales bear spines only occasionally. (4) The dorsal arm plates are nearly identical to those figured for *A. olivacea* of this size (Fig. 1B).

Figure 1D illustrates a paratype of *A. spinifer* whose disc diameter is smaller (ca. 3 mm) than that of the holotype. Here: (1) The primary plates, of which one central and three radial are figured, are large relative to the size of the disc, occupying a sizable fraction of the dorsal surface. (2) The radial shields are much shorter, relative to their width, and are not contiguous. (3) The scalation of the disc consists of even fewer fine overlapping scales, which bear scale spines only occasionally. Here again, several larger scales, particularly one in each interradial area, are quite noticeable, although other large scales are present around the central disc area. (4) The dorsal arm plates, which are basically rectangular, show some convexity at the distal edge and slight indentations laterally.

Growth changes on the ventral surface

Amphilimna olivacea. In the specimen with a disc 9.7 mm in diameter: (1) Seven sets of flanges of fused arm spines are borne by those arm segments overlain by the disc. (2) The oral shield is basically triangular with a distal edge that forms a slight outward bulge toward the middle. (3) On the arm plates overlain by the disk two tentacle scales are usually present. (4) Eight or nine arm spines are present on each side arm plate at the point where the arm becomes free of the disc. (5) The ventral surface of the disc is covered by many small overlapping scales bearing spines.

Figure 2B shows the smaller specimen of this species: (1) There are only three sets of flanges per arm. (2) The oral shield, with an even more convex distal side, almost forms a rhombus. (3) Two tentacle scales are often present on the arm plates overlain by the disc. (4) The arm bases have fewer arm spines (five or six) than in the above specimen. (5) The ventral surface of the disc is covered by fewer overlapping scales than in the above specimen. Some of these bear single scale spines.

Amphitarsus spinifer. The specimen illustrated in Figure 2C (the holotype) is almost the same size as the *A. olivacea* shown

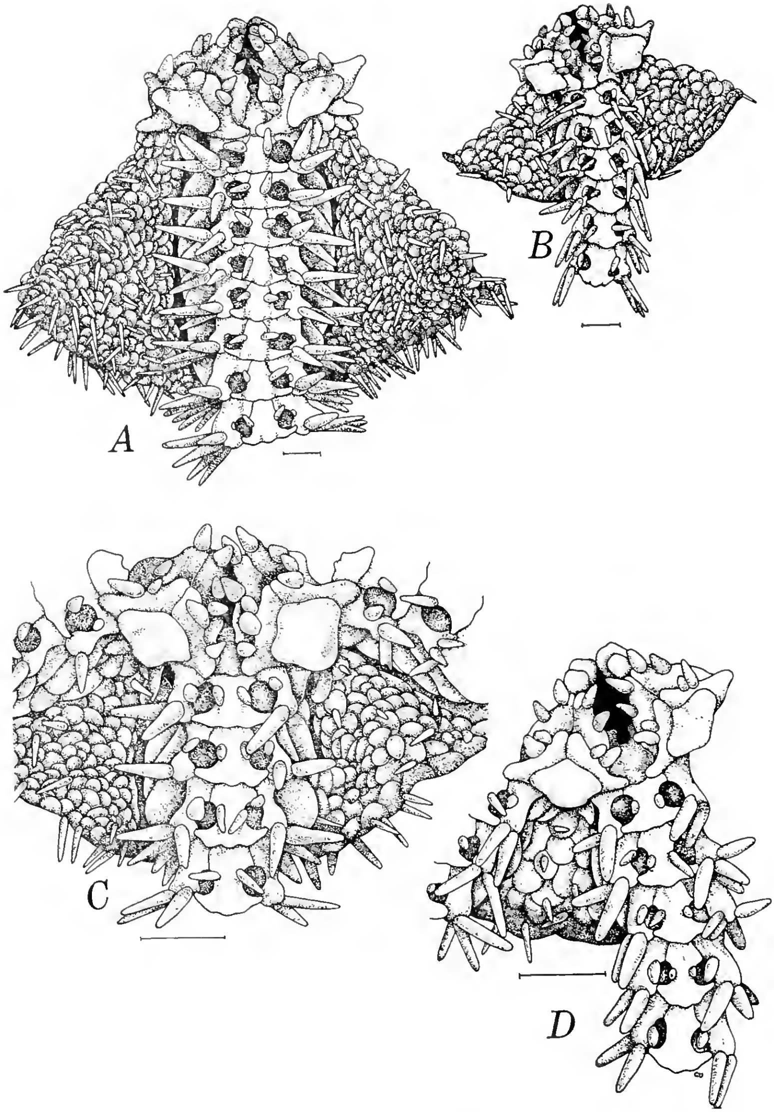

Figure 2. Ventral views of specimens arranged in order of decreasing size. A. *Amphilimna olivacea* (9.7 mm); B. *A. olivacea* (4.5 mm); C. *Amphitarsus spinifer* (3.8 mm); D. *A. spinifer* (ca. 3 mm).

in Figure 2B. In the characters considered, except perhaps for the length of the disc scale spines, it scarcely differs from *A. olivacea.*

Figure 2D shows the ventral aspect of the smaller specimen of *A. spinifer:* (1) The number of flanges in the genital area is reduced still further to two sets per arm. (2) The distal side of the oral shield is more rounded. (3) Two tentacle scales usually are present on the arm plates overlain by the disc. (4) The number of arm spines near the arm base (four or five) is less than that in the larger *A. spinifer* (above). (5) The ventral surface of the disc is covered by still fewer scales, which overlap less, and only a few of which bear spines.

CONCLUSION

In order to conclude on the basis of evidence from growth sequences that two supposed species, the larger *Amphilimna olivacea* and the smaller *Amphitarsus spinifer,* are in reality only one species, two criteria must be satisfied. First, for specimens of each species that overlap in size, one must show that the variation in important characteristics is negligible. Second, one must be able to offer a logical progression of growth stages from one to the other.

The first point is readily satisfied upon examination of specimens of the same size range. This has been done (see Figs. 1B, C & 2B, C) and the specimens are found to be very similar.

The second point, that growth sequences should generally agree within reasonable bounds with those of other species investigated, is also satisfied. Superficially the following sequences are consistent with knowledge of developmental series for other ophiuroid species (Schoener, 1967b, 1969). These points include the following: (1) The six primary plates of the dorsal disc surface may become less conspicuous as the specimens in a series increase in size. (2) The radial shields are initially small and may elongate with an increase in the size of the specimen. (3) More arm spines are added as the adult condition is approached. (4) There may be an increase in the number of specialized elements (e.g., flanges in the genital area) as the adult condition is reached. (5) There will be an increase in the number of scales covering the disc if their absolute size remains constant while the size of the specimen increases.

Several other characters remained fairly constant in this series. These were the deep notching of the disc at the distal ends of the radial shields, the shape of the dorsal and ventral arm plates, and the number of infradental papillae at the jaw apex.

Points on which no judgment is presently made concern the variation in the shape of the oral shield, which in any case seems slight, and the fact that there is no documented sequence of development in which radial shields in the smallest specimens are initially separated but later become contiguous. However, since our knowledge in this area is just being expanded, this may indeed occur in other species.

Based on the above evidence, it is concluded that the smaller species *Amphitarsus spinifer* Schoener is part of the developmental series of *Amphilimna olivacea* (Lyman), the latter name having priority.

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BREVIORA

Museum of Comparative Zoology

Cambridge, Mass. April, 1972 Number 388

INTENSE LOW-FREQUENCY SOUNDS FROM AN ANTARCTIC MINKE WHALE, *BALAENOPTERA ACUTOROSTRATA*

William E. Schevill and William A. Watkins

Abstract. Intense low-frequency underwater sounds, somewhat similar to those heard from other species of *Balaenoptera*, have been recorded from minke whales, *Balaenoptera acutorostrata* Lacépède 1804, in the Ross Sea, Antarctica.

The small *Balaenoptera* (minke whales) of the Antarctic had for many years been identified as *B. acutorostrata* Lacépède 1804, until Williamson (1959 and 1961) indicated that some of them might be referable to *B. bonaerensis* Burmeister 1867, which van Utrecht and van der Spoel (1962) considered no more than a variety. Since our Ross Sea whales showed us only the top of the back and the part of the head from the blowholes forward (Fig. 1), we could not judge whether they were this form or the typical *acutorostrata*, so we refrained from reporting the sounds till the relationship of these Antarctic minke whales to those in other parts of the world was more clearly defined. Ohsumi, Masaki, and Kawamura (1970) have now compared the southern and northern forms and concluded (p. 116) that any differences were minor and that the Antarctic minke whale was not taxonomically separable from the typical northern *Balaenoptera acutorostrata*, and this conclusion we happily accept.

Our recordings were made from the edge of the Ross ice shelf 2 km east of Cape Crozier, Ross Island, on 22 November 1964. A whale had been sighted earlier in the 4-km stretch of open water between the ice shelf and the loose pack-ice further out, but it was too far away for identification. A light northerly wind eventually closed this open water and drove the pack-ice against the ice shelf. Large chunks of ice were forced on edge, and the loose ice was pushed together against the shelf, forming a solid cover as far as the eye could see.

We had been listening underwater for ice sounds as the pack came in and had forgotten about the whale sighting, when we were startled by the characteristic sound of a whale blow in air. A minke whale had thrust its head out through a hole in the ice far enough to breathe (Fig. 1). In an 8-m whale, this means nearly 1.5 m. There were three holes nearby, apparently kept open by emperor penguins, *Aptenodytes forsteri* G. R. Gray 1844, in relatively thin ice that had formed behind a projecting tongue of the ice shelf. We were using the nearest for our hydrophone, and the whales appeared in one about 5 m further away.

The whale sounds had been noted, but not identified, in the underwater ambient before the whales' appearance. There were two minke whales, though at first we saw only one at a time. Later both were visible at once as they blew in adjacent holes. The whales came from the direction of the ice pack and would return again in that direction after a series of blows. Five to ten minutes elapsed between series of four to seven blows.

Examination of the recordings reveals that initially there were two whales producing sounds, one relatively close by and a second at a distance. Sounds produced when the whale was close by often took us by surprise and massively overloaded the sound equipment. The loud sounds were heard when a whale was near the breathing holes, and therefore near the hydrophone, either just before or just after a series of blows. The blows were barely audible underwater.

The background ambient on the day of these recordings was filled with a wide variety and range of sounds. Though most of these remain unidentified, occasionally some could be matched to ice movement and also to a single visit from a leopard seal, *Hydrurga leptonyx* (Blainville 1820). Others were recognized as sounds from Weddell seals, *Leptonychotes weddelli* (Lesson 1826). We had been working for some weeks in McMurdo Sound in an acoustically pure culture of *Leptonychotes* and we were confident that we could recognize most of their vocalizations. Throughout this entire day's listening, these seals were heard quite often as they moved from crack to crack under the more solid ice cover. They were audible except during the period of the approach of the minke whales. During this time, a period of about 30 minutes, the Weddell seals were silent.

EQUIPMENT AND METHODS

The sounds were recorded with an LC-34 (Atlantic Research) hydrophone and a WHOI-built amplifier and spring-driven recorder (Watkins, 1963). Analysis playback was on Crown (800 series) recorders. The combined frequency response was flat within ½ dB from 30 to 30,000 Hz. Spectograms were made on a Kay Electric 7029A Sound Spectograph.

The hydrophone was thrown from the ice shelf across thin ice through holes used by emperor penguins, *Aptenodytes forsteri*. The hydrophone was suspended 3 meters or more in the water from the ice edge, but since the cable was operating at low impedance, no noise was generated by motion of the cable against the ice.

CHARACTERISTICS OF THE WHALE SOUNDS

The minke whale sounds were intense. The loudest of these in undistorted recording are 60 to 65 dB above the local relatively high background ambient, which averaged about 0 dB re 1 dyne cm^2. Of course, we do not know how near the whales were, but we assume they were quite near, since the loudest sounds occurred either a few seconds before or after a whale was seen in a breathing hole. Thus, 65 dB re 1 dyne/cm^2 may be nearly the maximum (1 m) signal strength of these whale sounds.

The sounds were composed of a single downward sweep in frequency, starting at 130 to 115 Hz and sweeping to about 60 Hz (see Fig. 2). Since the frequency sweep continued throughout the sound, the rate of drop in frequency varied with both the span of frequencies and the duration of the call. The sweep rate was fairly regular throughout each sound.

Sounds that were recorded at a low enough level to be free from distortion had no harmonic structure; they appear to have been composed of nearly sinusoidal waves. The second and third traces visible with each sound in Figure 2 are from reflections off ice walls or the bottom.

The minke whale sounds began with gradually increasing intensity for the first few cycles and ended with a gradual reduction in intensity for the last few cycles. Thus the sounds appeared to rise out of background and disappear back into it. The endings of the sounds also were further obscured by reflections and reverberations. Measurement of the duration of a sound depended on its relative intensity over ambient. Individual minke whale sounds lasted from 0.2 to 0.3 seconds.

No repetitive pattern was evident in sequential sounds either from one individual or from both. Of nine sounds presumed to be from one whale and recorded on one continuous tape, the intervals between sounds (in seconds) were approximately 19, 8, 13, 97, 35, 10, 89, and 12.

The sounds were not all identical, but had a basic similarity in duration, frequency sweep, and intensity. Differences could not be attributed easily to characteristics of individual whales, though certainly that possibility exists.

DISCUSSION

Intense low-frequency sounds have been recorded in the presence of other species of *Balaenoptera*. Schevill and Watkins (1962) reported a 75- to 40-Hz sound from *B. physalus* (Linnaeus 1758), and Schevill, Watkins, and Backus (1964) identified a 20-Hz (23–18 Hz) sound also with *B. physalus*. More recently, other low-frequency sounds have been reported from *B. physalus*, 20 Hz to 100 Hz, and *B. edeni* Anderson 1879, with average frequency of 124 Hz, by Thompson and Cummings (1969), and from *B. musculus* (Linnaeus 1758), with most energy below 50 Hz, by Cummings and Thompson (1971). The intensity of most of these low frequency whale sounds has been estimated to be 60 dB or more re 1 dyne/cm^2 at 1 m.

Other sorts of sounds also have been reported from *Balaenoptera*. These include pulses at about 25 kHz from *B. musculus* by Beamish and Mitchell (1971), and chirps and whistles at 1500 to 2000 Hz from *B. physalus* by Perkins (1966). Our gear is capable of receiving such sounds, and with it we have listened to a few hundred *Balaenoptera* over many years, and yet we have recorded only lower-frequency sounds from them.

The minke whale sound is similar in most respects to both the 75- to 40-Hz and the 23- to 18-Hz sounds in our recordings of the larger fin whale, *B. physalus*. The one from *B. acutorostrata* and these two from *B. physalus* (1) are relatively intense, (2) are composed of low frequencies, (3) have a downward sweep in frequency, (4) are nonharmonic, nearly sine-wave, (5) are made up of about the same number of cycles duration at the same relative intensity (about 20 cycles at 40 dB above background), and (6) begin with gradually increasing intensity and end with dropping intensity. The differences in these sounds are mainly those related to frequency. This would seem to indicate a common method of sound production and similar acoustic structures.

Neither the 75- to 40-Hz finback whale sound nor the 120- to 60-Hz sound of the minke whale has shown the regular, repeated patterns often found in the 23- to 18-Hz finback sounds. (These latter are often called simply 20-Hz pulses because they usually have been examined through band-pass filters centered at 20 Hz.)

The conspicuous silence of *Leptonychotes* while the minke whales were about is puzzling. Did they confuse them with killer whales? One might expect the seals to be good enough cetologists to differentiate between killers and minkes. Killer whales, *Orcinus orca* (Linnaeus 1758), are frequent visitors to the ice edge, and the seals, one would suppose, might have developed some respect for them. There was no obvious panic, however, in the demeanor of a band of emperor penguins congregated near the holes. Nevertheless, they stayed away from the water during the whales' visit.

We presume that the minke whales sought out the holes in the thin ice because the shift in the heavy pack had closed other breathing spaces in the vicinity. Our failure to hear the whale sounds again after the minkes' disappearance suggests a swim under the pack to some other distant open water.

ACKNOWLEDGEMENTS

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Figure 1. A minke whale pushes its head through broken ice for a breath of air. The hole was about one-half this size before the whale began using it. Initially, they had to push their heads nearly vertically through the ice hole, but as more and more ice was broken by their efforts, the hole became large enough for nearly normal (horizontal) attitudes during breathing. Ross Island in background. Watkins phot.

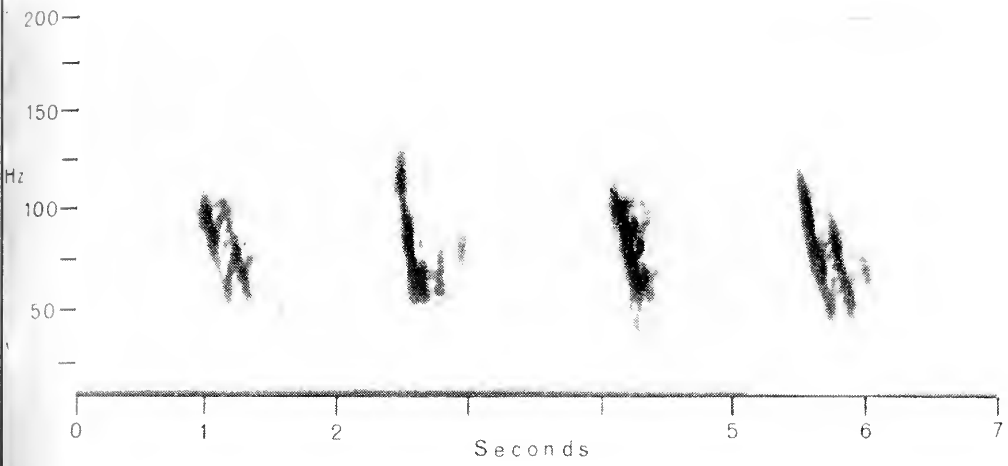

Figure 2. Four minke whale sounds are analyzed without intervening intervals—up to two minutes elapsed between sounds. The high level of the sounds relative to background permits analysis without obvious interference from ambient sound. The second and third traces accompanying the minke whale sounds are from reflections off the bottom or off ice walls. The slightly beaded appearance of the sound traces probably is a result of multiple-path sound transmission with constructive and destructive reinforcement of the sound as the wave length (from about 11.5 to 25 m) varies with the sweep in frequency. The effective analyzing filter bandwidth was 11 Hz.

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BREVIORA

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THE CHAÑARES (ARGENTINA) TRIASSIC REPTILE FAUNA. XIII.
AN EARLY ORNITHOSUCHID PSEUDOSUCHIAN, *GRACILISUCHUS STIPANICICORUM*, GEN. ET SP. NOV.

Alfred Sherwood Romer

Abstract. A description is given of the skull and skeleton of a small ornithosuchid thecodont, *Gracilisuchus stipanicicorum* gen. et sp. nov., from the Triassic (? Anisian) Chañares Formation of Argentina. The skull is of an advanced pseudosuchian character, with a large antorbital opening, a very large orbit and a lateral temporal opening of an advanced type. The front limbs are short, being about 3/5ths the length of the hind; the tibia is nearly as long as the femur. Armor consisted of a double row of dorsal scutes.

INTRODUCTION

Work in the Triassic of Argentina and southern Brazil in recent decades has resulted in the discovery of a considerable number of new thecodonts; some 21 genera have now been described from the Triassic of this area. Most are known from incomplete remains; however, in the last paper in this series (Romer, 1972), I have been able to give a fairly complete skeletal restoration of the long-snouted *Chanaresuchus*, and below I give a description of the nearly complete skull and skeleton of a small ornithosuchid.

Gracilisuchus stipanicicorum, gen. et sp. nov.

Combined generic and specific description. A small ornithosuchid, with a skull length on the order of 95 mm and a presacral column of 23 segments, with a length of about 21 cm. Skull of advanced pseudosuchian type. Premaxillae extending upward back of nares, excluding the maxillae from that opening. Antorbital fenestra large, included in a recessed area of maxilla and lacrimal; antorbital bar moderately narrow. No pineal opening; a tiny postparietal bone present. V-shape of lateral temporal opening so pronounced that the upper part of the opening is closed by apposition of squamosal to postorbital and jugal. Basicranial kineticism lost; the pterygoids meet medially beneath the basisphenoid region. Lateral flanges of pterygoids highly developed, extending directly outward the entire width between lower jaws. Normal stance possibly bipedal; femur and tibia combined about 1 1/2 times skull length and about 1 2/3 the length of humerus plus radius; tibia and fibula somewhat shorter than femur. Dorsal scutes are about 1/2 vertebral length and paired, each element having a vertical lateral portion and a horizontal median flange that overlaps its mate.

The generic name refers to the obviously graceful build of the little reptile. The specific name is in honor of Drs. Pedro and Maria Stipanicic, able students of Triassic stratigraphy and palaeobotany.

I am indebted to National Science Foundation grant GB-2454 for aid in the collecting of the specimen and grant GB-22658 for preparation and publication.

Holotype. La Plata Museum No. 64-XI-14-11 (Field no. 146). A slab (Fig. 1) exhibiting a skull in dorsal view, much of the presacral column and scattered limb and girdle material. Also present on the slab is the type material of *Lagosuchus talampayensis* (Romer, 1971), and originally a gomphodont skull was likewise present. Collected from the Chañares Formation in La Rioja Province, Argentina, about 2 km north of the Rio Chañares.

Other material. A number of further Chañares specimens include remains of the present animal. These are:

MCZ[1] 4117 (Field no. 153, *partim*). A nearly complete skull and jaws from the same locality as the holotype.

MCZ 4118 (Field no. 153, *partim*). In the same nodule as the last, but separated from it by a short distance, was a specimen including ventral elements of the skull, the jaws and a partial postcranial skeleton, including a well-preserved cervical region.

MCZ 4116 (Field no. 174). A slab including a crushed skull and jaws and considerable postcranial material, part of it pertaining to a smaller reptile. From the holotype locality.

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[1] Museum of Comparative Zoology.

Further *Gracilisuchus* material, collected by Sr. José Bonaparte, is in the Instituto Lillo, Tucumán. Notable is a specimen with an incomplete skull and the greater part of a skeleton that agrees with *Gracilisuchus* in all identifiable features; the individual is about 20 percent larger than the holotype.

CRANIUM

(Figures 1-4)

Cranial materials are present in all four specimens listed above. The skull in MCZ 4117 is nearly completely preserved, except for the palate, and is uncrushed. In the holotype the skull roof and right side of the face are seen on the upper side of the slab; ventrally there is present part of the palate and the disarticulated left maxilla and jugal. In MCZ 4118 the ventral margins of the skull and complete lower jaws are preserved. In MCZ 4116 the right aspect of the skull, crushed and elements disarticulated, is seen on one surface; on the opposite surface are disarticulated elements of the left side.

Skull length to the posterior end of the table is 85 mm in MCZ 4117, and appears to have been similar in the holotype and in 4116 and 4118. The general proportions are those to be expected in a moderately advanced pseudosuchian. As viewed dorsally, the shape is essentially triangular, expanding gradually from a slender snout to a greatest width across the temporal region. Anteriorly the skull outline curves up sharply above the external nares, but from this point backward there is little further increase in height, the roof being essentially flat and the height nowhere great. The external nares are moderately large. The facial length is not excessive, the distance from snout to orbital margin being somewhat less than half the total skull length. The antorbital vacuities are large, and set in an oval recess, which is bounded anteriorly by a pronounced curved line running upward along the maxilla; it is deeply overhung dorsally by the prominent lateral edge of the skull roof. The orbit is very large, its diameter being about 1/3 the skull length. It not only occupies nearly the entire height of the face, but also extends medially across much of the dorsal surface of the skull. The temporal region, in contrast, is short. The superior temporal fenestra is triangular in shape, narrow anteroposteriorly but extending broadly outward behind the postorbital bar. The lateral temporal opening is of unusual structure. As in advanced thecodonts generally, the posterior border is V-shaped, the apex of

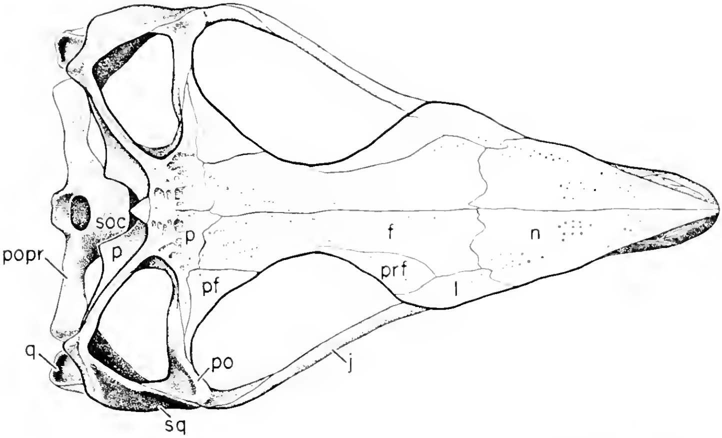

Figure 1. The skull in dorsal view. This and the following skull figures are based mainly on MCZ 4117 × 1. Abbreviations for Figs. 1 to 5: *a*, articular; *an*, angular; *c*, coronoid; *d*, dentary; *ec*, ectopterygoid; *f*, frontal; *j*, jugal; *l*, lacrimal; *m*, maxilla; *n*, nasal; *p*, parietal; *part*, prearticular; *pf*, postfrontal; *pm*, premaxilla; *po*, postorbital; *popr*, paroccipital process; *pp*, postparietal; *prf*, prefrontal; *pt*, pterygoid; *q*, quadrate; *qj*, quadratojugal; *san*, surangular; *soc*, supraoccipital; *sp*, splenial; *sq*, squamosal.

the V pointing anteriorly. Here, however, in contrast to normal advanced forms, the forward push of the V is so pronounced that the upper limb of the V is in contact with the postorbital and jugal; as a consequence the upper half of the fenestra is completely closed, the opening remaining being a ventral triangular area. A similar situation is present in the aetosaurs.

The premaxillae are thickened ventrally, with accommodation for tooth roots. Anteriorly each element sends a slender process upward to meet the nasal medial to the narial openings. Posteriorly the premaxilla sends a stout process upward to form part of the posterior border of the naris.

A pronounced ridge extends backward on either side of the skull roof along the upper margin of the antorbital region toward the upper anterodorsal margin of the orbit; this pair of ridges, formed anteriorly by the nasals, sharply separates the flattened dorsal surface of the skull from the essentially vertical lateral surfaces. Below this ridge the nasal extends downward to form the upper boundary of the naris. This flange is in contact with the premaxilla ventrally, both in front of and behind the naris. On the dorsal surface the nasals extend well backward, broad-

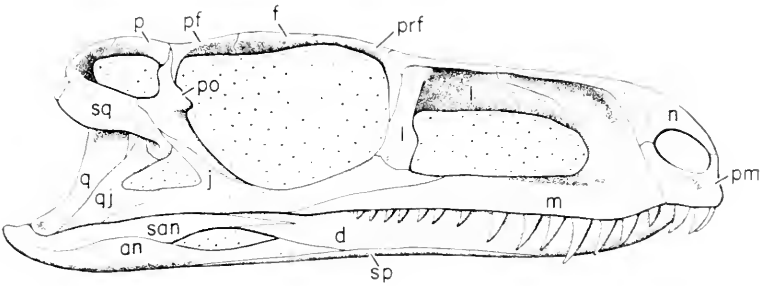

Figure 2. The skull in lateral view. × 1.

ening posteriorly. The lateral ridges form their lateral boundaries for most of this distance; part way along the upper margin of the facial region, however, the width of the nasals is somewhat constricted by the presence of the lacrimals. Nasals and frontals meet in a broad transverse suture, not readily discernible, a short distance anterior to the anterior margin of the orbits.

The frontals are elongate, their length being roughly that of the large orbits. Broad anteriorly, they are constricted in width by the strong medial curvature of the dorsal orbital margins, the prefrontals being interposed for some distance between them and the frontals. Posteriorly the frontals are bounded laterally by the postfrontals, and terminate at an irregular transverse suture with the parietals.

The last elements are short in longitudinal extent, occupying, roughly, only the length of skull roof opposite the short temporal region. There is no pineal opening; posteriorly the median suture is absent. Laterally the parietals send out a flange on either side, anterior to the superior temporal fenestra and behind the postfrontal, to gain a postorbital contact. Posterior to the upper fenestra the parietals send out on either side strong flanges that form the upper margins of the occipital surface and, along the posterior margins of the fenestrae, overlap posteriorly ascending flanges of the squamosals.

The postparietal, seen on MCZ 4117, persists as a small triangular wedge of bone that projects strongly backward from the middle point of the dorsal occipital surface; it is essentially the most anterior portion of the dorsal armor that continues down the back.

The maxilla is prominently developed. Its major ramus is a long strip of bone that carries the tooth bases and extends backward from a premaxillary contact to a point not far forward of the posterior border of the orbit. Anteriorly it forms the lower margin of the antorbital fenestra. Near the posterior limit of the fenestra the anterior end of the jugal is found above the maxilla, and from this point back the maxilla is reduced, to become a slender splint. Anteriorly the maxilla fails to reach the external naris. It sends upward a broad process, bounded posteriorly by the antorbital vacuity and anteriorly by the premaxilla, from which it is separated by a very prominent incised suture. Curving upward along the surface of this process is a well-marked ridge separating the proper outer surface from the depressed area in which the antorbital vacuity develops. Dorsally this maxillary process extends backward below the lateral skull ridge to form part of the upper margin of the antorbital vacuity.

The lacrimal forms most of the vertical bar of bone between orbit and antorbital vacuity. This bar is of limited width; it has a conspicuous ridge along its anterior border, and a less developed ridge posteriorly. Below, the lacrimal meets the jugal. Above, the lacrimal forms the projecting process between the orbital rim and the lateral ridge above the facial region, and extends forward above the antorbital opening. It has (unusually) a modest exposure on the dorsal surface, lateral to frontal and nasal. The prefrontal is a small wedge-shaped element, lateral to the frontal and posterior to the dorsal exposure of the lacrimal; it forms the anterior half of the curved dorsal margin of the orbit.

The postfrontal is a triangular element of modest size, lying above the posterodorsal margin of the orbit. Medially it is in contact with the frontal, posteriorly with a lateral flange of the parietal; laterally it is barely in contact with the postorbital.

The postorbital is centered at the point of meeting of the postorbital bar with the bar of bone separating upper and lower temporal openings. The bone is here thickened, with a prominent external knob, posterior and dorsal to which it is gently concave externally. A ventral flange forms much of the posterior margin of the orbit, overlapping the jugal anteriorly. Above, the bone is in contact with postfrontal and parietal along the upper part of the postorbital bar. A posterior flange joins with the squamosal in the formation of the bar separating the temporal openings.

The jugal is of typical construction, its main ramus lying below the orbit and extending from a point anterior to the orbit backward to a contact with the quadratojugal below the lateral temporal fenestra. Behind the orbit a ramus ascends, slimming as it goes, behind the lower branch of the postorbital.

The squamosal is a complex element. Its structural center lies at the posterior end of the bar separating the two temporal fenestrae. Anterodorsally a thin but deep flange extends forward to overlap laterally the posterolateral extension of the parietal. Anterolaterally a ramus extends forward to form, with the postorbital, the bar between the temporal openings. A backward extension of the bone from its center affords a broad area of articulation for the paroccipital process. Beneath this region the concave ventral surface of the bone supports the head of the quadrate. Forward and somewhat ventrally from this region a broad flange of bone forms a firm union with the dorsal end of the quadratojugal. In many pseudosuchians this flange forms the upper half of a V-shaped posterior border of the lateral temporal fenestra. Here, however, (as previously noted) an unusual condition exists. This flange turns so sharply forward that the upper half of the "normal" lateral opening is obliterated, and the flange is apposed to the postorbital, which forms the anterior margin of the upper part of the lateral opening under "normal" conditions.

The quadratojugal is a well-developed element. It forms the posterior part of the skull rim below the lateral temporal fenestra, between jugal and quadrate. A broad ramus extends upward and forward posterior to the lateral fenestra to terminate beneath the anteroventral ramus of the squamosal. The quadrate is highly developed. It presents a convex, transversely broadened, articular surface for the lower jaw on the under side of its posterior termination. From the medial edge of the articular area a sharply defined ridge runs upward and somewhat forward to terminate beneath the squamosal. The quadrate is broadly developed lateral to this ridge for nearly the entire height of the bone; this area is somewhat concave in transverse section. The lateral margin of the quadrate is in contact with the quadratojugal for most of the extent of the two bones. Not far above their ventral margins, however, there appears to be a small foramen, as in many early tetrapods, between the two bones, and quadrate and quadratojugal separate dorsally to reach their differing termini. Medial to the major vertical ridge on the quadrate there is seen a thin sheet of bone running medially for some distance in the position appropriate for the quadrate ramus of the pterygoid; at the bottom of this sheet is a curved ridge, running upward and anteromedially from the articular region of the

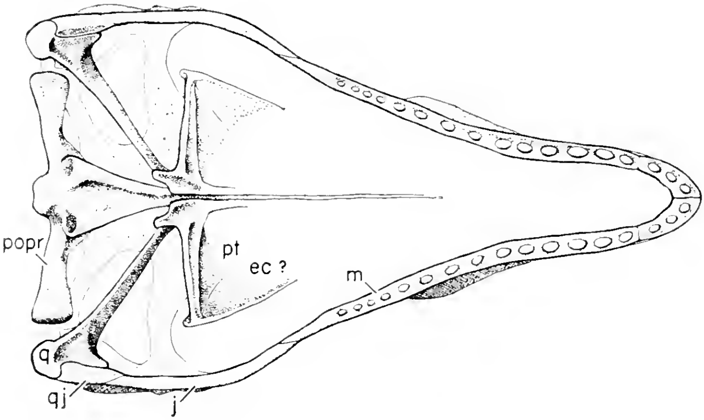

Figure 3. Palatal surface of the skull; the anterior portion of the palate is not preserved in available material. × 1.

quadrate. I am unable to determine how much of this bone pertains to the quadrate and how much to the pterygoid.

The upper rim of the occipital surface is formed by the two posterior flanges of the parietals, which curve backward, outward and somewhat downward to their lateral points of termination near the posterior angles of the squamosals. Between the two flanges, as noted earlier, is the small projecting postparietal; beneath, on either side, are the posttemporal fenestrae. Below and beneath the central part of these flanges is a broad plate of bone, the supraoccipital. It is essentially flat, but with a slight dorsoventral swelling in the mid-line. Fused with the supraoccipital on either side are the paroccipital processes, which extend outward to form a broad (but not tightly sutured) union with the squamosals. The paroccipital processes are relatively narrow proximally, expanding somewhat in vertical breadth distally and, except at their bases, thin anteroposteriorly; they are roughly oar-shaped. Exoccipitals and basioccipitals have been lost on MCZ 4118. They appear to be present in the crushed remains of the occiput in the holotype, but little detail can be made out.

The palatal surface is poorly preserved in available specimens. Posteriorly is a pair of well-developed basisphenoidal tubera. I have obtained no data regarding the lateral walls of the braincase in the otic region. No stapes has been discovered. The two quadrate rami of the conjoined quadrates and pterygoids slant strongly inward anteriorly, so that the two pterygoids are

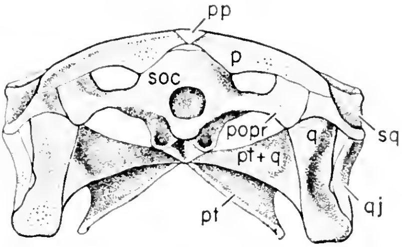

Figure 4. Occipital view of the skull. × 1.

apposed in the midline below the basisphenoid; it seems reasonably certain that movement of pterygoids on the braincase had been lost. A short backward median projection is present on each pterygoid at its point of apposition. Transverse pterygoid flanges are highly developed, extending straight out laterally and somewhat ventrally to occupy the total space available between the lower jaws when in occlusion. A pair of ridges extends outward along the under surface of each flange. Anterior to the flange, a curved sheet of bone, on which there appears to be a suture between pterygoid and ectopterygoid, slants upward anteriorly for a short distance. No data are available regarding the anterior portion of the palate.

The jaws (Figs. 2, 5) are slender. The symphysis is moderately elongate but shallow and is formed entirely by the dentaries. The dentary occupies practically the entire outer surface of the jaw for more than half its length. Posteriorly the dentary has a V-shaped suture with the surangular dorsally and a diagonal suture with the angular ventrally. Between dentary and surangular above and angular below is a typical archosaur lateral mandibular fenestra. There is a well-developed retroarticular process behind the broadly concave articular cavity. A splenial is well developed, occupying a considerable area on the inner surface of the jaw, but is barely visible externally. The prearticular forms a buttress at the anterior margin of the articular surface and thence extends forward and downward below the adductor fossa. The jaw is strongly compressed mediolaterally, and hence the large fossa looks medially rather than dorsally. The dorsal rim of the fossa is marked by a well-developed longitudinal ridge along the upper margin of the surangular. I am not sure whether or not a coronoid was present at the anterior margin of the fossa; the material is imperfect but suggests that a thin sheet of coronoid may have been present anterior to the adductor fossa.

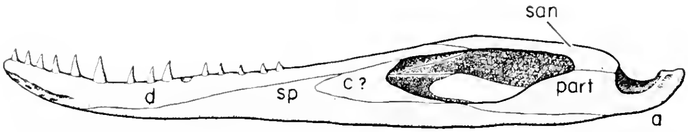

Figure 5. Internal surface of the lower jaw. Sutures in the presumed coronoid region are uncertain. × 1.

The teeth of *Gracilisuchus* are of the typical thecodont type common among carnivorous archosaurs — somewhat flattened mediolaterally, sharp-pointed and curved somewhat posteriorly toward their tips. Only two small teeth are definitely preserved in the only specimen in which the premaxillae are present, but the space available suggests the presence of a third. A disarticulated maxilla of the type skull has fortunately preserved a nearly complete series of maxillary teeth, not fully thecodont. About 14 appear to have been present. From a small first tooth, there is a steady increase in size to the fourth, following which there is a steady reduction to small elements for the last half dozen of the series. The lower teeth are not fully preserved, but the evidence suggests that none were of large size, and that there was a rather even row of small teeth, spaced about 2.5 mm apart, to a total of 16 or so.

AXIAL SKELETON

A considerable amount of vertebral material of *Gracilisuchus* is present in the collection. The holotype when entombed possessed a complete articulated presacral series (Fig. 6). However, the nodule in which the specimen was preserved had undergone considerable damage before collection. A split had occurred in the nodule that slanted back down most of the length of the series of dorsal vertebrae and, with the loss of a large chip adjacent to it, caused the complete loss of the posterior cervical and anterior dorsal vertebrae and damage to the remainder of the dorsals. The second and third vertebrae from the end of the series are obviously sacrals. Most of the ribs of the right side are preserved in their original position. This aids greatly in determining the spacing of the missing vertebrae, as does, further, a calculation, from known lengths of cervical and posterior dorsals, of the number of vertebrae contained in the missing segment of the column. As a result, it seems rather certain that 23 presacrals were present in life — a reasonable thecodont count.

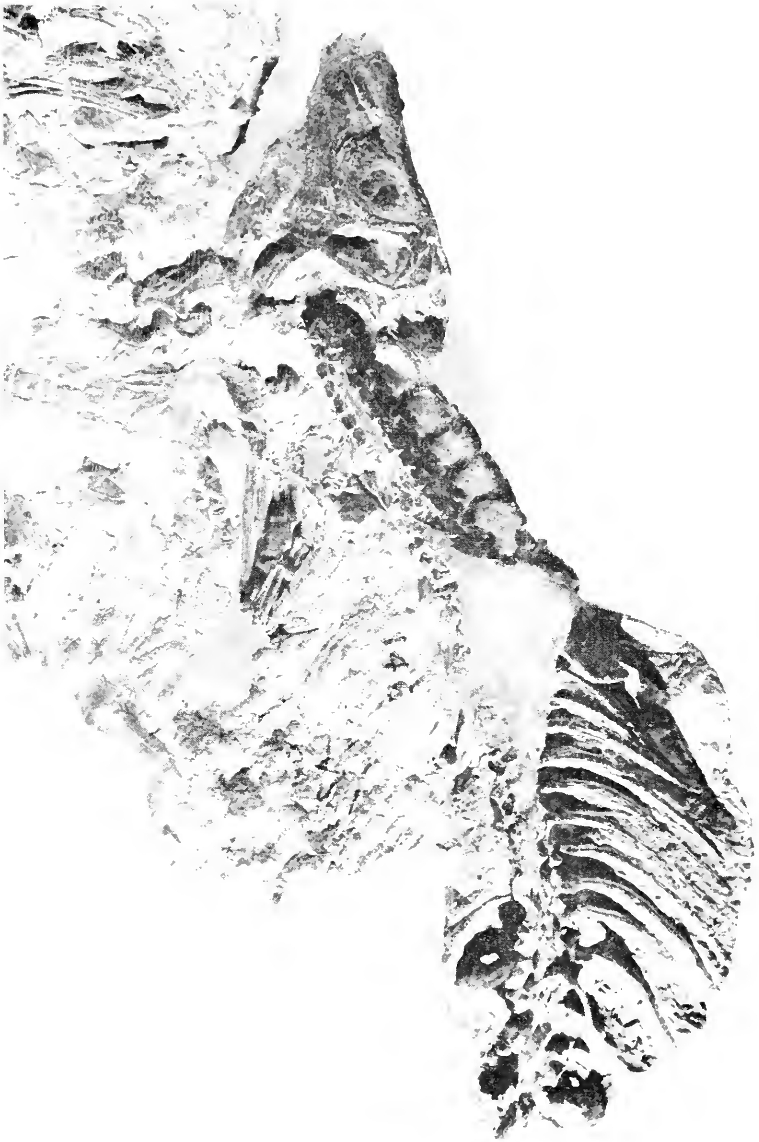

Figure 6. The holotype skeleton, in dorsal view. × 1/2.

In MCZ 4118 a number of short sequences of articulated vertebrae are present:

(1) A series of cervicals articulated with the fragmentary skull.

(2) Six articulated centra that appear to lie in the cervical-dorsal transition.

(3) Six vertebrae, three well preserved, lying close to the skull-cervical series; they are probably anterior dorsals.

(4) Five poorly preserved vertebrae, presumably dorsals.

(5) Nine vertebrae, probably posterior dorsals, sacrals and proximal caudals.

(6) Two poorly preserved dorsals, with ribs.

(7) Ten caudals, probably from the middle of the tail.

These series will be referred to below by number. Excluding no. 6, 35 vertebrae are present, most of which are surely presacrals. It is obvious that not all belong to one individual; some, apart from nos. 1 and 3, may have been associated with MCZ 4117, a skull found in the same nodule.

The Tucumán specimen mentioned above has present much of the column; in all observed respects it agrees well with the material from the holotype and no. 4118. MCZ 4116 contains a mélange of vertebral material, some of which appears to belong to *Gracilisuchus* (as does the skull included in this slab).

The cervicals are best seen in the series (no. 1) connected with the skull remains in 4118 (Fig. 7); a similar but less well-preserved series is present in the holotype. The atlas is partially concealed by other materials, but as far as can be seen, has a typical archosaur structure — a well-developed intercentrum, above which are paired neural arches, and back of this articular ring a small atlas centrum and a small axis intercentrum. The axis has a well-developed centrum and a neural arch and spine of stout construction. The vertebrae in the cervical region posterior to the axis are similar in pattern, but with a less expanded neural spine. In these vertebrae the spines slant forward dorsally; in typical members of this series they are, as preserved, covered by dermal armor at their tips; isolated posterior cervicals and anterior dorsals show that their tips were flattened, obviously for close apposition of armor scutes. Two well-developed apophyses for rib articulation are seen on each centrum from the axis backward. The capitular articulation is a short parapophysis developed low down anteriorly on the centrum and terminating in a round articular area. The area for tubercular attachment is a short transverse process slanting sharply down-

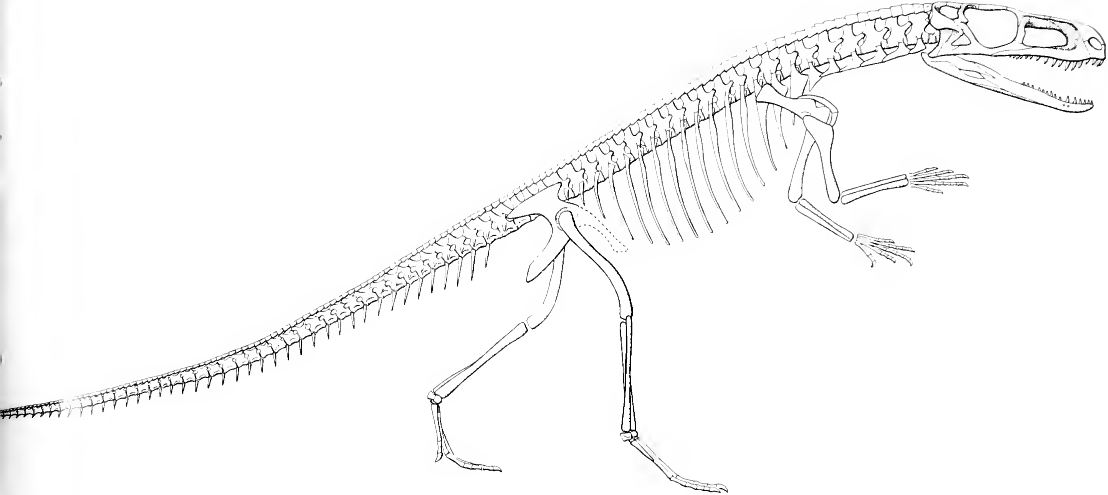

Plate 1. Skeleton of *Gracilisuchus stipanicicorum*, restored. Dermal shoulder elements, manus, pubis, and distal part of tail unknown. × 1/2.

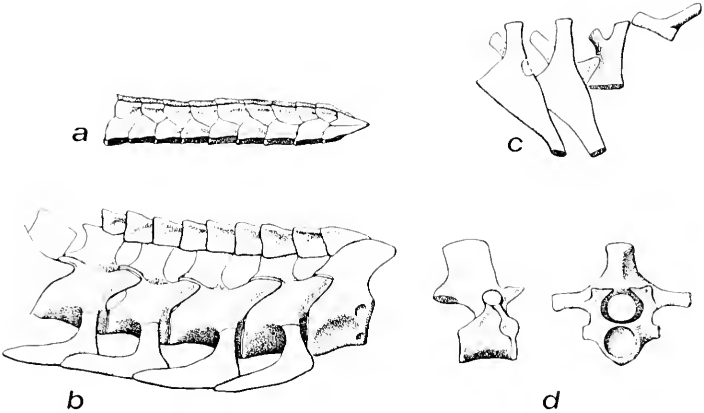

Figure 7. *a*, Dorsal scutes of the cervical region, seen from above. *b*, The cervical region in side view (the atlas is not included). *c*, Incomplete ribs of the right side, transitional between cervical and dorsal series. *d*, A dorsal vertebra in lateral and anterior views. All from MCZ 4118. × 1.

ward from a point near the anterior edge of the neural arch. By the time the seventh vertebra is reached, the diapophysis has moved to a point somewhat higher on the arch and is directed more laterally. The parapophysis, however, appears to have been persistently ventral in position in the cervical region. No intercentra are preserved back of the atlas. In MCZ 4118 cervicals two to six are completely preserved, the seventh is incomplete; in the holotype six vertebrae are similarly preserved. In MCZ 4118 the typical cervicals average 10.5 mm in length and in the holotype the length is approximately the same. From the axis back all centra are keeled ventrally.

Of the posterior cervicals and anterior dorsals, nothing can be made out on the holotype. Associated, however, with 4118 are two series of vertebrae that appear to represent this area. One such series (no. 2) includes six articulated centra and a fraction of the next posterior centrum; central lengths here average 8.5 mm. Neural arches and spines are not preserved, but ribs are present on four, the first two well preserved. Since the first rib of the series resembles that which (as noted later) appears to be associated with vertebra 7 in the holotype, it is reasonable to assume that this series includes vertebrae 7–12 as well as part of centrum 13. In presumed vertebrae 7–9 the capitulum still articulates well down the side of the centrum, and the build of tubercular process indicates that in these segments the transverse process still slanted strongly downward.

Further vertebrae from the anterior part of the column are present in series no. 3, three in articulation and well preserved. We are dealing here with typical dorsals (Fig. 7). Vertebral lengths average close to 8 mm. Rib attachments are markedly different from those of the series described above. The diapophyses now extend directly out from the arches. In the first of the three complete vertebrae the parapophysis lies about at the boundary between centrum and arch at the anterior edge of the vertebra; in the third member of the series, the parapophysis is well up on the side of the arch, not far below and anterior to the base of the diapophysis. The neural spines are broad anteroposteriorly, but low, with a height of but 7 mm above the zygapophysis. Their upper ends are broadly oval, for apposition to the dorsal armor. In the arch region the surface is poorly preserved, so that little can be seen regarding rib articulations.

Series 4, 5 and 6 are poorly preserved and crushed, so that it is difficult to determine the nature of the apophyses, and no ribs are attached, except in no. 6 (where the vertebrae show little). An ilium lies close to the posterior end of series 5, suggesting that this sequence may include proximal caudals and sacrals as well as posterior dorsals. No chevrons are present, and the condition of preservation of the lateral surfaces of the vertebrae is such that it is impossible to determine whether sacrals are included. It seems clear that, as in archosaurs generally, the capitular articulation has joined the tubercular one in originating from the transverse process; details, however, are not clear. In no. 5 central lengths are about 8 mm. In series 6 the mean central length is a little over 7 mm; the neural spines are broad anteroposteriorly but low, rising only about 5 mm above the zygapophyses, and the total height of a vertebra is about 13 mm. As preserved, the centra in series 5 and 6 are prominently keeled ventrally and thin from side to side, but this may be due to post-mortem compression.

One further series of vertebrae on the 4118 slab, no. 7, includes 10 articulated caudal vertebrae, evidently from the midportion of the tail. Central length of an anterior member of this series is 6 mm, that of posterior members 5.5 mm. Chevrons are present, the most anterior one being 10.5 mm in length; in contrast, that between the sixth and seventh of the series is but 7 mm long. The vertebrae are still fairly tall, an anterior member measuring 8 mm from bottom of centrum to zygapophysis, while at the posterior end of the series this height is somewhat reduced. The first two members of the series have well-developed spines, slanting backward and rising to a vertical height above the zygapophyses of 6 mm. Posteriorly the spines are reduced, and at the end of the series are merely low triangles above the zygapophyses.

As noted earlier, sacral vertebrae are present, although poorly preserved, in the type. The Tucumán specimen (Fig. 8) includes well-preserved sacrals in articulation with ilia. Beyond them are 16 articulated caudal vertebrae. Anterior members of this series have a central length of about 9 mm, posterior segments about 7.5 mm. In the anterior members of the series the neural spines are narrow anteroposteriorly, but moderately high, with heights of 10 mm or so above the zygapophyses; they are tilted posteriorly. In the posterior members of this series the spines are much reduced in height. The first chevron is present between vertebrae 3 and 4. Most chevrons are imperfect distally, but that between vertebrae 8 and 9 is 17 mm long. If we compare this series with that of no. 7 in MCZ 4118 — and take into account the larger size of the Tucumán specimen — it would seem that the 4118 series includes segments comparable to the posterior part of the Tucumán series.

Vertebrae present on the holotype slab, although disconnected from the main specimen, appear to represent much of the length of the tail. One series of seven vertebrae, and part of an eighth, is articulated and for the most part well preserved. Each measures 8 mm in length. The neural spines are low, and capped by dermal plates to give a total height of about 8 mm above the level of the zygapophyses. The transverse processes are incompletely preserved. There then follows a series of about 14 partially disarticulated and poorly preserved vertebrae which, as indicated by long transverse processes, are definitely caudals. Of several that are moderately well preserved, the length of the centrum is, again, about 8 mm; the width over the transverse processes is 15 mm. Beginning near the end of this series is a further series of about 15 poorly preserved caudals of smaller size, with lengths of 5.5 to 6 mm in the distal members. There is thus definite evidence of 39 caudals making up a considerable part of the presumed length of the tail.

Cervical ribs (Fig. 7) are well seen in both 4118 and the holotype. There is no evidence as to the presence or absence of an atlantal rib. Typical members have the highly specialized pattern developed among certain early archosaurs and retained today in crocodilians. Each rib is essentially plow-shaped, the two "handles" represented by converging rami running outward from parapophysis and diapophysis. The "blade" of the plow, formed distally by the union of the two "handles," includes a short point anteriorly and a long posterior extension. In typical cervicals each "blade" overlaps its more posterior neighbor to make a continuous rib series from the axis as far back, at least, as vertebra 7. As in the case of the vertebrae, the rib transition to the dorsal series is somewhat uncertain. In series 2 of no. 4118 (Fig. 7), four incomplete ribs are present on the left, and one on the right. The first three ribs extend strongly forward from the point of union of capitulum and tuberculum to form a triangular sheet of bone, the front end of which underlies the next anterior rib. The main shaft of the rib extends outward and downward in line with the tuberculum, rather than turning backward as in typical cervicals; shaft lengths are uncertain. The width of the proximal rib expansion (presumably associated with serratus muscles) decreases from the first to the third of the series, and rib 4 appears to lack any expansion.

In the holotype most of the dorsal ribs are preserved. Mid-dorsals have average lengths of 62 mm. There is, as expected, a diminution in length toward the sacrum. The fourth presacral rib measures but about 46 mm, the three following, as preserved, 39, 18 and 10 mm. The main shaft of typical dorsal ribs averages but about 1 mm in diameter for most of their length; they thicken somewhat toward their heads. The direct proximal course of each rib is toward the tubercular attachment; the capitular head slants downward medially from the course of the shaft to extend several millimeters further than the tuberculum. The ribs show considerable curvature proximally, little distally, thus suggesting (reasonably) that the trunk was relatively high and narrow in its proportions.

DERMAL ARMOR

As in many other pseudosuchians, *Gracilisuchus* was armored dorsally. Best preserved is the armor of the cervical region (Fig. 7). The plates, thin but highly sculptured, are paired, and approximately two pairs are present for each vertebral segment. When articulated, the series of plates form a dorsal shield with a flat area, about 5 mm wide, running longitudinally down the column over the neural spines and with, on either side, a vertical sheathing about 5 mm in height. A sharp ridge separates dorsal and lateral portions of each plate laterally; each plate overlaps its posterior neighbor. The plates of either side join to form the dorsal area, each member of a pair overlapping dorsally (as laterally) its posterior neighbor, and with members of each pair overlapping its partner; in 4118 the left plates overlap the right. Anteriorly, over the atlas region, the plates appear to narrow dorsally as a pointed terminus, but details are uncertain.

The plating of the dorsal region is imperfectly preserved in available material. Only small plate fragments are present in the isolated dorsal series found with 4118. In the badly preserved dorsal series of the holotype, a lateral plate covering is seen in the area of the third to fifth presacral neural spines, indicating that the type of plating seen in the cervical region was continued down the back. In the holotype the series of proximal caudals described definitely carry dorsal scutes, although details are somewhat obscure.

No articulated series of abdominal ribs is preserved, but in the holotype a scattered series of typical archosaur gastralia are present in the area near the shoulder girdle and front legs described above. Those gastralia that are completely preserved measure about 35 mm in length. They are essentially straight for most of their length, but gently curved toward their presumed medial ends.

APPENDICULAR SKELETON

Much of the girdles and appendages are preserved, although partially disarticulated, in the holotype; a number of elements are preserved in MCZ 4118; disarticulated elements are to be found on the MCZ 4116 slab.

In *Gracilisuchus* the front limbs are much shorter than the hind, and hence, as expected, the shoulder girdle is of small size. A right scapulocoracoid (Fig. 8) is present in the type (as well as an incomplete left scapula). The height of the scapula is 24 mm. The structure is typically thecodont; the scapular blade is slender, but ventrally the anteroposterior width increases to 11 mm before the anterior margin retreats to the clearly marked scapulocoracoid suture. The back margin ventrally is strongly bevelled off for a prominent area of articulation for the humerus, facing diagonally outward and backward. A somewhat less marked articular area is present below on the coracoid. This latter element, with rounded borders, is much broader anteroposteriorly than dorsoventrally, the measurements concerned

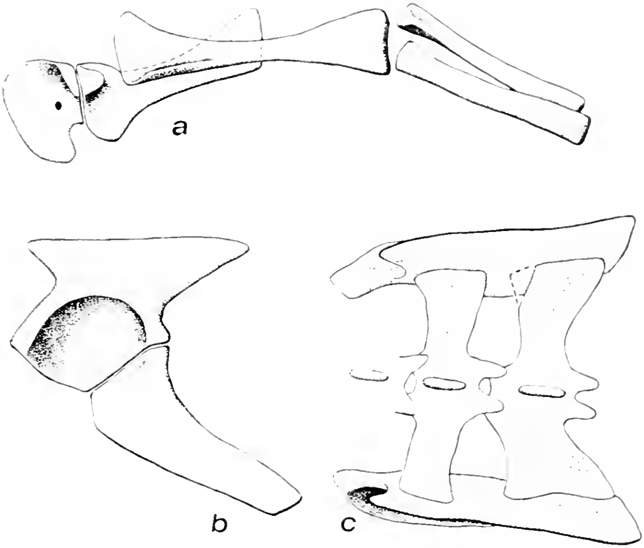

Figure 8. *a*, Right shoulder girdle, humerus, radius, and ulna. From the holotype. *b*, Left ilium and ischium. *c*, Sacral ribs and ilia, seen from above. From a specimen in the Instituto Lillo, Tucumán. All × 1.

being 17 mm and 11 mm; there is thus no suggestion of crocodiloid build. Just below the suture with the scapula the coracoid is slightly notched anteriorly; below this point the bone expands anteriorly to a considerable degree. A coracoid foramen is present anteroventral to the articular area. A similar scapulocoracoid is present on MCZ 4116. Of dermal girdle elements, none are identifiable with certainty in the material studied. Of pelvic girdle elements (Fig. 8), ilia are present in the holotype, in MCZ 4116, MCZ 4118, and in the Tucumán specimen mentioned. The element is of generalized thecodont proportions, with an iliac blade extending only a short distance anterior to the acetabulum, but much better developed posteriorly. The upper edge of the blade is thin; below, however, it swells convexly on the inner surface to allow for excavation of the acetabulum externally. The acetabular margin, semicircular in outline, is well defined; it is deeply incised into the bone, particularly anteriorly, where the margin develops as an overhanging shelf. The lower margin of the bone is convex in outline, with some differentiation of pubic and ischiadic contacts. It is obvious that the pelvis was imperforate.

Little evidence of the ventral elements of the girdle can be identified in the material. I have found nothing in the available specimens that I can identify with confidence as pertaining to the pubis. Imperfectly seen ischia are present in the Tucumán specimen and a pair of conjoined ischia are present in MCZ 4116. Unfortunately, the front margins of the ischia are imperfectly preserved, so that only a fraction of the acetabular margin is present and nothing can be said concerning the relations of ischium and pubis. The bones are bladelike, tapering posteriorly and having a long median contact between the two elements.

Of the short front legs, the long bones of both sides are present in semi-articulated fashion close to the right scapulocoracoid of the holotype (Fig. 8). A humerus is present in 4118, and two incompletely preserved specimens are present in 4116. Except for the last, the bones are exposed from the ventral surface. The structure is that typical of primitive archosaurs generally — hourglass shaped, moderately expanded at either end, and constricted at mid-length of the shaft. There is a well-developed deltopectoral crest. Distally, there is a circular convex area for articulation with the head of the radius; lateral to this the bone is somewhat notched for reception of the olecranon.

The right radius and ulna (Fig. 8) are present and articulated with the humerus in the holotype; the left radius and ulna are incomplete distally. I have not been able to identify these elements in other specimens. As preserved, they show little character; both are slender elongate cylinders. The ulna is somewhat expanded proximally, but there is no olecranon ossification.

Regrettably there are no identifiable remains of the manus preserved.

Femora (Fig. 9a) are present in the holotype, nos. 4116, 4118, and the Tucumán specimen mentioned earlier; in the 4116 slab there are four femora of appropriate size and shape, indicating the presence of two individuals of *Gracilisuchus.* The bone has the typical sigmoid curvature of a proper archosaur. The head is turned somewhat medially from the shaft, but this curvature is less pronounced and the distinction between head and shaft less marked than in *Lagosuchus*, for example. There is no evidence of the presence of a "fourth trochanter." Tibia and fibula are present in articulation with the femur on the right side of the holotype, and these elements are present also in nos. 4116, 4118, and the Tucumán specimen (Fig. 9b and c). These elements are long and slender but where associated are nevertheless somewhat shorter than the femur. As always, the tibia is

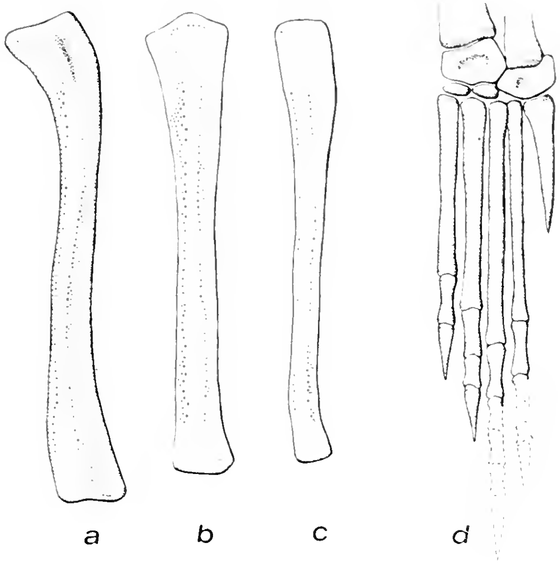

Figure 9. *a*, *b*, *c*, Left femur, tibia, and fibula. *d*, Left pes, composite. All × 1.

much stronger than the fibula, with an expanded triangular head, a well-developed cnemial crest, and a broadly oval distal area for astragalar articulation. The fibula is moderately broad but flattened throughout, with a gently sigmoid curvature.

The pes (Fig. 9d) is incompletely known. In the foot pertaining to the right leg of the holotype the usual two small distal tarsals are present. But little is preserved of the two proximal tarsals, and nothing worthy of description can be made out from tarsal remains associated with tibia and fibula in MCZ 4118. Astragalus and calcaneum are, however, moderately well preserved in the Tucumán skeleton mentioned earlier. The astragalus is a stout element, broad mediolaterally and moderately deep proximodistally; the anterior surface is somewhat concave. At its lateral margin the astragalus, as articulated, is in contact with the fibula, and below this area a diagonal surface of contact with the calcaneum is present. The calcaneum is less developed proximodistally. Details of the astragalocalcanear articulation cannot be determined; the calcaneum, however, had a well-developed "heel" in the fashion of crocodilians and many pseudosuchians.

Data on the digits of the pes are available only in the holotype and the Tucumán skeleton; the foot of the former is of the right side, of the latter, the left. Neither is complete distally. In the holotype metatarsals I–IV are present, but metatarsal IV is incomplete. Metatarsal IV is notably more slender than I–III. Metatarsal lengths as preserved are: 12 +, 23, 28 and 24 + mm. In the Tucumán specimen all five metatarsals are present, with lengths of 24, 28, 33, 32 and 18 mm; metatarsal V is of the "hooked" type, pointed distally. On the holotype no phalanges are present on toe I, but on digit II all three phalanges are present, with lengths of 7, 6, and 8 mm. On toe III a single phalanx is imperfectly preserved; no digits are present with metatarsal IV. In the Tucumán specimen, the two phalanges of digit I are present with lengths of 6 and 8 mm. On digit II all three phalanges are present, the third incomplete, the first two with lengths of 7 and 4 mm. On digit III three phalanges are present, but only the first, with a length of 10 mm, is well preserved. With digit IV there is found only a single phalanx, 7 mm long.

Allowing for a disparity in size of about 20 percent, the data from the two specimens agree well and allow a complete construction of the foot except for the more distal phalanges of toes III and IV. Assuming that as regards these phalanges, the pattern is that found in other advanced thecodonts and primitive saurischians, the restoration shown in Figure 9d cannot be far from the actual condition. It may be noted that in the specimens with articulated foot material, the toes are closely appressed to one another, as in my figure, with no trace of the fan-shaped spreading seen in many reptiles.

RESTORATION

Between the various available specimens, nearly the entire skeletal structure of *Gracilisuchus* is identifiable, and hence a skeletal restoration is justified (Plate 1). As usual in archosaurs in which the front limbs are notably shorter than the hind, the question arises as to whether a bipedal or quadrupedal pose is suitable. In the case of *Chanaresuchus* (Romer, 1972) I restored the animal as a quadruped, despite considerable disparity in limb lengths, because of the probably amphibious, crocodile-like nature of the animal. *Gracilisuchus*, as already mentioned (and discussed below), is quite surely a relative of *Ornithosuchus*, and I have followed Walker's restoration of that reptile in restoring *Gracilisuchus* as a biped. It is possible that the normal pose of *Gracilisuchus* was a quadrupedal one; however, I feel sure that, if pressed, this animal was able to run in the bipedal manner in which I have restored it.

RELATIONSHIPS

It is quite clear, I think, that *Gracilisuchus* is a relative of *Ornithosuchus* of the later Elgin beds of Scotland, ably described by Walker in 1964. The skull structure is closely comparable in most regards, as are various postcranial features. Walker has suggested certain late Triassic saurischian genera as possible *Ornithosuchus* relatives which might belong with this genus in a common family Ornithosuchidae, and Bonaparte (1969b) has recognized two Argentinian genera (*Venaticosuchus* and *Riojasuchus*) that seem quite surely to belong in this family. *Gracilisuchus*, from the Chañares beds — quite probably Anisian in age — is the oldest (and smallest) of forms that may pertain to this apparently common and perhaps widespread Triassic family. In a few features (such as the partial closure of the lateral temporal fenestra) the genus *Gracilisuchus* is perhaps slightly aberrant, but it seems quite surely close to the base of this stock.

Walker argues further that *Ornithosuchus* is a carnosaur — a proper dinosaur rather than a thecodont ancestor of dinosaurs. I provisionally adopted this interpretation when I published my 1966 edition of *Vertebrate Paleontology*. I confess, however, to now having reservations on this assignment (cf. Bonaparte, 1969a). Certainly the ornithosuchids show a number of features that might be expected in a carnosaur ancestor. But in certain features *Gracilisuchus* surely is below a proper dinosaur "grade" in structure: the apparent complete closure of the acetabulum, for example. Again, saurischians are completely devoid of armor, and I would be loath to believe that the dorsal armor seen in *Gracilisuchus* and *Ornithosuchus* would have been developed and secondarily lost. I do not wish to enter the controversy over the evolution of tarsal structure, but the presence in ornithosuchians of a "crocodilian" type of tarsus is, to say the least, an argument against placing the family in the Carnosauria, although not necessarily debarring the group from an ancestral position. Certainly the ornithosuchids show a trend in development that is in many ways similar to that which led to the carnosaurs. But for the time, it is, I think, better to regard them as forms related to and paralleling the line leading to the carnosaurs rather than members of that group.

As our knowledge of thecodonts increases (as it is currently doing at a rapid rate), it seems clear that while crocodilians, pterosaurs, bird ancestors and ornithischians have struck off on a variety of "tangents," the saurischians show merely an improvement on structural patterns already evident among the thecodonts. It has been generally held that the Saurischia are a "natural" order, monophyletic in origin. But recently it has been advocated (Charig *et al.*, 1965) that the sauropods are only distantly related to the "theropods" and may have arisen independently from ancestral thecodonts, and it is not impossible that among "theropods," carnosaurs and coelurosaurs may have had independent origins (cf. Bonaparte, 1969a). I am constitutionally allergic to unnecessary advocacy of polyphyletism, but I fear that we are as yet far from a solution to questions of relationships between various thecodont and saurischian groups.

TABLE I

Length of limb bones, in mm

	Holotype	MCZ 4118	MCZ 4116	Tucumán specimen
Humerus	38	44	44	—
Radius	30	—	—	—
Ulna	31	—	—	—
Femur	58, 60	68	64, 62, 61, 60	81
Tibia	56	59, 64	61, 56	73
Fibula	55	64	47+	65

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B R E V I O R A

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THE CHAÑARES (ARGENTINA) TRIASSIC REPTILE FAUNA. XIV. *LEWISUCHUS ADMIXTUS*, GEN. ET SP. NOV., A FURTHER THECODONT FROM THE CHAÑARES BEDS

Alfred Sherwood Romer

Abstract. Incomplete remains of a new thecodont from the Chañares Formation, *Lewisuchus admixtus*, are described and figured. Incomplete skull remains indicate that the posterior border of the lateral temporal opening was nearly vertical; the basal articulation with the palate was freely movable. A maxilla indicates elongation of the snout. Much of the presacral column is present; the cervical vertebrae are somewhat elongate, the ribs unspecialized. Scapulocoracoids are preserved, but no pelvic material; limb material is incomplete and disarticulated; femur and tibia are slender and of approximately equal length; the pes is long and slender. A single row of thin dorsal scales is present. *Lewisuchus* is a relatively primitive pseudosuchian that may be related to coelurosaur ancestry.

INTRODUCTION

After much preparation and a general survey of the Chañares collection, it became apparent that six thecodonts of various sorts were present in the material; these have been described in previous papers in this series. Recently, however, Mr. Arnold Lewis, in preparing a concretion containing a mixed assortment of reptilian remains, discovered that in addition to parts of a gomphodont skeleton and miscellaneous materials of small thecodonts, there was present a considerable fraction of a skeleton and skull of a thecodont of relatively good size which was obviously new, and is described below.

I am indebted to the National Science Foundation grant GB-2454 for aid in the collecting of the specimen and grant GB-22658 for preparation and publication.

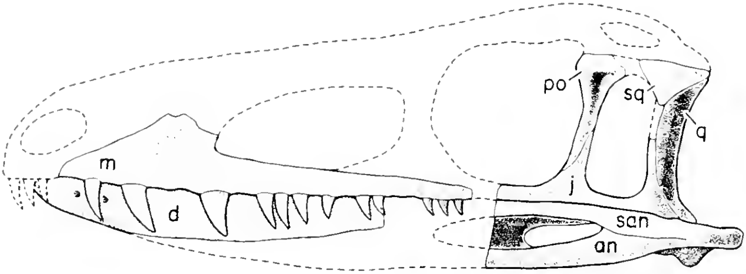

Figure 1. Lateral view of the skull, restored. *an*, angular; *d*, dentary; *j*, jugal; *m*, maxilla; *po*, postorbital; *q*, quadrate; *san*, surangular; *sq*, squamosal. The jugal-quadratojugal suture is obscure. × 2/3.

Lewisuchus admixtus, gen. et sp. nov.

Holotype. Museo de La Plata 1964-XI-14-14, consisting of much of the presacral column, part of the skull and jaws, scapulororacoids and some limb material, contained in a concretion including also remains of a gomphodont and smaller thecodonts. The specimen was collected from the Chañares Formation of La Rioja Province, Argentina, about 4 km north of the mouth of the Chañares River.

The generic name is in honor of Chief Preparator Arnold D. Lewis, who discovered the remains during preparation of the nodule containing them. The specific name refers to the mixture of materials in the nodule.

DESCRIPTION

Skull and jaws (Figs. 1–5). In one portion of the nodule were found the "cheek" region of the skull in articulation with the back end of the mandible, and close by, the occipital plate and basicranium, as well as a limited amount of other skull material. Separately were found an incomplete maxilla with dentition, an appropriate dentary, and a small segment of another maxilla and dentary.

Of the skull remains, the region of the left lateral temporal opening is well preserved (Fig. 1). The fenestra is subquadrate in outline, relatively narrow anteroposteriorly, the posterior margin descending vertically to the region of the jaw articulation. The jugal forms most of the straight lower margin of the skull in this area, the portion preserved running back from the area below the orbit to a contact with the quadratojugal, and including a triangular process ascending between orbit and lateral temporal opening to a diagonal articulation with the postorbital. The latter bone extends down nearly to the posteroventral angle of the orbit, narrowing distally; this ventral portion of the bone has a vertical groove at mid-width. At the level of the top of the lateral fenestra the postorbital is thickened, with a pronounced transverse ridge on its outer surface. The bone is broken off shortly above this point.

The quadratojugal completes posteriorly the ventrolateral skull margin. Posteriorly, adjacent to the quadrate, it expands in triangular fashion and sends a slender process, curving somewhat forward, up along the anterior margin of the quadrate. This process, as preserved, terminates about half-way up the posterior margin of the lateral fenestra.

The quadrate is nearly complete. Below, it presents a broad area for jaw articulation; this area, however, is not well preserved and the surface was perhaps cartilaginous in life. Its external ramus sweeps far upward behind the lateral fenestra, with a mildly convex anterior border, and with a concave cross section. At the posterior margin of this ramus there is, as in thecodonts generally, a sharp ridge, internal to which is the ramus articulating with the pterygoid, little developed dorsally but of considerable extent further ventrally. Lying above the head of the quadrate is a triangular piece of bone, quite surely broken off dorsally, with its apex directed downward along the anterior edge of the quadrate, its posterior margin following the curved upper edge of the quadrate. Its curved anterior margin apparently formed the posterodorsal angle of the lateral fenestra. This is surely a fragment of the squamosal. It is probable that in life squamosal and quadratojugal were in contact along the anterior margin of the quadrate. Above the preserved portions of the postorbital and squamosal are several bone fragments of indeterminate nature which may have pertained to the missing skull roof.

Internal to the temporal area described above, but not articulated with it, is a nearly complete braincase (Figs. 2–4) mostly in a good state of preservation. No sutures are apparent. The occipital plate is complete. Above is a broad supraoccipital area, with a median vertical ridge dorsally. On either side the upper margins curve forward into the otic region of the braincase; below this, on either side, paroccipital processes, broadened at their tips, run outward and somewhat downward and posteriorly.

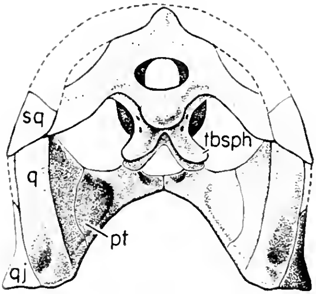

Figure 2. Posterior view of the skull; roof restored. *pt*, pterygoid; *q*, quadrate; *qj*, quadratojugal; *sq*, squamosal; *tbsph*, basisphenoidal tubera. × 1.

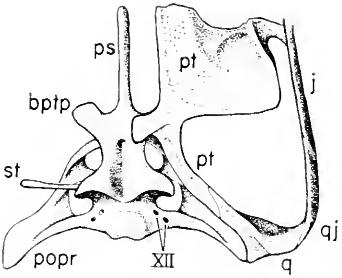

Figure 3. Ventral view of posterior part of skull; quadrate and dermal bones shown on right side of figure; ventral view of braincase on left. *bptp*, basipterygoid process of basisphenoid; *j*, jugal; *popr*, paroccipital process; *ps*, cultriform process of parasphenoid; *pt*, pterygoid; *q*, quadrate; *qj*, quadratojugal; *st*, stapes; *XII*, openings for hypoglossal nerve. × 1.

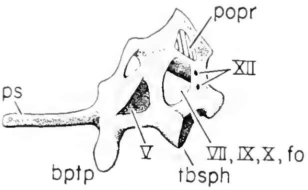

Figure 4. Lateral view of braincase. *bptp*, basipterygoid process; *fo*, foramen ovalis; *popr*, paroccipital process, cut off at base; *ps*, cultriform process of parasphenoid; *tbsph*, basisphenoidal tubera. Roman numerals indicate presumed region of nerve exits. × 1.

Below the large foramen magnum is the occipital condyle. Its surface is broad and somewhat subdivided posteriorly, and faces as much ventrally as posteriorly, suggesting a head posture appropriate to a possible bipedal pose. The basicranial region is well preserved. Just anterior to the condyle are highly developed basisphenoidal tubera. Broad posteriorly, they diminish in size anteriorly as they converge, with a deep longitudinal median groove between them. Anterior to the region of the bases of the tubera are highly developed basipterygoid processes, which extend strongly downward, outward, and somewhat anteriorly. It is obvious that at their curved articular termini there was free movement between the processes and the pterygoids. Extending forward between the base of the basipterygoid processes is the slender cultriform process of the parasphenoid, incomplete anteriorly.

The upper margins of the braincase stop at a point where presumably the roof of the brain cavity was continued by the dermal roofing bones. Laterally (Fig. 4), the upper margins curve forward on either side. The upper part of the lateral braincase walls slants medially; below this, a prominent if rounded ridge runs forward from the anterior surface of the paroccipital process, separating from the upper part of the wall a lateral surface which lies in a vertical plane and ventrally turns somewhat medially.

Three bars or "struts" constitute the lateral braincase wall connecting the upper portion of the braincase with the basicranial region. The most posterior, adjacent to the foramen magnum, is formed by the exoccipital, presumably reinforced anteriorly by opisthotic ossification. Two foramina are present in this strut. At least one was obviously occupied by nerve XII; possibly the other served for passage of the vagus nerve, but the opening is small and I tend to believe that this was a second hypoglossal foramen, and that the vagus emerged anterior to this strut.

Between the posterior and middle struts there is a large unossified area in the side wall of the otic region; presumably in this area lay the exits of nerve VII, the vagus foramen and the fenestra ovalis. The upper portion of the interval between posterior and middle struts is ossified, the ossification lying deep to the struts concerned. The middle strut is presumably formed by a prootic ossification, with nerve V emerging anteriorly beneath it. The most anterior strut, presumably a laterosphenoid ossification, descends to meet the basisphenoid at the base of the basipterygoid process. Dorsally the presumed laterosphenoid bifurcates, leaving an opening (? a fenestra epioptica) between its branches and the dorsal taenia marginalis. No more anterior ossification is preserved in the braincase. The dorsal surface of the cultriform process is grooved, presumably for reception of a cartilaginous sphenethmoidal braincase segment.

Much of the left pterygoid is preserved, although it is somewhat displaced. The quadrate ramus is present. Its ventral border is strongly ridged, continuing a ridge present more posteriorly on the quadrate. Anteriorly this ridge curves upward, separating a thinner posterior portion of the ramus from a thicker anterior area; presumably this marks the boundary of the tympanic cavity. The area for articulation with the basipterygoid process is a recess on the medial border of the bone at the junction of quadrate and palatal rami. The posterior portion of the palatal ramus is preserved; there is no evidence of palatal teeth. A well-developed lateral flange appears to have extended directly laterally, with a slight ventral curvature distally. A ridged medial border of the ramus is preserved for a distance. From the tip of the lateral flange the lateral, ridged, margin of the palatal plate curves forward and somewhat medially and dorsally; for the short distance preserved, the lateral border twists sharply outward and gains contact with the jugal. It is probable that this region pertains to an ectopterygoid, and there is some evidence of a line of suture between this element and the pterygoid.

On the right side a slender splint of bone, about 7 mm long, extends outward from the braincase region anterior to the paroccipital process. This is reasonably identified as a stapes.

No more anterior portions of the skull are present in articulation with, or near, the posterior skull elements so far described. Probably pertaining to this skull are tooth-bearing elements that are certainly thecodont in nature and of appropriate size. A tooth-bearing strip of bone, 73 mm in length, is surely an incomplete right maxilla (Fig. 1). The teeth are incompletely preserved, but some 18 teeth or alveoli can be counted. A maximum size appears to be developed not far from the anterior end, posterior to which there is a gradual diminution in tooth size. Externally, near the anterior end there is a curved ridge that presumably marks the border of the depression containing the antorbital fenestra. Part of the upper margin of the maxilla appears to be a finished surface bounding the fenestra. The internal surface of the bone is considerably swollen in the area in which the bases of the larger teeth were contained; above this

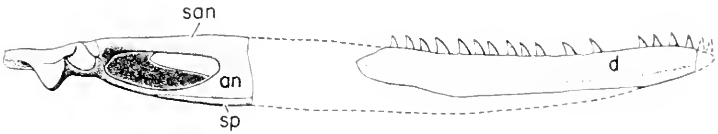

Figure 5. Inner view of lower jaw, restored. *an*, angular; *d*, dentary; *san*, surangular; *sp*, splenial. × 2/3.

is a thin area that is obviously part of the maxillary extension upward anterior to the antorbital fenestra. It may be noted that the tooth row is essentially straight, without the ventral convexity noticeable in carnosaurs and even in ornithosuchids.

A fragment that pertains to a left maxilla shows a series of teeth clearly decreasing in size posteriorly. As in thecodonts generally, the teeth are somewhat compressed mediolaterally, conical, sharp-pointed, and recurved posteriorly toward their tips.

The posterior portion of the left mandible is present in essentially natural relations with the cheek elements and quadrate (Figs. 1, 5). The anterior end of the preserved portion lies in the region of the external mandibular foramen, showing above this opening the surangular and, below, the angular and posterior end of the splenial. Internally the jaw portion preserved shows the suture outline of the mandibular fossa. It is probable that in life the outer surface of the ramus was tilted strongly medially, but, even so, it would appear that the fossa faced as much medially as dorsally. Above the fossa the jaw, as preserved, appears to show a broad horizontal shelf along the course of the surangular. The articular surface of the mandible is large, broadened lateromedially, and divided into a smaller anterior and larger posterior portion; the articulation is so oriented that the inner margin is somewhat more anteriorly placed. There is a well-developed retroarticular process and, in addition, a strong flange directed ventromedially behind the articular area.

Presumably belonging to this specimen is an isolated tooth-bearing element, obviously a dentary, 62 mm in length, which bears about 20 teeth or alveoli (Figs. 1, 5). As frequently in thecodont jaws, there is no great regional difference in tooth size along the series. It is probable, from the contours of the bone, that little is absent anteriorly. Two small foramina for blood vessels are present close to the front end; internally a longitudinal meckelian groove is present, above which the bone is thickened for tooth roots.

In Figure 1 I have attempted to restore the skull in lateral view. Because of the relative length of the maxilla, it is obvious that the "snout" was much longer, relatively, than in many thecodonts.

Axial skeleton. Not connected with the cranial remains first described, but reasonably associated because of thecodont nature and proper size, is a series of 17 articulated vertebrae, beginning with the axis; part of this series is shown in Figure 6. Anterior to the axis are imperfect remains that appear to represent the atlas centrum and axis intercentrum (no intercentra are present more posteriorly). The axis is well developed, with a relatively low but long neural spine, with a curved upper margin. The cervical vertebrae are elongate as compared with the rest of the column; the axis centrum is 14 mm in length, and the more posterior cervicals are approximately similar, compared to an average of 11 mm in dorsal members of the series. Neural spines are not well preserved in the cervical region (the axis apart). In vertebra 8 the spine is low, extending but 9 mm above the level of the zygapophyses. The back border of the spine is essentially vertical, but the anterior border slants strongly forward dorsally, so that, from a width of 5 mm across the base, the dorsal margin is 10 mm in extent. There is no thickening of the dorsal margin for armor support (such as is seen in *Gracilisuchus*). In the dorsal region the spine bases are stouter, but the anterior slant of the anterior margin persists. There are some poorly preserved traces of scutes above the cervical vertebrae, apparently thin and probably in a single row.

As preserved, the cervical centra appear to be thin, compressed from side to side except for prominent vertical ridges at either end. Even here, however, there appears to be no sharp ventral longitudinal ridge, and as we proceed posteriorly the centra become thicker and but gently rounded ventrally. In the cervical region the sides of the centra show a longitudinal depression; farther back, with major development of the transverse processes, this depression is part of a more expanded excavation, bounded above by the roots of the transverse processes. The articular area for the rib capitulum lies, in the cervical region, at the base of the ridge forming the anterior margin of the centrum; it is, however, little marked in the column as preserved. Presumably this articular area ascended toward or to the arch in the posterior part of the series but there is little evidence preserved in the specimen. In the column as preserved the diapophysis is not

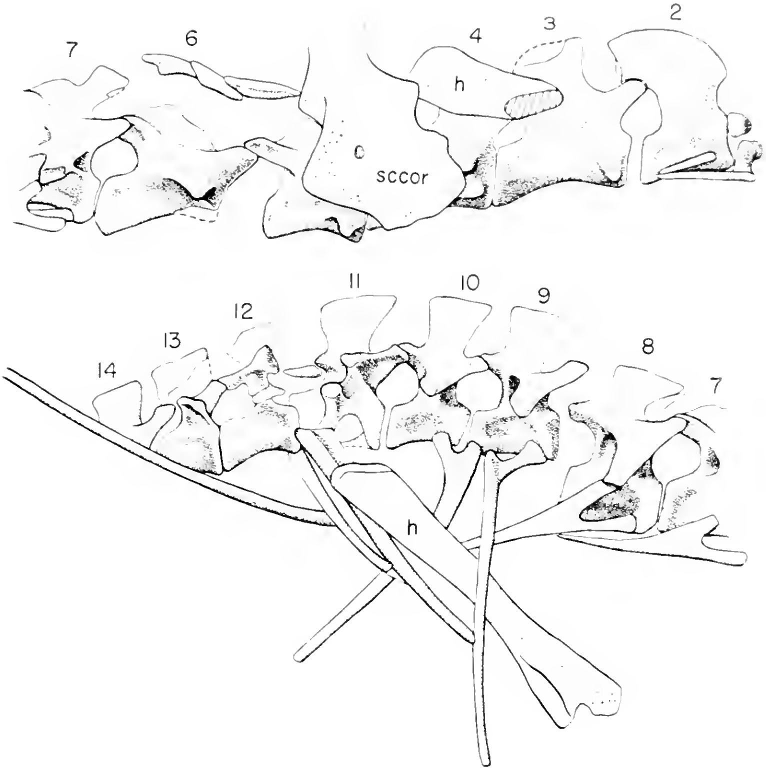

Figure 6. Right lateral view of cervical and anterior dorsal vertebrae and ribs. *h*, head of right humerus and incomplete left humerus; *sccor*, inner view of right scapulocoracoid. × 1.

prominently developed in the cervical vertebrae; in the dorsal region, however, the transverse processes become prominent, extending strongly outward and somewhat downward and backward. The process is supported ventrally by ridges extending upward to its base from both anterior and posterior margins of the centrum; above, a stout ridge connects the base of the process with the anterior zygapophysis, and a less developed ridge extends to the region of the postzygapophysis.

Close to the posterior end of the articulated series are three further vertebrae of appropriate size for *Lewisuchus*. Details are not well preserved, but presumably these vertebrae were from the "lumbar" or sacral region. Several further isolated vertebrae are present in the concretion, not well preserved except for one which is clearly a posterior dorsal.

Ribs are in general incompletely preserved (Fig. 6). Close to the base of the axis centrum is a short rodlike structure, expanded at one end, which is presumably an incomplete axial rib; adjacent to it is a slender rod, 14 mm long, which may be an atlantal rib. There are no ribs preserved associated with cervicals 3–6; ribs are present, although incomplete, with vertebrae 7–10. All are markedly two-headed; there is no evidence of the development of accessory processes of the rib heads described in a number of other thecodonts. The preserved portions of these ribs, measured from the tubercula, are 20, 15, 45, and 37 mm long. Although none of the four is complete, the first two appear to be slender and close to their termini where broken off; the last two are more stoutly built and seem surely to have been true dorsal ribs. A few further incomplete rib segments are present close to the articulated rib series. In another part of the nodule are several articulated dorsal ribs of a size appropriate for *Lewisuchus*; one has a length of about 80 mm. The curvature of these ribs suggests a deep but narrow trunk. Close to the three vertebrae mentioned above as possible lumbars or sacrals are two structures with triangular outlines and with a developed articular area at the narrow end; these may be sacral ribs.

Appendicular elements. Close to, and quite surely pertaining to the articulated vertebral series are two scapulocoracoids (Fig. 7), the left seen from the outer surface, the right from the inner side. Scapula and coracoid are well fused, with no apparent suture. The scapular blade is unusually tall and slender. Distally it expands somewhat; the distal margin is taller posteriorly, slanting downward toward the anterior margin. The lower part of the scapula expands both anteriorly and posteriorly, with a thickened acromial ridge anteriorly and a somewhat comparable posterior ridge buttressing the upper glenoid rim. The ventral margins of the coracoids are imperfectly preserved, but the bone seems to be primitive in structure, with no evidence of a crocodiloid posteroventral extension, and without evidence of any anterior "incision" in the plate.

There is no material interpretable as being a clavicle or interclavicle of this specimen. And nothing found in this concretion can be identified as pertaining to the pelvic girdle of *Lewisuchus.*

There is a considerable amount of limb material strewn through the concretion, but most appears referable to a gompho-

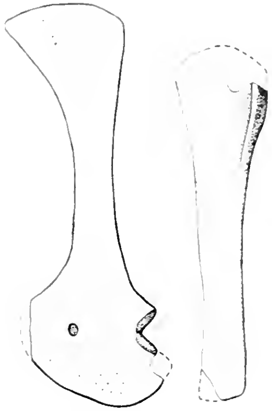

Figure 7. *Left*, left scapulocoracoid; *right*, incomplete left humerus in ventral view. × 1.

dont or to one or more thecodonts of smaller size. Only a small amount of material appears to be of a size and nature appropriate to *Lewisuchus.*

Close to the right scapulocoracoid is the head of a humerus obviously of slender build and a second imperfect humerus (Fig. 7); its head seems comparable to that just mentioned. The shaft is slender; the distal end is missing, but if extrapolated from the part present, on the analogy of *Hesperosuchus* (Colbert, 1952, fig. 22), the length in life must have been on the order of 70 to 75 mm. I find no elements that are interpretable as radius or ulna. A femur of appropriate size (Fig. 8) measures 105 mm in length. The bone is badly crushed proximally; it nevertheless shows a well-developed greater trochanter and an apparently spherical head turned in sharply from the shaft. The bone is slender, the shaft having a diameter of but 7 mm. Unfortunately the distal end is imperfect.

A slender tibia, represented mainly by an impression in the matrix, is 106 mm in length. Near the shoulder region (but also close to the vertebrae mentioned as perhaps being in the lumbosacral region) is a group of podial elements (Fig. 8B). Two slender bones, measuring 31 and 30 mm in length, are surely metapodials; semi-articulated with the second are three phalanges, the terminal one clawed. Near the first of the two metapodials is a relatively long phalanx, and beyond it a second series of three articulated phalanges, terminating in a clawed element.

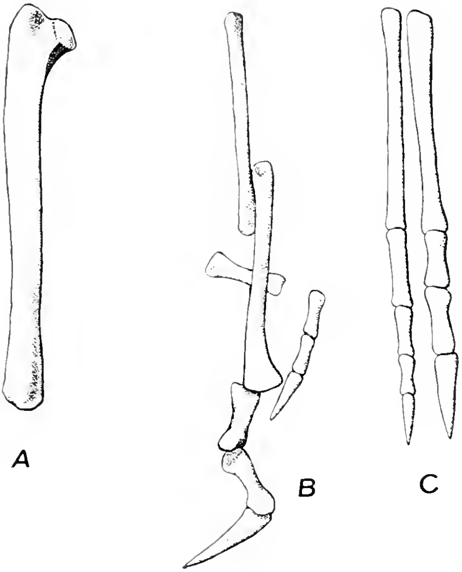

Figure 8. *A*, Right femur in dorsal view (incomplete distally); *B*, elements of second and third toes of right pes; *C*, the same, articulated. × 1.

It is most reasonable to interpret the two metapodials and the seemingly associated phalanges as toes II and III of the right pes. When articulated (Fig. 8C), it is obvious that digit II is stronger than III, and nearly as long, suggesting comparison with the proterochampsid type of foot (Romer, 1972a).

DISCUSSION

Because of the inadequacy of the material, I have refrained from attempting a skeletal restoration of *Lewisuchus*. In default of good skull material, allocation of *Lewisuchus* to a definite position in the order Thecodontia is difficult. The modest trend toward strengthening of the inner toes immediately suggests comparison with *Chanaresuchus* (Romer, 1971; 1972a) and the proterochampsids, an assignment with which facial elongation is compatible. But strengthening of the inner toes is not confined to the proterochampsids, and the subquadrate configuration of the lateral temporal opening is sufficient to debar *Lewisuchus* from the Proterochampsidae, and indeed, from the suborder Proterosuchia, in which the lateral opening is relatively long with the quadrate slanting backward ventrally. *Lewisuchus* is thus probably assignable to the Pseudosuchia.

Lewisuchus retains certain primitive features, such as the free basal articulation between palate and braincase, and the nearly straight back margin of the lateral temporal fenestra, which lacks the V-shape here found in many advanced forms. On the other hand, the long slender tibia, about equal to the femur in length, and the long metapodials, suggest a strong advance towards a truly bipedal gait.

Lewisuchus does not appear to be closely comparable to other described pseudosuchians. It differs in many obvious features from the ornithosuchids (cf. Romer, 1972b). It is possibly related to *Hesperosuchus* of Colbert (1952), but this form is poorly known and, furthermore, appears to differ in certain features, such as the incipient development of accessory rib flanges, absent in *Lewisuchus.* Elongation of cervical vertebrae suggests comparison with *Teleocrater*, an incompletely known form from the Manda beds, under description by Charig (1957). *Lewisuchus* may possibly be a form leading toward the coelurosaurs. Not improbably *Lewisuchus* may eventually merit being made the type of a family of its own. But for the time being it is perhaps best left as a pseudosuchian *incertae sedis.*

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B R E V I O R A

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THE RELATIONSHIP OF ISLAND AREA AND ISOLATION TO COLOR POLYMORPHISM IN *LIGUUS FASCIATUS* (PULMONATA, BULIMULIDAE)

Michael A. Rex

Abstract. *Liguus fasciatus* is a highly polymorphic arboreal pulmonate living on small islands called hammocks in the Florida Everglades. Color variation in this snail has in other studies been assumed to be random and of no selective significance. Multiple regression analysis showed that hammock area was a statistically significant predictor of color morph diversity, and that measures of isolation were either insignificant or significant but subordinate to the effect of area. From this result it was inferred that color variation in *Liguus* was regulated by available ecological diversity (hammock area) even when interhammock migration appeared to be extensive. Color polymorphism in this snail might be imposed by visual predation, larger hammocks with more heterogeneous floral composition having more morphs because they offer more possibilities for cryptic or aposematic associations to avoid predators.

INTRODUCTION

Conchologists have long considered color variation in the remarkably polymorphic *Liguus fasciatus* to be random and of no adaptive significance. "On the whole it is not apparent that any form of selection has been a major factor in the evolution of Florida *Liguus*" (Pilsbry 1946: 47). Ecological uniformity of habitats led Pilsbry (1912, 1946) to attribute differences in color and form between monomorphic colonies to isolation alone, and to explain variation in mixed colonies by random mutation and recombination of hypothetical Mendelian alternatives.

However, recent studies indicate that random genetic events do not, as once thought, constitute the most important mode of evolution in land snails. Crampton's (1916, 1925, 1932) contention that intraspecific variation in *Partula* was due to genetic drift has been contested by selectionists both on the basis of his collecting methodology (Mayr 1942; Cain and Sheppard 1950; Ford 1964) and on reexamination of his own data (Bailey 1956). Gulick (1873, 1905) was unable to correlate variation in *Achatinella* with ecological diversity, but Welch (1938, 1942, 1958) found changes in both color and form with altitude in achatinellids when temperature and moisture gradients were pronounced. Diver (1940) and Lamotte (1952) proposed that color variation in *Cepaea nemoralis* resulted from genetic drift, though it is now evident that relative frequencies of color and banding patterns in *Cepaea* are regulated to some extent by visual predation (review *in* Cain and Sheppard, 1954) and climatic factors (Lamotte 1959, 1966; Wolda 1967; Arnold 1968, 1969). Furthermore, Murray (1964) demonstrated that hermaphroditism, sperm storage, and multiple matings in *C. nemoralis* function to maximize effective population size, thereby reducing the probability of genetic drift in small colonies. Gould (1969) disclosed the adaptive significance of both color and form in his study of temporal character variation in *Poecilozonites*.

In the present paper I show that the number of color morphs in populations of *Liguus fasciatus* living on small islands can be predicted by island size and isolation. It is suggested that polymorphism in this snail is maintained by a selective balance of phenotypes.

Liguus is particularly suitable for investigating effects of environmental factors on phenotypic diversity. The snail lives on small islands called hammocks in the Florida Everglades. Hammocks are slightly elevated remnants of Pleistocene coral reefs that support a tropical hardwood vegetation. They are surrounded by sparse pine woods or swamp, both of which are inhospitable to *Liguus*. Thus, habitat size and distance between individual populations are well defined and easily measured.

LIGUUS MATERIAL

Liguus colonies, once abundant in Florida, have now been decimated to near extinction by land clearing, glade fires, amateur collectors, and introduced rats. Fortunately, a few careful investigations were carried out before the onslaught. Material used in this study came from extensive collections made by W. J. Clench and W. S. Schevill during February and March, 1931, from an assemblage of hammocks on Long Pine Key, Dade County, Florida (Fig. 1). The hammocks ranged in size

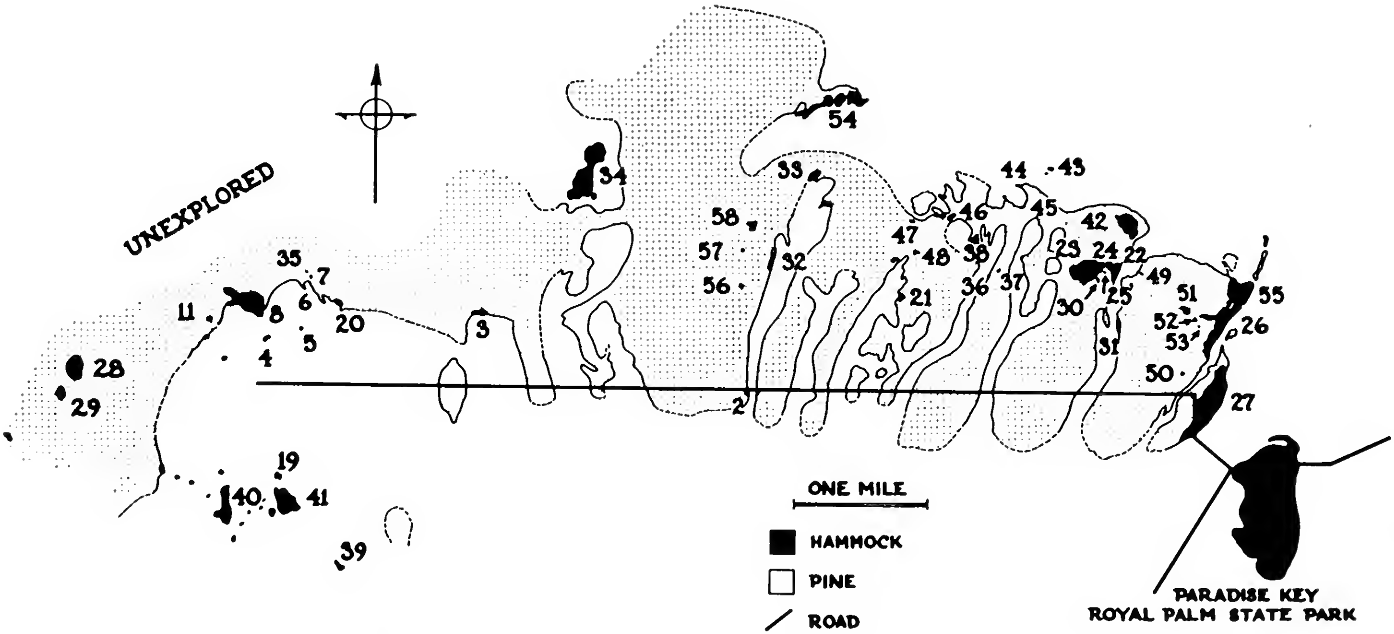

Figure 1. Distribution of hammocks in Long Pine Key, Florida. Area left blank is glade. *Liguus* material was available only for those hammocks which are numbered.

from 0.34 to 43.80 acres. According to Clench (personal communication), an endeavor was made to collect samples of all the varieties present in each hammock visited, but not necessarily in proportion to their natural frequency distribution (nonrandom). The material, comprising several thousand shells from 48 hammocks, was sorted by Clench as to varieties and placed in the mollusk collections of the Museum of Comparative Zoology, Harvard University.

I have considered the Long Pine Key material to include nine color morphs, which are described briefly below. The morphs clearly have some genetic integrity. By examining several clutches of eggs, Pilsbry (1946) showed that separate patterns segregated out, but the exact extent to which this occurs is unknown. Pilsbry (1946) classified the morphs of *L. fasciatus* into subspecies, forms, and varieties. The subspecific designations represented different color patterns and had no geographic connotation. The forms were based on the colors present in the patterns and the presence or absence of pink coloration on the early whorls and columellar callus. The varieties were usually named stages in the continuous variation present in the forms. His system for sorting out morphs is convenient and I have largely adhered to it here. But the genetic criteria on which his hierarchy was based are unacceptable. For instance, the rare variety *deckerti* (see below) found in three widely separate localities in Florida was thought to have arisen from the form *castaneozonatus* through mutational "loss" of the factor for pink coloration (1946: 70). Its white apex and columellar callus could, however, be the result of a number of conceivable schemes involving matings with morphs having white apices, dominance interactions, recombination, and close linkage. The genetic mechanisms governing coloration in these snails are probably complex and I have chosen not to make any underlying assumptions about them. For purposes of this paper it is sufficient to recognize that *L. fasciatus* is a highly variable species in which more or less disjunct color morphs can be discerned and that the number of morphs present in a population is some indication of its genetic variance.

MORPHS PRESENT IN LONG PINE KEY

Names listed are those used by Pilsbry (1946) and the patterns refer to Figure 2.

1. *eburneus:* shell completely white.

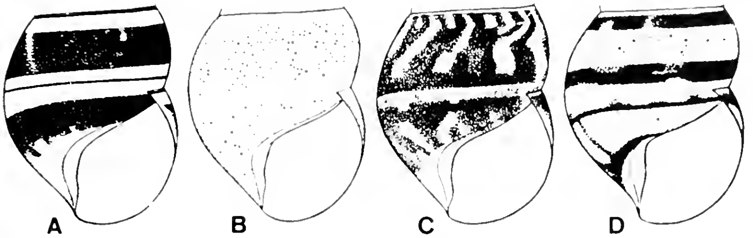

Figure 2. Basic color patterns for *Liguus fasciatus* present on Long Pine Key, Florida (from Pilsbry, 1946). See text for explanation.

2. *cingulatus:* faint yellow spiral zones (Pattern A) on a white background; apex and columellar callus white.
3. *roseatus:* yellow spiral zones (Pattern A) on a white background; apex and columellar callus pink.
4. *castaneozonatus:* splotchy to solid brown spiral zones (Pattern A) on a white background; apex and columellar callus pink.
5. *deckerti:* brown spiral zones (Pattern A); apex and columellar callus white.
6. *luteus:* uniform faint yellow coloration (Pattern B); apex and columellar callus white.
7. *ornatus:* uniform yellow coloration (Pattern B) intensifying to amber near the lip; apex and columellar callus pink.
8. *testudineus:* variegated and banded (Pattern C or D), with brown coloration on white to yellowish background; apex pink with pink or white columellar callus.
9. *marmoratus:* variegated and banded (Pattern C or D) with brown coloration on a white background; apex and columellar callus white.

Patterns C and D are endpoints of continuous variation, the dense variegation or "flames" of C gradually superimposing the bands and lightly variegated pattern in D. There appear to be no good objective criteria for discriminating various stages in this continuous variation. Thus, the distinction between morphs 9 and 10 is one of apical coloration.

METHODS

Computerized stepwise multiple regression analysis using program BMDO2R (Dixon, 1968) was performed to determine whether the degree of polymorphism in populations from different hammocks correlated with any of several independent variables measuring area or isolation.

No general discussion of the estimating equations of multiple regression is presented here as they have now been so extensively employed in ecological studies (cf. Ebeling *et al.,* 1970; Hamilton *et al.*, 1963; Hamilton *et al.*, 1964; Hamilton and Rubinoff 1963, 1964, 1967; Johnson *et al.,* 1968; Pomeroy, 1967; Vuilleumier, 1970).

The methodology allows one to determine both whether a statistically significant prediction of the dependent variable can be made using some or all of the independent variables, and which independent variables are most important. The square of the multiple correlation coefficient R^2 estimates the amount of variance in the dependent variable explained by the combined effects of the independent variables. The significance of the entire regression was tested by the variance ratio F, which is the mean square due to regression divided by residual mean square. The significance of the contribution of each independent variable to the total explained variance in the dependent variable (R^2) was tested by using the t– ratio, which equals the partial regression coefficient divided by the standard error (Snedecor and Cochran, 1967). Three versions of the regression were carried out: a linear model, a semi-log model using log-transformed independent variables, and a log-log model.

The dependent variable was simply the number of morphs present on each hammock. Independent variables were restricted to those which could be measured from a large map of the collecting site prepared by W. S. Schevill (Fig. 1). Previous studies in island biogeography, in which multiple regression models were used to predict species diversity (cf. esp. Hamilton and Rubinoff 1963, 1964, 1967; Vuilleumier 1970), suggested several independent variables. The following were tested for their ability to predict the number of morphs: (1) Hammock Area. This variable is commonly used as an index of ecological diversity. Larger hammocks were expected to have more microhabitats; i.e., more plant species, more possibilities for cryptic associations, greater foliage height diversity, etc. (2) Distance to Hammock 27. Hammock 27 (Fig. 1) was the largest island and may have been an effective dispersal center for the entire group of hammocks even though it was peripherally located. It also had the fortuitous advantage of being close to Paradise Key, an enormous hammock which probably exerted influence over the morph diversity of Long Pine Key hammocks, but which was not included in this study because data on the number of color morphs present were unavailable. This variable tested effectiveness of isolation from a possible source area of high phenotypic variability. Hammock 27 had eight of the nine color morphs. Three additional variables determined the effects of isolation in a more localized sense. (3) Distance to the nearest large hammock, a large hammock being defined as any of hammocks 54, 23, 26, 8, 34, 27. (4) Distance to the nearest hammock. (5) Size of the nearest hammock.

RESULTS

The relative influence of each independent variable and an analysis of variance are given in Table 1. In all three models hammock area was the most significant ($P < .001$) predictor of the number of morphs present. Area made a higher contribution to R^2 in the semi-log model (.39) than in the linear model (.30), an indication that the data are somewhat curvilinear with respect to area.

Variables measuring isolation, with the exception of distance to hammock 27, proved to be insignificant. Distance to hammock 27 made a significant contribution to R^2 in the linear ($P < .05$) and semi-log ($P < .025$) models. This suggested that a slight phenotypic diversity gradient extended westward from hammock 27. If hammock 27 was, or was near, the effective population center, then perhaps the population was simply expanding westward. There was some evidence to support this contention in the distribution of individual morphs. Two morphs, *ornatus* and *marmoratus*, did not extend farther west than hammocks 34 and 56 respectively and *deckerti* was confined to hammocks 55 and 26. They were the least frequent in occurrence and were found predominantly on large hammocks. These morphs might still have been in the process of dispersing westward. When they were removed from the analysis, the number of morphs still correlated significantly with hammock size ($.01 \geqslant P \geqslant .001$). But distance measures correlated so poorly when added to the multiple regression models that the significance of the entire regression was reduced to $P < .05$ in the linear and log-log versions. Otherwise, the morphs showed no evident propensity for east or west. Even though distance to hammock 27 made a significant contribution to R^2, its effect was clearly subordinate to that of area.

TABLE 1. Relative influence of independent variables and analysis of variance for multiple regression equations used to predict the number of color morphs in populations of *Liguus fasciatus* living on hammocks.

Independent variables	*Linear Model* Contribution to R^2	$t(42)$	P*	*Semi-log Model* Contribution to R^2	$t(42)$	P	*Log-log Model* Contribution to R^2	$t(42)$	P
X_1 Hammock area	.3013	4.5705	$< .001$	.3876	4.6934	$< .001$	.2895	3.6073	$< .001$
X_2 Distance to hammock 27	.0662	2.2924	$< .05$	.0925	2.5184	$< .025$	.0297	1.3450	$> .10$
X_3 Distance to nearest large hammock	.0166	1.1729	$> .20$	.0017	.3782	$> .50$	.0011	.2569	$> .50$
X_4 Distance to nearest hammock	.0050	.5218	$> .50$	.0036	.6214	$> .50$	.0011	.3205	$> .50$
X_5 Size of nearest hammock	.0010	.2604	$> .50$	.0031	.5053	$> .50$	.0034	.4415	$> .50$
Total R^2	.3901			.4885			.3248		
Analysis of variance for entire equation	$F_{(5,42)} = 5.372$, $P < .01$			$F_{(5,42)} = 8.022$, $P < .01$			$F_{(5,42)} = 4.041$, $P < .01$		

*P = Probability that calculated values result from chance. All other symbols discussed in text. Subscripts represent degrees of freedom.

Regression equations are:

Linear model, $Y = 3.8164 + 4.3240X_1 - 0.0463X_2 + 0.1264X_3 - 0.1277X_4 + 0.2654X_5$;
Semi-log model, $Y = 7.2483 + 1.8446 \log X_1 - 1.0776 \log X_2 + 0.1250 \log X_3 - 0.3262 \log X_4 - 0.1850 \log X_5$;
Log-log model, $\log Y = 0.8701 + 0.2125 \log X_1 - 0.0863\ X_2 + 0.0127 \log X_3 - 0.0252 \log X_4 - 0.0242\ X_5$.

It is worth noting that in three cases independent variables measuring isolation had significant simple correlation coefficients with the number of morphs: 1) distance to the nearest large hammock, $r = -.407$, $P < .01$; 2) distance to hammock 27, $r = -.398$, $P < .01$, both in the semi-log model; and 3) distance to the nearest large hammock, $r = -.310$, $P < .05$ in the log-log model. These isolation variables were de-emphasized in the multiple regression analyses because they did not correlate with the dependent variable as significantly as area ($r = .549$, .538, .623, $P < .001$, in the linear, log-log, and semilog versions respectively), did not explain as much of the variance in the dependent variable as area, and were partially redundant with one another.

Associations between intraspecific variability, interspecific competition, faunal diversity, etc. and various physical or biological environmental parameters are often obscure. The usefulness of multiple regression lies in the ability to discern a hierarchy of importance among independent variables relating to some dependent variable from a matrix of correlations between all variables. In this particular study it indicated that hammock area was more important than isolation in predicting the amount of color variation in populations of *L. fasciatus.* It is possible, however, that the distance measurements and transformations used may not have been the relevant ones for predictive purposes.

MacArthur and Wilson (1967: 132–133) concluded on the basis of theoretical considerations that in colonization "stepping stones" should be less important to passive dispersers than to active dispersers. Snails probably disperse passively and one would expect direct distance measurements to be most appropriate in this kind of study. When hammock-hopping distances[1] were tried in place of variables 2 and 3, however, the results remained very nearly the same as those presented in Table 1. R^2 for the linear, semi-log, and log-log model was .39, .51 and .34 respectively, and probability levels for significant variables were identical, with the exception of variable 2 in the semi-log model which was significant at $P < .005$ instead of $P < .025$

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[1] Hammock-hopping was measured by using intervening hammocks as stepping stones rather than using direct distance. Also, measurements were made through the pine wood or to the narrowest passage through glade if glade must be crossed, the assumption being that it would be difficult for an actively dispersing pulmonate to cross bodies of water.

(a difference of less than .02 in the contribution of variable 2 to R^2).

Distinction in mode of dispersal that might otherwise be indicated by using either direct or hammock-hopping distances could be blurred by the small size of the study area as a whole. Predatory birds and high winds are likely agents of dispersal and they probably transport snails a highly variable range of distances. Simpson (1929) occasionally found live *Liguus* far into the open pine wood which he thought were propagules on their way to colonize new hammocks. He gives a delightfully anthropocentric account of *Liguus* "obeying an instinct for founding new colonies." It seems more likely that the snails he found were dropped by birds.

An analysis of variance for the entire regression for each model is given in Table 1. All three models provided significant ($P < .01$) results. The best predictive value (highest R^2) was afforded by the semi-log model. In all models, however, at least half of the variance in the number of morphs was left unaccounted for. This "error" ($E = 1 - R^2$) was due to several factors. First, there were undoubtedly important variables that were not considered simply because the data were unavailable. For instance, more precise measurements of ecological diversity such as the number and kind of plant species occurring on each hammock may have been important. Secondly, there were errors in measuring the independent variables used in the appraisal of polymorphism. Some morphs must have been occasionally overlooked during collecting. Finally, there is the certainty that not all of the variance could ever be attributed to ecological parameters, part of it being due to genetic mechanisms such as balanced polymorphism (heterozygote superiority) and part of it actually being random.

DISCUSSION

I infer from the inability of isolation to predict the number of color morphs and the widespread distribution of the morphs in general that interhammock migration, however it occurs, is a fairly frequent event, but that its contribution to maintaining polymorphism in *Liguus* is strongly mediated by hammock area. The question now arises: Why is hammock area a good predictor of color variation? A speculative hypothesis is the following.

Boettger (1931) first suggested, without giving supporting data, that the degree of color polymorphism in *Cepaea* is regulated by background heterogeneity through selection by visual predation. The quantitative studies of Cain and Sheppard (see review 1954) corroborated Boettger completely. More diverse backgrounds such as hedgerows, rough herbage, and mixed deciduous woods supported more variable populations of *Cepaea* than the more uniform beechwoods or short turf. Further, cryptic associations between color morphs and background color appeared to confer a selective advantage in eluding predators. For instance, in a study of *Cepaea* in Wytham Woods, Sheppard (1951) found that brown and pink morphs were at an advantage in mid-April when the forest floor was brown, the more conspicuous yellow morphs being selectively predated by thrushes. In May when the forest became green the reverse situation obtained, yellow then being at an advantage.

A similar mechanism might regulate morph diversity in *Liguus.* Larger hammocks with greater foliage height diversity and a greater number of plant species might provide more possibilities for cryptic associations to avoid predators. Natural predators of *Liguus* include the opossum (Pilsbry, 1946), the crow, and "other large birds" (Simpson, 1929). Colonies on small hammocks having limited floral heterogeneity might continually have morph diversity depleted by predators.

Eisner and Wilson (1970) recently suggested the obverse of this hypothesis: that coloration in *Liguus* is aposematic (rather than cryptic). When disturbed the snail withdraws into its shell and discharges large quantities of liquid. Simpson (1929) thought this fluid secretion enabled the snail to slip from the beaks of predatory birds, but Eisner and Wilson believed it to be a chemical defense mechanism. The success of cryptic or aposematic coloration depends on suitable background color. Since none of the wide variety of morphs will appear conspicuous in all situations, perhaps the snail employs a mixed strategy involving both kinds of coloration. Further observations are needed.

The possibility of low morph diversity on small hammocks being due to genetic drift is not discounted, but seems unlikely for reasons presented against Pilsbry's argument below. Other hypotheses, such as regarding polymorphism as a manifestation of niche subdivision (Van Valen 1965), are conceivable, but lack substantiating evidence.

An explanation for the previously noted curvilinearity of the data with respect to area might be that the number of cryptic associations utilized by this snail is attained at intermediate hammock size, and the probability of adding a new and different association with further increase in area is negligible.

Pilsbry's argument that variation in *Liguus* is random seems untenable for the following reason: Interhammock migration, as already mentioned, appears to be quite extensive. Since the snail is hermaphroditic and has multiple matings a single fertilized immigrant can introduce considerable variation into a colony (Pilsbry, 1912, found at least three separate morphs in one clutch of nine eggs from a single adult). In the early stages of colonization, larger hammocks might be expected to have populations with greater morph diversity simply because they represent larger target areas for propagules; this might be the case with *ornatus*, *marmoratus*, and *deckerti*. The great abundance of *Liguus* at Long Pine Key and further north in Florida suggests, however, that the snail has populated southern Florida for a rather long period of time, possibly since the last glaciation, and that it has essentially achieved a steady state. This being the case, and if variation occurred randomly and were unaffected by selection, then there would be no reason to expect populations living on larger hammocks to be more variable than those living on smaller ones. The highly significant positive correlation of hammock area and the number of morphs ($P < .001$) indicates, however, that morph diversity on smaller hammocks is maintained at a low level. Visual predation might be an important selective agent reducing variation on small hammocks. Visual predators are known for *Liguus* and a similar mechanism has been shown to operate with another polymorphic pulmonate.

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B R E V I O R A

Museum of Comparative Zoology

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A FOSSIL PELOMEDUSID TURTLE FROM PUERTO RICO

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Abstract. A fossil turtle shell, too incompletely preserved to merit a formal binomial taxonomic designation, from the Oligocene San Sebastian Formation of Puerto Rico is here described. It represents the first record of a truly endemic pelomedusid in the Caribbean region. The specimen appears to be more closely related to South American pelomedusids than to any of the North American members of the family, which are known only as fossils. Presumably the Puerto Rican pelomedusid was derived either from South American ancestors or from some progenitor that gave rise to both it and the South American forms.

Fossil turtles from the Caribbean region are few and fragmentary. Our knowledge of these has most recently been reviewed by Williams (1950) and then further extended in a subsequent publication (Williams, 1952). In his earlier paper, Williams (p. 8) briefly mentioned a specimen from Puerto Rico ". . . represented by numerous fragments of plastron, pelvis, and of the buttress region of the carapace . . ." which had been donated to the American Museum of Natural History in 1924 by Señor Narcisco Rabell Cabrero. Williams noted that "the exact locality and circumstances of the find are uncertain" and that it "was unfortunately so incomplete as to afford no generic characters." Nevertheless, an accompanying map (Williams, 1950, fig. 1), in which the specimen is identified simply as an emydine, indicates that it was found in the southeastern quadrant of the island.

The fossil turtle to which Williams alluded, however, is not an emydine nor was it collected in southeastern Puerto Rico. It is, instead, a pelomedusid from the northwestern part of the island. Apparently this specimen was once part of a larger collection of vertebrate remains from the San Sebastian Forma-

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tion, which outcrops in the vicinity of the city of that same name[1].

To the best of my knowledge, none of this material has ever been described, nor, except for the specimen that forms the subject of this paper, can its present whereabouts be established.

The San Sebastian Formation is generally considered to be of middle to late Oligocene age (Schuchert, 1935: 467–468; Weyl, 1966, table 15; Khudoley and Meyerhoff, 1971, fig. 27), although there is some possibility that at least the upper part of it may be early Miocene in age (Khudoley and Meyerhoff, 1971: 145–146). This formation is part of a larger series of middle Tertiary limestones and shales that form an extensive east-west trending belt more than 100 kilometers long across northwestern Puerto Rico. The sediments in this belt are generally believed to represent a widespread mid-Tertiary marine transgression over this sector of the island. Shale is the predominant sediment within the San Sebastian Formation, although a wide variety of other lithofacies also occur — gravels, sands, lignitic clays, limestones, and chalks. Fossils have been found throughout this formation, which is in the neighborhood of 700 feet thick; marine invertebrates are abundant, as are a variety of fossil land plants believed to represent a tropical flora typical of that now found bordering on lagoons and estuaries. From this evidence it would appear that the sediments of which the formation is comprised were deposited partly under brackish and partly under near-shore marine conditions. The few fragments of matrix still adhering to the turtle shell here described indicate that the specimen was recovered from a limestone facies.

The shell (#1836 in the collection of the department of vertebrate paleontology at the American Museum of Natural History) is badly fragmented, and its partial reconstruction has only been possible as the result of much patient piecing together by a number of persons (Drs. Walter Auffenberg, Eugene Gaffney,

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[1] Correspondence (now on file in the department of vertebrate paleontology at the American Museum of Natural History) from Professor James F. Kemp, of the department of geology at Columbia University, to Walter Granger mentions the existence of a number of specimens in addition to the fossil turtle. These were said to include teeth, jaws, and vertebrae. According to the son of Señor Rabell Cabrero, who still lives in San Sebastian, the specimens that his father collected probably came from limestone exposures along the main road from San Sebastian to Lares (personal communication, Mr. and Mrs. Alan Patterson).

and the author) over a period of several years. Much of the left side of the shell has been preserved so that, although it is far from complete (Figs. 1 and 2), many of its essential features can be determined. Save for the epi-and entoplastra, most of the left side of the plastron remains. Much less of the carapace, unfortunately, is known; only the posterior neurals as well as some of the left pleurals and peripherals still exist. In addition, the pelvis is largely intact. Moreover, cleanly broken surfaces on many of the isolated bone fragments that I have not been successful in reassembling indicate that at the time of its discovery the shell was somewhat more complete than at present, but how much of it actually has been subsequently lost during the nearly fifty intervening years is conjectural.

Originally the carapace must have measured well over half a meter in length. In transverse section, it is low-arched, with a strong lateral carina at the bridge. Nearly all of the last two neurals and the left side of the one immediately preceding these have been preserved. They are arranged in an uninterrupted series. The last is pentagonal, while the preceding two are hexagonal ("coffin shaped"). Their dorsal surfaces are unkeeled. The neurals become progressively shorter posteriorly (5.95 cm, 4.45 cm, and 2.95 cm in length from front to back). Although it is impossible to determine the exact widths of any of the three neurals, it is clear that the last was broader than long, the next-to-last was of approximately the same width as length, and the most anterior was somewhat longer than broad. These proportions are typical of most pelomedusids. Some of the scute sulci that were superimposed on the dorsal surface can still be detected; these are shown in Figure 1. The hour-glass configuration at the junction between the fourth and fifth vertebrals is similarly developed elsewhere among the pelomedusids only in the African species *Pelusios sinuatus*, to the best of my knowledge. The external surface of the shell (plastron as well as carapace) is essentially smooth, without the concentric striations or vermiculated sculpture characteristic of some pelomedusids. Roughened areas, posterolateral to the last neural on the visceral surface, indicate where the pelvis was fused to the carapace. The axial buttresses appear to have been robust, but the extent to which the inguinal buttresses may have been developed cannot be ascertained, owing to the incomplete preservation of the carapace.

As preserved, the midline length of the plastron is 35.7 centimeters. I estimate that its total length must have been somewhat greater than 50 centimeters. The posterior plastral lobe was

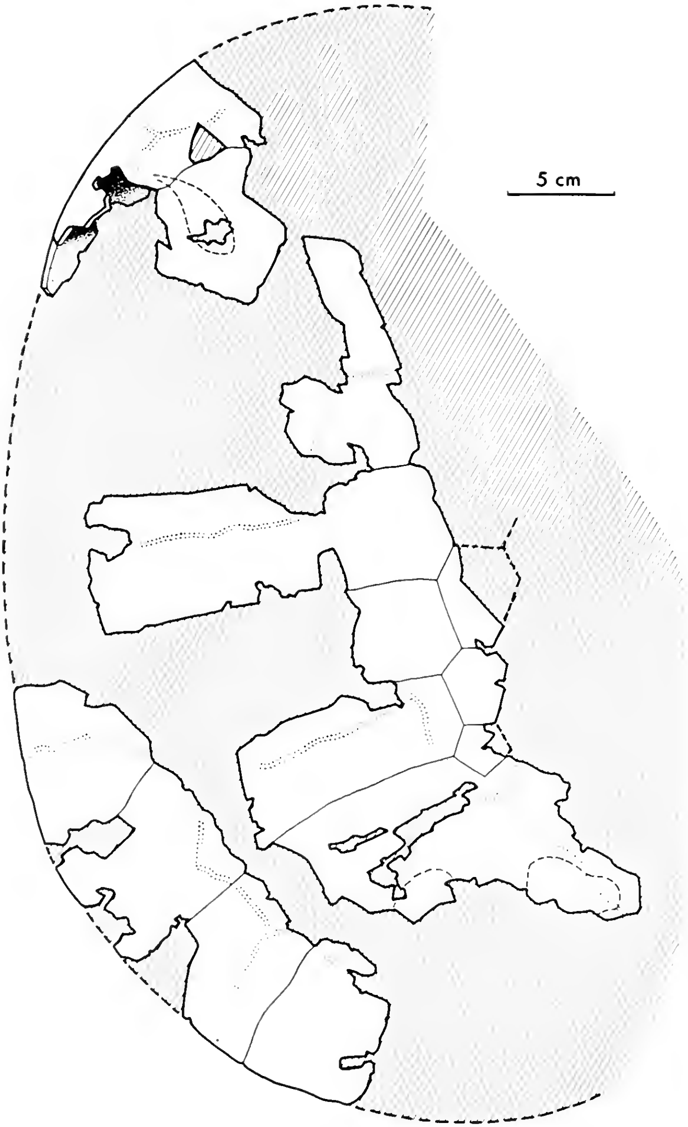

Figure 1. External view of what remains of the carapace of the Puerto Rican pelomedusid (AMNH 1836); the anterior end is toward the top of the page. The positions on the visceral surface of the left axial buttress as well as of the iliac scars of the pelvis are indicated by broken lines. Those scute sulci that can still be discerned are represented by parallel dotted lines. Missing portions of the shell are indicated by shaded areas.

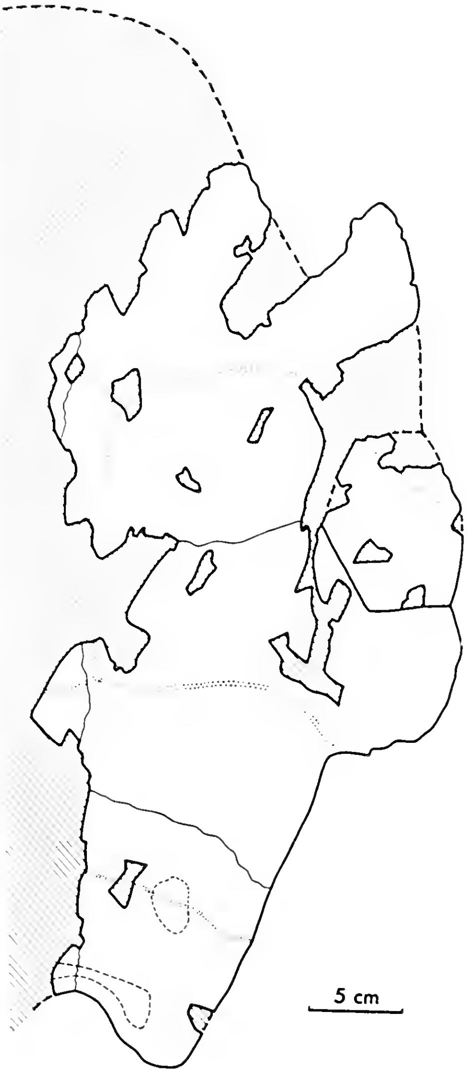

Figure 2. External view of what remains of the plastron of the Puerto Rican pelomedusid (AMNH 1836); the anterior end is toward the top of the page. The positions of the pelvic scars on the visceral surface are indicated by broken lines. The scute sulci and missing portions of the shell are depicted as in Figure 1.

evidently slightly wider than the anterior one; its width to the midline at the inguinal notch is 13.7 centimeters, whereas the corresponding width from the axial notch to the midline is approximately 12 centimeters. The sides of the posterior lobe are straight rather than curved and converge toward the rear. The anal notch is broad. The external surface of the posterior lobe is flat rather than depressed inward, which suggests (but does not conclusively demonstrate) that the specimen may have been a female. The bone forming the posterior lobe becomes gradually and uniformly thinner toward the rear. Pelvic scars are present on the visceral surface of the plastron. These are disposed in essentially the same manner as in any of the living pelomedusids. Only the left mesoplastron has been preserved; it is large and hexagonal in shape, but unlike most pelomedusids it is not more or less equidimensional. Instead, it is appreciably longer (9.9 cm) in its anteroposterior axis than in its tranverse one (8.1 cm). The pectoral-abdominal scute sulcus curves backward laterally to cross the front portion of the mesoplastron. Otherwise, there is nothing noteworthy about the remainder of the plastral scute sulci that can still be discerned.

The pelvis is the best preserved part of the specimen. Nevertheless, parts of the pubes and ischia are missing on both sides, although somewhat more remains of the right side than of the left (Plate 1). In its general appearance, the pelvis is similar to the structure typical of most living and fossil pelomedusids.

There can be no question that the specimen here described represents a pelomedusid; the presence of mesoplastra together with a pelvis that is fused to the shell assures this determination. More precise placement of this Puerto Rican pelomedusid within the family, however, is difficult. In the New World, only two clearly definable pelomedusid genera — *Bothremys* (Gaffney and Zangerl, 1968) and *Taphrosphys* (Hay, 1908) — have been reported outside the confines of South America[1], and these are known only as fossils. The Caribbean form does not belong to either of these genera. *Bothremys* differs from it in having mesoplastra that are broader than long (Schmidt, 1940: 7 and fig. 5; Zangerl, 1948: 38 and figs. 3, 15), as well as an anterior plastral lobe that is slightly broader than the posterior one at

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[1] Two other North American fossil genera, *Amblypeza* and *Naiadochelys*, have been described on the basis of extremely fragmentary material and referred to the Pelomedusidae (Hay, 1908: 122, 125), but I regard both of these as *nomina vana* (Wood, MS).

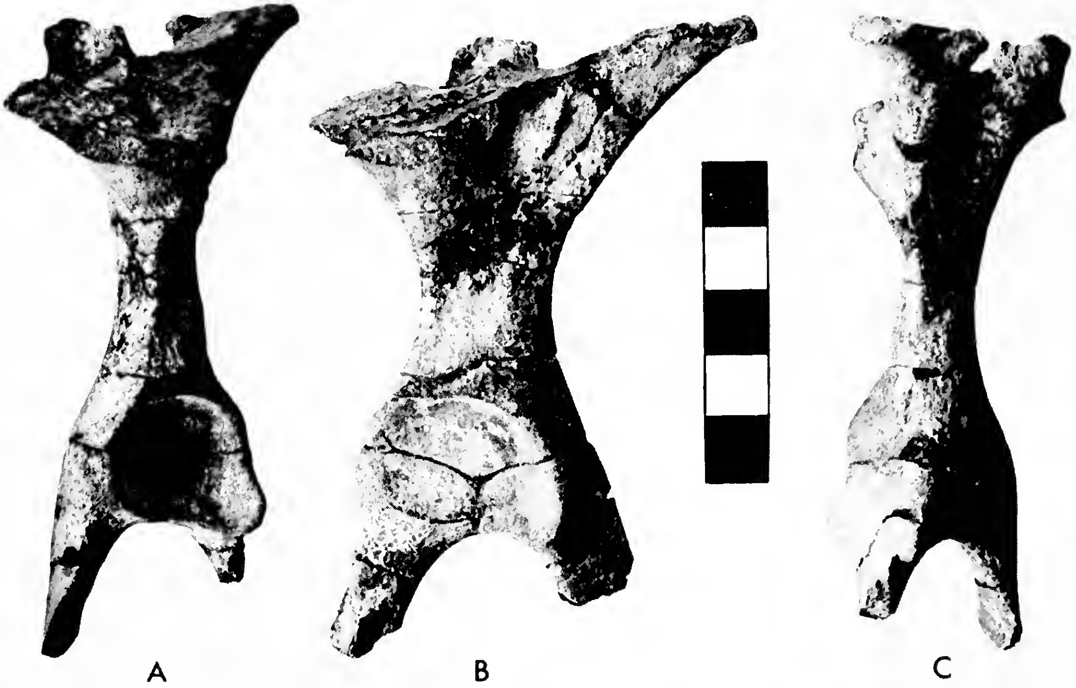

Plate 1. The right side of the pelvis of the Puerto Rican pelomedusid: A) posterolateral view; B) lateral view; C) anteromedial view. The scale represents a length of five centimeters.

its maximum width (Zangerl, 1948: 38). *Taphrosphys* differs principally in the shape and position of the pelvic scars on the internal surface of the plastron (Hay, 1908, fig. 118) in addition to having its anterior plastral lobe broader than the posterior one.[2]

Representatives of three pelomedusid genera are known in the South American paleontological record.[3] Two of these — *Apodichelys* (Price, 1954a) and *Roxochelys* (Price, 1954b) — are known only as fossils from Brazil, while the third — *Podocnemis* — still has living species in South America as well as in Madagascar. *Apodichelys* is based on a single specimen of very small size, the internal mold of a shell. Its anterior plastral lobe was considerably broader than the posterior one, and for this reason it is unlikely to be related to the Caribbean form. The type and only described specimen of *Roxochelys* consists of a small portion from the front of a carapace and an anterior plastral lobe. Comparable parts of the Caribbean specimen have not been preserved, so that possible relationships between the Brazilian and Puerto Rican forms cannot yet be evaluated. Fortunately, several nearly complete shells of *Roxochelys* have recently been discovered, but until they are described meaningful comparisons cannot be undertaken. Wood and Gamero (1971) recently have summarized our knowledge of the South American fossil forms that have been referred to *Podocnemis,* while Siebenrock (1902) and Williams (1954) have reviewed the living species of the genus. Except for the proportions of its mesoplastron and the outlines of the last two vertebral scutes, the Caribbean specimen falls within the limits of morphological variability known to occur in *Podocnemis.*

From the foregoing discussion, it seems reasonable to state that the Caribbean specimen is probably more closely related to South American pelomedusids than to those from North America. But difficulties arise in trying to determine the most appropriate way to express this relationship. The shape of the

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[2] This information is based on a recently discovered specimen, #18706 in the collections of Princeton University, that is much more complete than any that were available to Hay. Dr. E. S. Gaffney has studied but not yet described this specimen, and I appreciate his courtesy in permitting me to use the information mentioned here.

[3] Staesche (1929) has referred some fragments from the late Cretaceous or early Tertiary of Argentina to a fourth genus, *Naiadochelys,* but such an attribution is highly doubtful in view of the fact that the type material from North America cannot be adequately characterized at present.

mesoplastron and the vertebral scute pattern might be considered sufficiently distinctive for the recognition of either a new species of *Podocnemis* or perhaps even of a new genus. Numerous fossil pelomedusid taxa have been named and described in the past on the basis of an equally small list of purportedly diagnostic features. In view of the fact that the shell is so incompletely known, however, I prefer to refrain from giving it any kind of formal taxonomic designation at either the generic or the specific level, for at least three possibilities exist: the shell may belong to either *Podocnemis*, *Roxochelys*, or a third previously unrecognized genus. At present I do not believe that currently available evidence is adequate to discriminate among these choices. Consequently I will merely designate the Puerto Rican specimen as Pelomedusidae *gen. et sp. indet.*

Outside of South America, only one other fossil pelomedusid of Tertiary age has previously been described in the New World. This is the specimen, consisting solely of the anterior half of the plastron, that Collins and Lynn (1936) originally described as *Taphrosphys miocenica* and that Gaffney and Zangerl (1968) later (and correctly, I believe) referred to *Bothremys*. This specimen, now lost (Gaffney and Zangerl, 1968: 209), is of Miocene age. Collins and Lynn (1936: 162) assumed that *B. miocenica* must have been a fresh water form because all living pelomedusids occur in fresh water habitats. They further assumed that their specimen had been carried out to sea before being covered by sediment. In view of the fact that many pelomedusids in the past (including, I suspect, all other previously described North American fossil pelomedusids) were evidently adapted to marine conditions (Wood, MS), as well as that the bulk of fossils associated with *B. miocenica* include strictly oceanic cheloniid turtles, cetaceans, and marine invertebrates, it seems reasonable to postulate that this species was probably a marine form that was not transported any particularly great distance before burial.

Circumstantial evidence indicates that the Puerto Rican pelomedusid was probably also a marine form. As already mentioned, the fauna that was reportedly discovered in association with it cannot now be located, thus eliminating a potentially important source of environmental information. Fortunately, however, one other fossil vertebrate previously has been described from the San Sebastian Formation and this species — the dugongid sirenian *Caribosiren turneri* (Reinhart, 1959) — may be helpful in determining the depositional environment in which the remains of the Puerto Rican pelomedusid were buried. *Caribosiren* was found in a limestone outcrop along the road between the towns of San Sebastian and Lares (Reinhart, 1959: 8); consequently, it seems probable that this species was recovered from the same general area as the locality where Señor Rabell Cabrero discovered his fossil turtle. The close proximity, if not coincidence, of the localities where these fossil vertebrates were found strongly suggests that they lived in the same aquatic habitat. The limestones from which *Caribosiren* was disinterred contained abundant foraminifera and molluscs and these indicate a shallow-water marine habitat (Reinhart, 1959: 16-17). Living dugongids, furthermore, are confined to marine waters (Walker, 1968: 1332). Therefore, it seems reasonable to suppose that *Caribosiren* was also fully adapted to a marine existence. All these considerations lead me to believe, by inference, that the Puerto Rican pelomedusid was in all probablity a truly marine turtle.

Other pelomedusids, although not fossil ones, previously have been reported from the Caribbean region. Palacký (1897: 14) cursorily mentioned the occurrence of *Podocnemis dumeriliana* on Guadeloupe without specifying any further details. The validity of this record is dubious, however, for, as Barbour (1934: 111) has noted: ". . . apparently material from a host of localities around the Caribbean basin, at one time or another, was assembled at one of these French islands [Guadeloupe or Martinique] before being shipped to Paris, where the material now bears a locality label indicating the point of shipment only." Barbour further quoted a publication dating from 1862 which stated that tortoises " '. . . are brought for sale to the islands from the coast (Venezuela) . . .' " This reference specifically singles out an area where *P. dumeriliana* naturally occurs. Either one of these explanations could account for the reported presence of this species on Guadeloupe. In view of the fact that no one has subsequently found *P. dumeriliana* on this island, it seems reasonable to regard Palacký's comment on its distribution as erroneous.

A different pelomedusid genus does, however, actually occur on Guadeloupe. Pinchon (1967: 561) has recorded its presence there: "C'est une Tortue originaire d'Afrique tropicale, *Pelusios subniger*; elle fut certainement introduite par l'homme mais on ignore absolument quand et comment." According to Pinchon (personal communication), representatives of this species can be found only on the eastern, nonmountainous half of the island

(Grand Terre), particularly in ponds in the vicinity of the town of Moule, and even here they are not particularly abundant. Although no examples of *Pelusios* from Guadeloupe have yet been carefully examined, there are no readily apparent differences serving to distinguish this population from African ones of the same species (which is, it may be worth noting, widespread in sub-Saharan Africa). It is for this reason, in addition to the fact that *Pelusios* does not occur in the fossil record except in Africa, that it seems reasonable to suppose that the Guadeloupe population has been introduced to the island within historic times.

Of the two reported occurrences of living pelomedusids in the Caribbean region, therefore, one is erroneous and the other represents what is almost certainly a relatively recently introduced population that has achieved limited success at best. Consequently, the Puerto Rican specimen is the first record of a truly endemic pelomedusid in the Caribbean. On the basis of morphological similarities, furthermore, it seems likely that the Puerto Rican form was derived either from South American ancestors or from some progenitor that gave rise to both it and at least some of the South American forms.

ACKNOWLEDGMENTS

I am indebted to Dr. E. S. Gaffney of the American Museum of Natural History for his kindness in permitting me to study the fossil turtle described in this paper. Miss Charlotte Holton, also of the American Museum, was of great assistance in my efforts to locate correspondence relating to the specimen. Shelter from the hazards of the New York subway system was amicably provided by Mr. and Mrs. R. H. Wadsworth during several visits to the American Museum for research on the specimen here described. Dr. Frank Whitmore, vertebrate paleontologist for the United States Geological Survey at Washington, D. C., was most helpful in directing my attention to Reinhart's publication on *Caribosiren*. Mr. and Mrs. Alan Patterson kindly interviewed the son of Señor Rabell Cabrero on my behalf during their visit to San Sebastian in late December, 1971; the information they were able to uncover proved to be of great interest. I am in addition much obliged to Père R. Pinchon of Fort de France, Martinique, and Dr. P. C. H. Pritchard, of the University of Florida, for information concerning the occurrence of *Pelusios subniger* on Guadeloupe. Prof. E. E. Williams of Harvard University first prompted my interest in the Puerto Rican fossil turtle and then critically read the resulting manuscript. Miss Victoria Kohler and Mr. Don Crowe assisted in the preparation of the photographic plate. Finally, I would like to express my gratitude to the National Geographic Society for its generous support of my research on pelomedusid turtles.

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B R E V I O R A

Museum of Comparative Zoology

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MINUTE JAMAICAN PROSOBRANCH GASTROPODS: *STOASTOMA* AND ITS CONGENERS

Kenneth J. Boss

Abstract. Several generic level taxa have been allied to the minute terrestrial helicinid *Stoastoma* (Mollusca; Gastropoda; Prosobranchia). The type-species of each taxon is illustrated for the first time and the status of each is discussed. The nominal congeners are four recognizable genera that are virtually restricted to Jamaica: *Wilkinsonaea, Lewisia, Stoastoma* with its synonym *Hemicyclostoma,* and *Fadyenia* with its synonyms *Metcalfeia, Petitia, Lindsleya,* and *Blandia.*

INTRODUCTION

Among the terrestrial prosobranch gastropods, the family Helicinidae is exceptionally rich in species and is developed in two primary regions of the world, southeastern Asia and the West Indies. In the latter are several radiations that have been accorded subfamilial and generic rank (Keen, 1960). One genus, *Stoastoma* C. B. Adams, consists of species with minute shells, usually in the size range of 1–3 mm in diameter. Of the New World helicinids, it has been almost totally neglected, because of nomenclatorial problems and the tiny size of the shells. This paper reviews the generic units of *Stoastoma* and provides the first illustrations of their type-species.

In 1849 C. B. Adams described the genus *Stoastoma.* Subsequent to Adams' death in 1853, Edward Chitty, an amateur conchologist, English lawyer, and judge who lived in Jamaica, took up the task of describing land snails from this Antillean island. In 1857, after his return to England, Chitty published an overzealous paper on *Stoastoma* in which he recognized the group as a separate family, the Stoastomidae, and proposed seven new genera, sixty-one new species, and two new varieties from Jamaica. Although these descriptions pay considerable attention to conchological detail, none of the species was illustrated and there is some confusion as to the type-species of the subgenera.

Clench and Turner (1950) provided a list of Chitty's taxa but did not figure any *Stoastoma.* Baker (1922, 1934) and Wenz (1938) treated some aspects of the taxonomy of *Stoastoma,* while Keen (1960), though listing the taxa and synonymizing some of the subgenera, did not figure any type-species. Herein are illustrated the type-species of the generic taxa described by Adams and Chitty, along with corrected type designations.

Type designations have been given by Baker (1922), Wenz (1938), Clench and Turner (1950), and Keen (1960) but most of Chitty's taxa, in accordance with the International Code of Zoological Nomenclature (Article 68 [C], Recommendation 69 B [2]), have their type-species by virtual tautonymy. Pfeiffer (1858, 1865, 1876) also provided lists of species.

C. B. Adams frequently did not give any specific type locality for his species; the localities provided herein are those of the lectotypes here designated. Principle citations are also provided.

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Mr. John Peake of the British Museum (Natural History) kindly arranged for the loan of specimens from the Chitty Collection. The manuscript was critically read by Dr. R. D. Turner and Messrs. R. I. Johnson and M. K. Jacobson.

LIST OF THE TAXA

Blandia Chitty 1857, PZSL, pp. 167 & 169 [type-species, by virtual tautonymy, *Stoastoma blandianum* C. B. Adams 1849, lectotype here selected and figured (Figs. 20–22), MCZ 177243; type-locality, Pease River, Manchester, Jamaica]; Pfeiffer, 1865: 207; 1876: 237; Baker, 1922: 57; Pilsbry, 1930: 230; Baker, 1934: 14; Wenz, 1938: 446; Clench and Turner, 1950: 9; Keen, 1960: 288.

Fadyenia Chitty 1857, PZSL, pp. 167 & 168 [type-species, by virtual tautonymy, *Stoastoma fadyenianum* C. B. Adams 1849, lectotype here selected and figured (Figs. 23–25), MCZ 177233; type-locality, hills SW of Port Henderson, Jamaica]; Pfeiffer, 1865: 190; 1876: 237; Baker, 1922: 57; Baker, 1934: 3; Wenz, 1938: 446; Clench and Turner, 1950: 9; Keen, 1960: 288.

Hemicyclostoma Chitty 1857, PZSL, p. 163 (*nomen nudum*); Pfeiffer, 1865: 191 [type-species, by original designation, *Stoastoma pisum* C. B. Adams 1849, lectotype here selected and figured (Figs. 1–3), MCZ 177234], *non* Gray 1840.

Lewisia Chitty 1857, PZSL, pp. 167 & 168 [type-species, by subsequent designation (Baker, 1922: 57), *Stoastoma philippianum* C. B. Adams 1851, lectotype here selected and figured (Figs. 10-12), MCZ 177241; type-locality, Burnt Hill near Ackendown, Westmoreland, Jamaica]; Pfeiffer, 1865: 185; 1876: 237; Baker, 1934: 14; Wenz, 1938: 447 (incorrectly designated *Stoastoma agassizianum* C. B. Adams 1849 as type-species); Clench and Turner, 1950: 10 (incorrectly designated *Stoastoma agassizianum* C. B. Adams 1849 as type-species); Keen, 1960: 228.

Lindsleya Chitty 1857, PZSL, pp. 167 & 169 [type-species, by virtual tautonymy, *Stoastoma lindsleyanum* C. B. Adams 1849, lectotype here selected and figured (Figs. 4–6), MCZ 177238; type-locality, Manchester, Jamaica]; Pfeiffer, 1865: 200; 1876: 237; Baker, 1922: 57; Baker, 1934: 3; Wenz, 1938: 446; Clench and Turner, 1950: 10; Keen, 1960: 288.

Metcalfeia Chitty 1857, PZSL, pp. 167 & 168 [type-species, *Metcalfeia metcalfeiana* Chitty 1857, by virtual tautonymy, lectotype here selected and figured (Figs. 7–9), BMNH 57.12.1.218; type-locality, Hanover, Jamaica]; Pfeiffer, 1865: 192; 1876: 237; Baker, 1922: 57 (incorrectly designated *Stoastoma chittyanum* C. B. Adams 1849 as type-species); Baker, 1934: 3; Wenz, 1938: 446; Clench and Turner, 1950: 10 (designated *M. metcalfciana* Chitty 1857 as type-species); Keen, 1960: 288.

Petitia Chitty 1857, PZSL, pp. 167 & 168 [type-species, by virtual tautonymy, *Stoastoma petitianum* C. B. Adams 1851, lectotype here selected and figured (Figs. 17–19), MCZ 177237; type-locality, Pease River, Manchester, Jamaica]; Pfeiffer, 1865: 196; 1876: 237; Baker, 1922: 57: 1934: 14; Wenz, 1938: 446; Clench and Turner, 1950: 11; Keen, 1960: 288.

Stoastoma C. B. Adams 1849 (September), Monograph of *Stoastoma*, a new genus of new operculated land shells, pp. 1–16, Amherst, Massachusetts; 1849 (September), Contributions to Conchology, no. 1, p. 16 [type-species, by subsequent designation, Chitty 1857, PZSL, p. 167, *Stoastoma pisum* Adams 1849, lectotype here selected and figured (Figs. 1–3), MCZ 177234; type-locality, Manchester, Jamaica]; Pfeiffer, 1858: 170; 1865: 184; 1876: 237; Baker, 1922: 57; Wenz, 1938: 446; Keen, 1960: 287.

Wilkinsonaea Chitty 1857, PZSL, pp. 167 & 168 [type-species, by virtual tautonymy, *Stoastoma vilkinsoniae* C. B. Adams 1851[1]; lectotype here selected and figured (Figs. 13–16), MCZ 177251; type-locality, Yallah's Hill, Jamaica]; Pfeiffer, 1865: 186; 1876: 237; Baker, 1922: 57 as *Wilkinsonia wilkinsoniae;* 1934: 14; Wenz, 1938: 446 (incorrectly designated *Stoastoma gouldianum* C. B. Adams 1849 as type-species); Clench and Turner, 1950: 12.

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[1] The spelling of this specific name was altered to *'wilkinsonaeana'* by Chitty, 1857: 168, to *'wilkinsoniae'* by Baker, 1922: 57, and to *'vilkonsoniae'* by Clench and Turner, 1950: 12.

DISCUSSION

Pilsbry and Brown (1910) noted the occurrence of *Stoastoma pisum*, a terrestrial form living on stones, in the vicinity of Mandeville, Jamaica. They figured the radula and stated that it confirmed the position of the genus in the family Helicinidae. That is, the radula of *S. pisum* exhibits the essential features of a helicinid radula (Troschel, 1857): a single rachidian tooth, flanked by A, B and C centrals, a lateral complex consisting of a comb-lateral and an accessory plate, and a marginal complex consisting of numerous teeth or uncini. This gives the formula (MC) (LC) CBARABC (LC) (MC). As illustrated by Baker (1922), its specific features include an A central with a single large outer hook (resembling *Lucidella*), a B central with three heavy lobes, and a C central with four. The comb lateral has three large cusps and the inner marginals (first 14) are unicuspid, whereas the other six are bicuspid.

In his extensive study on the radula of the Helicinidae, Baker (1922) retained *Stoastoma*, provisionally placing most of the Chitty subgenera into its synonymy and claiming that it forms a connecting link between the subfamilies Vianinae and Helicininae. He pointed out further (1922: 58) that, "Since Chitty's description of the many species and 'genera,' the group seems to have received little attention." He also tentatively included *Lindsleya* in the synonymy of *Lucidella* because of a similarity in radular structure.

Subsequently, Baker (1934) again dealt with some of Chitty's generic taxa. He separated *Stoastoma s. s.* and considered *Fadyenia* at the generic level, allocating *Lewisia, Wilkinsonaea, Blandia, Petitia, Metcalfeia* and *Lindsleya* either into synonymy or to unclearly defined groups. For example, *Lewisia* was recognized as a subgenus of *Fadyenia* and *Wilkinsonaea* tentatively synonymized. Likewise, *Blandia* was assigned a subgeneric status with *Petitia* as a synonym. And lastly, *Fadyenia s. s.* included both *Metcalfeia* and *Lindsleya*.

Keen (1960) also considered these taxa. *Stoastoma s. s.*, with its exact synonym *Hemicyclostoma*, was referred to the nominate subfamily. *Fadyenia*, placed in the Ceratodiscinae, was divided into three subgenera: *Fadyenia s. s.* with *Lindsleya* and *Metcalfeia* as synonyms, *Blandia* with *Petitia* and *Wilkinsonaea* as synonyms, and *Lewisia*.

The study of the type-species of Chitty's genera indicates that there should be some rearrangement of the taxa. Based on the structure and morphological features of the shell, four distinct groups can be recognized and these characteristics are such as to be accorded generic rank.

As in other helicinids, the internal portion of the shell is absorbed in *Stoastoma*, a feature long ago pointed out by Bland (1858). The shells of most of the species described by Chitty and Adams are uniquely tiny and rather strongly sculptured. Accentuated surface features are apparently rather rare in the Helicinidae, having been noted in some *Emoda*-like forms which are accorded generic rank by Clench and Jacobson (1971). Among all the groups, *Stoastoma s. s.* is distinct in the size of the shell alone, being two or three times larger than any of the forms described by Chitty. Additionally there is a spur-like flaring of the base of the aperture (Fig. 3). The shell is heavy, strong, and globose. All of Chitty's other generic taxa differ in being smaller and more delicate.

Lewisia (Figs. 10–12) is distinguished by its lack of sculpture. Its smooth discoid or lens-like shell is distinctive. Additionally it is imperforate with the umbilicus sealed and with a spiral ridge extending to the base of the aperture. Chitty (1857) characterized *Lewisia* as being "Quasi double-mouthed." I imagine that he was referring specifically to a teratological specimen of *Lewisia agassiziana* C. B. Adams. The type-lot of this species (BMNH 54.4.24.473–474) contains two specimens, one of which has an unusual sac-like growth over the umbilical area. A similar structure also occurs in the unique (single) specimen of *L. macandrewiana* Chitty, according to his description. The dominant features of the type-species of *Lewisia*, i.e., its smooth, imperforate shell, are apparently not shared by the species that Chitty included in *Lewisia*, namely *agassiziana* C. B. Adams, *woodwardiana* Chitty and *macandrewiana* Chitty. These nominate species are sculptured; *Lewisia* may then be monotypic.

Likewise, *Wilkinsonaea* is most unusual (Boss, 1972). Of a depressed sub-discoidal shape, it possesses markedly strong spiral sculpturing or carinae in the form of ridges which terminate as bulbous, digitiform extensions of the aperture. With an open umbilicus, it preserves its unique nature by possessing a very unusual operculum, which is deeply concave, finely punctate and auriculate at both extremities. Also the last whorl is extraordinarily produced and detached from the body whorl.

All of Chitty's other generic taxa are synonymous and can be placed in *Fadyenia*, since it has page priority and Baker (1934) utilized it preferentially. The shells vary in size from the very small subdiscoidal *Stoastoma blandianum* with only 3½ whorls to the larger globose *S. lindsleyanum* with 5½ whorls. However, conchological features indicating a basic similarity among all the type-species include: a variably developed, but distinct sculpture consisting of numerous spiral striations; a detached portion of the last whorl; an irregularly semicircular aperture with the central margin smooth and more or less straight and the external margin frequently formed into a recurved lip and variously scalloped by the terminations of the spiral carinae; a relatively deep, open umbilicus. The taxa synonymized under *Fadyenia* include *Metcalfeia, Petitia, Lindsleya,* and *Blandia.*

In addition to the species of *Stoastoma, Wilkinsonaea, Lewisia,* and *Fadyenia* described by Chitty and C. B. Adams from Jamaica, several other West Indian forms have been ascribed to *Stoastoma.* Pfeiffer (1857: 51) described *S. portoricense* from the island of that name collected by Hjalmarson on a plantation near Manati. Crosse (1892: 46) remarked how this form links Puerto Rico and Jamaica zoogeographically. Although Dall and Simpson (1901: 447) cited its occurrence, van der Schalie (1948: 22–23, pl. 1, fig. 7) was the first to figure the species and provide a list of several localities. Apparently the species is not a marked calciphile, occurs at elevations to 3000 feet, and is predominantly distributed in the northern and western parts of the island. Although nominally placed in *Fadyenia* by van der Schalie, the shell is distinctly more highly spired than Jamaican species. Its small size, somewhat detached outer whorl, and umbilication show some affinity with Jamaican *Fadyenia.*

From Haiti, Weinland (1862) described *Stoastoma haitianum,* which was collected some distance from Jeremie in the southwest of the island; he stated that the species was related to *S. philippianum* C. B. Adams. Pfeiffer (1862), in his comments on Weinland's paper, remarked that this was an important find, considering the habitat. He related the species to *Metcalfeia,* particularly *S. chittyanum* C. B. Adams. Crosse (1891) also noted that with the occurrence of a species of *Stoastoma* on Haiti, the islands of Puerto Rico and Haiti were zoogeographically related to Jamaica. A second species from Hispaniola was described as *S. domingensis* by Vanatta (1920: 206, pl. 6, figs. 4, 5) from one mile NW of Sanchez, Santo Domingo. Although he did not mention Weinland's species, he compared the form with *S. leanum* C. B. Adams from

Jamaica, a species that Chitty (1857) had placed in *Lindsleya*. *S. domingensis* is very similar to *S. portoricense* and can be referred to *Fadyenia* on the same basis and with the same reservation that *portoricense* is.

An exceptionally tiny shell (0.7 mm in height) was described by Pilsbry as *S. atomus* (1930: 230, pl. 15, figs. 4, 4a, 4b). It was taken near George Town, Grand Cayman Island. Pilsbry placed the species in *Blandia* and stated that it was comparable to *S. blandianum* C. B. Adams. Indeed, a comparison of his figures with those of *S. blandianum* (Figs. 20-22) shows that the species are very similar, though *S. atomus* is decidedly smaller. Pilsbry also commented that though *Stoastoma* and its relatives belonged to the Helicinidae on the basis of the radula, they were unique in their "peculiar gait." In his list of Cayman Island land mollusks, Clench (1964) also included *S. atomus*.

Lastly Baker (1922) described a *Lucidella venezuelensis* from Palma Sola, Estado Falcon, Venezuela, which he referred to *Fadyenia* (*in litt.* to M. K. Jacobson, 17 Nov. 1949). Providing a figure of the shell and relating the species to *S. domingensis*, he recounted the species more thoroughly in 1923.

The three species, *venezuelensis*, *domingensis*, and *portoricense* are all quite similar to one another. Though tentatively placed in *Fadyenia*, they are distinguished from the Jamaican forms by being distinctly higher or more conic in shape, with a characteristically detached and somewhat depressed outer whorl. In contrast, Pilsbry's species from the Caymans is virtually conspecific with *blandianum*.

In summary, of the generic level taxa attributed to the so-called Stoastomidae by Chitty (1857), four genera, which are virtually restricted to Jamaica, are recognizable and retained in the Helicinidae: *Wilkinsonaea*, *Lewisia*, *Stoastoma* with its synonym *Hemicyclostoma*, and *Fadyenia* with its synonyms *Metcalfeia*, *Petitia*, *Lindsleya* and *Blandia*.

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Plate I.

Figures 1–3. The type-species of *Stoastoma s. s. Stoastoma pisum* C. B. Adams 1849, Monograph of *Stoastoma,* p. 11, lectotype, here selected, MCZ 177234, dia. = 3.7 mm, ht. = 3.3 mm; dorsal, apertural, and ventral views.

Figures 4–6. The type-species of *Lindsleya* Chitty. *Stoastoma lindsleyanum* C. B. Adams 1849, Monograph of *Stoastoma,* p. 12, lectotype, here selected, MCZ 177238, dia. = 2.6 mm, ht. = 2.2 mm; dorsal, apertural, and ventral views.

Figures 7–9. The type-species of *Metcalfeia* Chitty. *Metcalfeia metcalfeiana* Chitty 1857, p. 179, lectotype, here selected BMNH 57.12.1.218, dia. = 2.6 mm, ht. = 2.2 mm; dorsal, apertural, and ventral views.

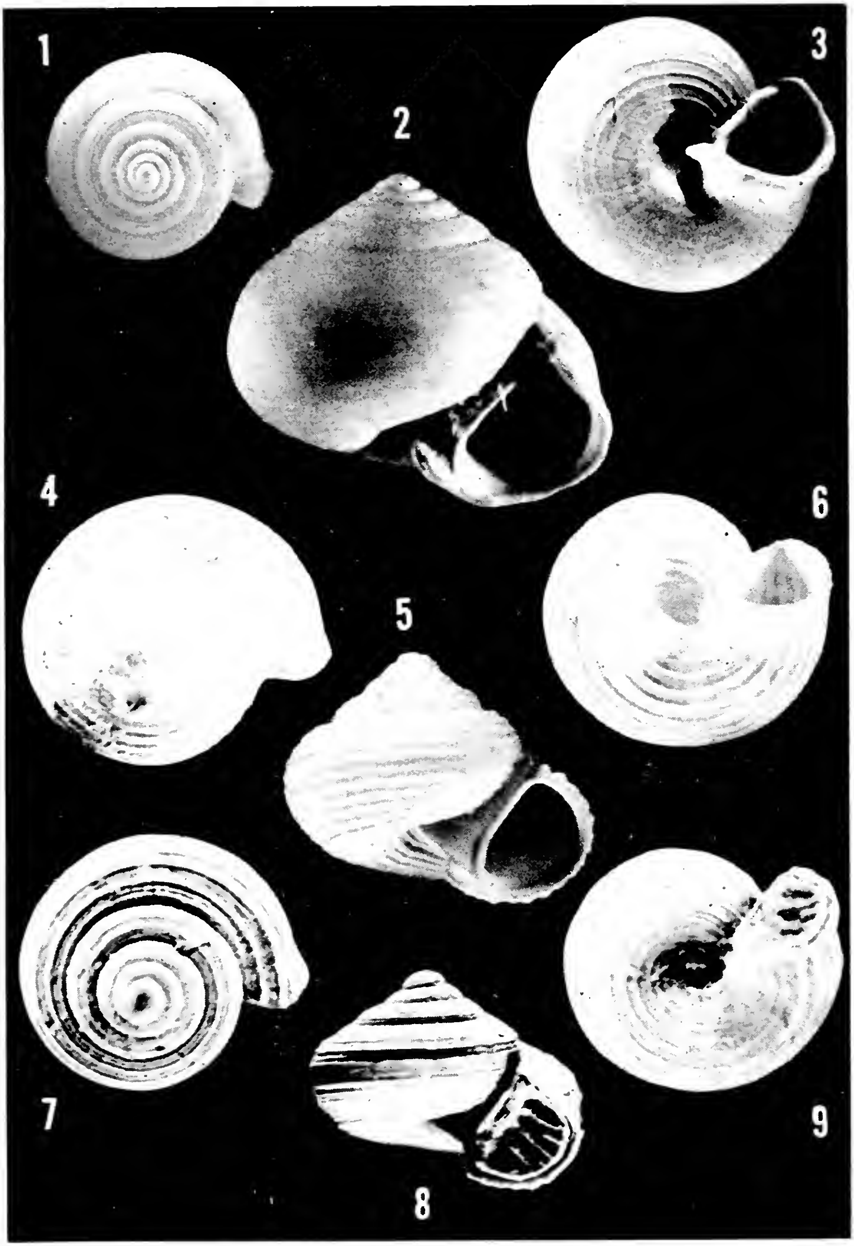
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Plate II.

Figures 10–12. The type-species of *Lewisia* Chitty. *Stoastoma philippianum* C. B. Adams 1851, Contributions to Conchology, 9: 158, lectotype, here selected, MCZ 177241, dia. = 2.2 mm, ht. = 1.1 mm; dorsal, apertural, and ventral views.

Figures 13–16. The type-species of *Wilkinsonaea* Chitty. *Stoastoma wilkinsoniae* C. B. Adams 1851, Contributions to Conchology, 8: 148, lectotype, here selected, MCZ 177251 (lost after photographs made), about 1.8 mm in diameter and 0.9 mm in height; dorsal, two apertural (showing protrusion of digitate aperture), and ventral views.

Figures 17–19. The type-species of *Petitia* Chitty. *Stoastoma petitianum* C. B. Adams 1851, Contributions to Conchology, 8: 151, lectotype, here selected, MCZ 177237, dia. = 1.7 mm, ht. = 1.1 mm; dorsal, apertural, and ventral views.

Figures 20–22. The type-species of *Blandia* Chitty. *Stoastoma blandianum* C. B. Adams 1849, Monograph of *Stoastoma,* p. 6, lectotype here selected, MCZ 177243, dia. = 1.3 mm, ht. = 0.7 mm; dorsal, apertural, and ventral views.

Figures 23–25. The type-species of *Fadyenia* Chitty. *Stoastoma fadyenianum* C. B. Adams 1849, Monograph of *Stoastoma,* p. 7, lectotype, here selected, MCZ 177233, dia. = 2.1 mm, ht. = 1.7 mm; dorsal, apertural, and ventral views.

All specimens were coated with magnesium before being photographed.


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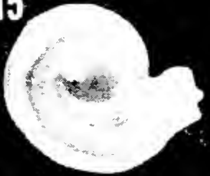
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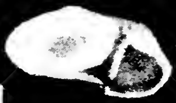
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B R E V I O R A

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THE CHAÑARES (ARGENTINA) TRIASSIC REPTILE FAUNA.

XV. FURTHER REMAINS OF THE THECODONTS *LAGERPETON* AND *LAGOSUCHUS*

Alfred Sherwood Romer

Abstract. Further fragmentary postcranial remains in the Chañares material attributable to the pseudosuchians *Lagerpeton chanarensis* and *Lagosuchus talampayensis* are described and figured. A sepcimen including a peculiar pelvis, hind leg, and vertebrae is described as *Lagosuchus lilloensis* sp. nov.

In addition to material definitely attributable to the seven thecodonts previously described in this series of papers on the Chañares fauna, various nodules collected in 1964–65 include numerous fragmentary remains of thecodonts, mainly of small size. I have gone over this series of specimens and attempted to identify such materials. Some apparently represent immature specimens of *Gracilisuchus* and *Chanaresuchus;* some remain problematical; still others seem certainly to pertain to the small thecodonts that I have described as *Lagerpeton chanarensis* and *Lagosuchus talampayensis* (Romer, 1971).

Lagerpeton chanarensis. I have previously described the type specimen, consisting of the slender hind leg of a small pseudosuchian in which the elongate pes differs from the typical pseudosuchian pattern in that digit 4 is longer than digit 3, and digit 1 is unusually short; I also mentioned the presence in the Instituto Lillo collections of an almost identical specimen. I may note that in the type the lengths of femur, tibia, and metapodials 1–4 are, in order: 77, 92, 8, 24, 45, and 48 mm.

Further materials apparently belonging to *Lagerpeton* are present in several Chañares nodules. In one nodule which, in addition to much of a gomphodont skeleton, included the type of *Lewisuchus admixtus* (Romer, 1972) and a few bones of *Lagosuchus,* there are materials that appear to pertain to *Lagerpeton*

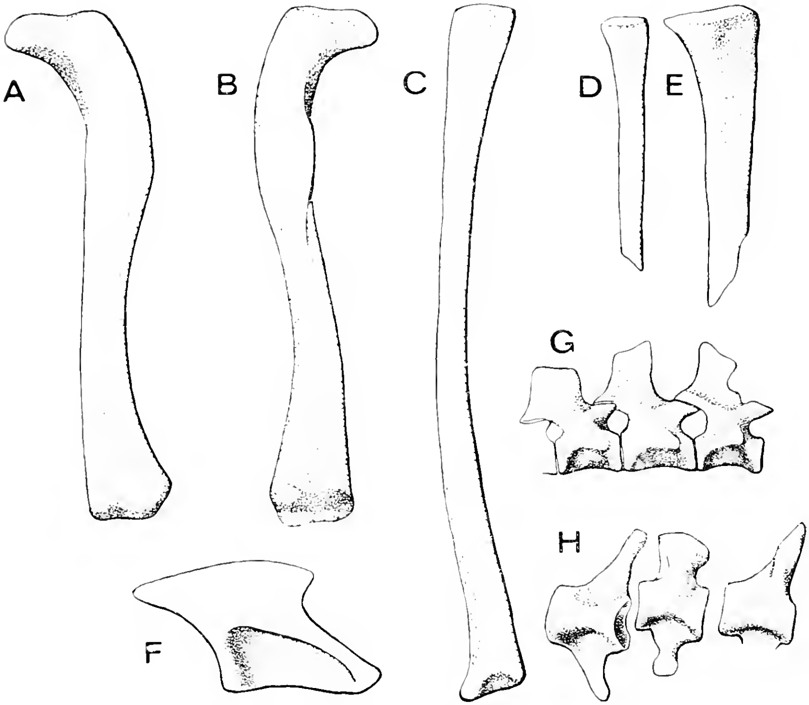

Figure 1. *Lagerpeton chanarensis.* Material in nodule with the *Lewisuchus* type. *A,* Left femur in dorsal view, head restored from right femur; *B,* the same in ventral view; *C,* fibula; *D,* partial fibula; *E,* partial tibia; *F,* right ilium; *G,* dorsal vertebrae; *H,* presumed sacrals, in ventral view. × 1.

(MCZ 4121), but represent an individual somewhat smaller than the two previously described (Fig. 1). Lying close together and presumably associated, they include two femora, with lengths of 58 and 62 mm, a fibula 84 mm long, proximal parts of a tibia and of a second fibula, a right ilium and part of the left, and a number of vertebrae. The limb elements compare well in structure with those of the type. The femur has a strongly developed sigmoid curvature, the head is well set off from the shaft, and the longitudinal ridge representing the fourth trochanter is well developed. The fibula is expanded distally for articulation with the tarsals. The acetabular cavity of the ilium, deeply incised, extends unusually far posterodorsally, and the inner surface of the bone is deeply grooved for the sacral ribs. There

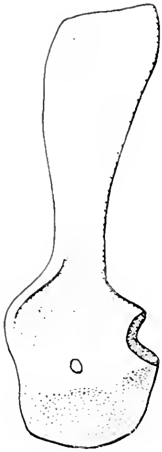

Figure 2. Left scapulocoracoid of *Lagosuchus talampayensis.* × + 3.

are several short series of vertebrae, rather imperfectly preserved. I figure several elements of a series of 12 dorsals, with mean central lengths of 7.5 mm. Near the right ilium are three vertebrae seen in ventral view, with central lengths of 6.5 mm; these bear short stout ribs, and are apparently sacrals. In the nodule, but somewhat separated, are remains of two scapulocoracoids, the better one of which is shown in Figure 2. This measures 42 mm in height. The scapular blade is relatively tall and narrow at the base. There is a modestly developed acromial ridge. Scapula and coracoid are firmly united, as preserved. The coracoid is deep dorsoventrally and narrow anteroposteriorly. The glenoid appears to face more directly backward than in most pseudosuchians.

MCZ 3691 is a slab mainly showing the confused remains of two partially articulated gomphodont skeletons. Present, however, are two pairs of slender tibiae and fibulae; none are completely preserved and exposed, but one tibia has, as far as visible, a length of 80 mm. These elements quite surely belong to *Lagerpeton.*

Lagosuchus talampayensis. The type remains of this form (Fig. 3) were contained on a slab (La Plata Museum 64-XI-14-11) that also includes the holotype of *Gracilisuchus stipanicicorum* (Romer, 1972). Present on the slab are incomplete remains of both hind legs and an incomplete humerus with articulated radius and ulna. Lengths of femur, tibia, and

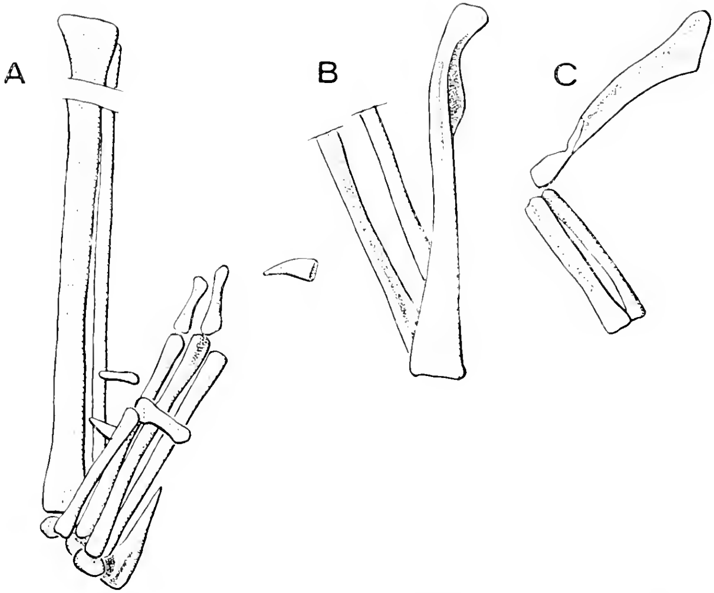

Figure 3. Holotype of *Lagosuchus talampayensis*. *A*, Tibia, fibula, and pes; *B*, femur and incomplete tibia and fibula; *C*, incomplete humerus, radius, and ulna. × 4/3.

metatarsals 1–4 are, in order: 38–39, 47–48, 15, 23, 26, and 25 mm. In the type only a few phalanges are preserved, but it was obvious from the metapodial lengths that digit 4 would have been slightly shorter than digit 3; metapodial 1, it will be noted, is relatively longer than in *Lagerpeton*. The foot restoration given in Figure 2 of my earlier paper (1971) was completed from the problematical Instituto Lillo specimen discussed below. Vertebrae present on this slab, which I previously thought pertained to this form, appear on closer study to be caudals of *Gracilisuchus*.

MCZ 4116 is a slab on which are numerous bones of *Gracilisuchus*. At one corner, however, are a few remains of *Lagosuchus*. These include: a femur 37 mm long closely resembling the type, articulated with which is the proximal end of a tibia; a series of dorsal vertebrae (Fig. 4); fragmentary remains of the pelvis. The vertebrae have central lengths of slightly over 5 mm.

In the Tucumán collections there is a hind leg that corresponds closely with the type in pattern. Measurements of femur, tibia,

Figure 4. *Lagosuchus talampayensis*, MCZ 4116. A series of dorsal vertebrae. × 2.

and metatarsals 2–4 are, in sequence: 42, 48, 24, 28, and 27 mm, thus closely approximating the holotype in size.

Lagosuchus lilloensis sp. nov.

This species is based on a specimen in the Instituto Lillo, Tucumán, collected by Sr. Bonaparte from the Chañares beds, and kindly loaned to me for study. Included are a complete right limb (Fig. 5), the left limb complete except for phalanges, a series of vertebrae including the sacral region and the proximal part of the tail (Fig. 6), and much of the pelvis. Except for larger size, the hind leg elements closely resemble those of the type. Length measurements of femur, tibia, and metatarsals 1–4 are, in sequence: 55, 71, 23, 35, 39, and 38 mm. The specimen is almost exactly 50 per cent larger than the holotype. If the lengths of the comparable elements of that specimen be multiplied by 3/2, we obtain: 57, 72, 22.5, 34.5, 39, and 37.5 mm. In view of this close correspondence in proportions, I felt justified in concluding that the two were specifically identical, used the foot of this Tucumán specimen in restoring the foot (Romer, 1971: fig. 2), and assumed that the small holotype was presumably a young individual, the present specimen an adult. Now, however, we have three specimens of femur of holotype size, only one larger. It is highly improbable that in a collection there would be three immature forms against only one adult. The differences are too great to be considered as sexual or due to individual variation. I am therefore forced to the conclusion that the present specimen represents a distinct species of *Lagosuchus*, which can be at present differentiated from the genotypic species only on the basis of its 50 per cent larger size.

The vertebral series preserved appears to be of normal thecodont type; the second and third of the series appear to be sacrals, with imperfectly preserved ribs and with central lengths of 6.5 mm; the caudals average 7 mm in central length. The

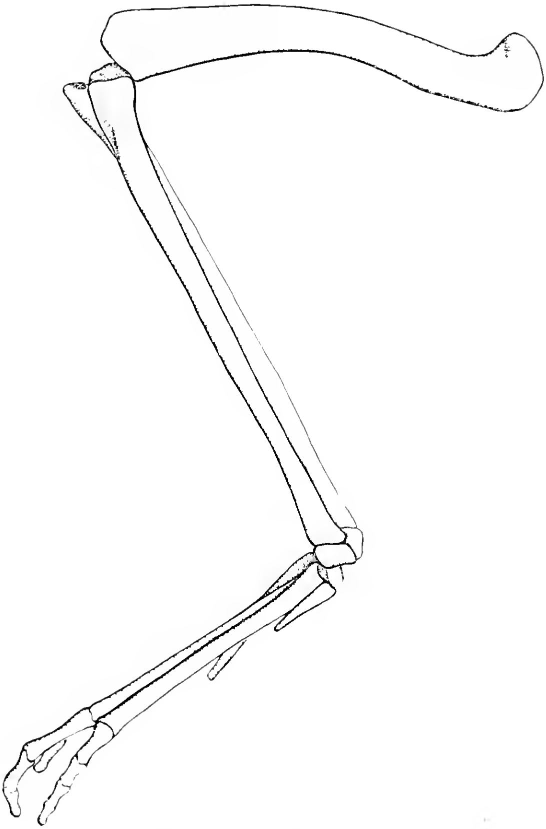

Figure 5. *Lagosuchus lilloensis,* holotype. Left hind leg, complete except for unguals. × 1.

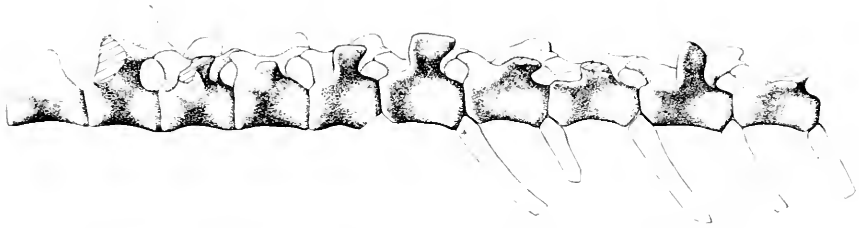

Figure 6. *Lagosuchus lilloensis*, holotype. A series of vertebrae including sacrum of proximal part of the tail. × 3/2.

first chevron present is between presumed caudals 3 and 4. Much of the pelvis is preserved. Interpretation of its peculiar structure should best be delayed until a more complete specimen is found.

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THE CHAÑARES (ARGENTINA) TRIASSIC REPTILE FAUNA. XVI. THECODONT CLASSIFICATION

Alfred Sherwood Romer

Abstract. The various non-phytosaurian genera of the order Thecodontia and Triassic crocodilians are reviewed and assembled in a classification. Four suborders of thecodonts are recognized: Proterosuchia, Parasuchia, Aetosauria, and Pseudosuchia.

Although it has long been agreed that the order Thecodontia is the basic stock from which arose the important later archosaur groups — dinosaurs, pterosaurs, crocodiles, and bird ancestors — we suffered until recent decades from a very limited knowledge of the membership of the order. Apart from the abundant phytosaurs of the late Triassic, we knew only a score or so genera of thecodonts, mainly late survivors. Today the picture is greatly changed, mainly owing to work in South America and Africa, so that we have about three times as many named non-phytosaurian thecodont genera (many, unfortunately, known from very incomplete materials). Further increases are certain to occur in the near future, as a result of recent and current work in a variety of regions: East Africa (Attridge *et al.*, 1964), Australia (Bartholomai and Howie, 1970), Antarctica (Kitching *et al.*, 1972), India (under the auspices of the Indian Statistical Institute), and North America. In consequence of this recent activity, a number of workers have been led to discuss the classification and phylogeny of the order. Summaries have been made by Rozhdestvenskii (1964) for the Russian treatise on paleontology, and by Hoffstetter (1955) for the French treatise. Huene has reviewed the group on numerous occasions (most recently in 1956 and 1962); Hughes (1963) has summarized postcranial patterns in basic members of the group; Walker has discussed the classification of thecodonts and primitive crocodilians in several papers (particularly 1968, 1970). My own recent studies of seven new Chañares genera (work supported by grants from the National Science Foundation) force me likewise to review the group. Which I do herewith.

The origin of the archosaurs is far from clear. Because they are diapsids they are frequently associated with the groups now generally termed Lepidosauria (Eosuchia, Squamata, Rhynchocephalia), but apart from the temporal region there is little resemblance between even the earliest representatives of the two groups. Except for a fragmentary late Permian specimen from Russia, there is no trace of an archosaur earlier than the *Lystrosaurus* zone at the base of the Triassic. Reig (1967, 1970) has advanced the theory that they were derived from the pelycosaur family Varanopsidae, closely related to the forms that gave rise to the therapsids; but as I have pointed out (1971d), nearly all the supposed points of resemblance that Reig cites are merely primitive reptilian features found in pelycosaurs and inherited by them (and by archosaurs) from primitive captorhinomorph cotylosaurs. *Petrolacosaurus* of the late Carboniferous (Peabody, 1952) very probably has a diapsid temporal region, and may possibly be related to the ancestry of either the lepidosaurs or archosaurs or both; but in other regards it is very primitive, differing little from romeriid captorhinomorphs, or their relatives among the pelycosaurs. There is a gap of a full period between the appearance of *Petrolacosaurus* and of either of the major diapsid groups.

It was long customary to divide the Thecodontia into two suborders, the Parasuchia, for the phytosaurs (relatively prominent in the group as known in older times), and the Pseudosuchia, in which were "lumped" all other members of the order. In recent decades it has become apparent that certain early and primitive types may well be separated from the more typical pseudosuchians to form a suborder Proterosuchia (cf. Reig, 1970), and some recent essays in classification have advocated still further subdivisions.

It was long believed by many workers (including myself) that there was from the beginning a strong trend toward bipedal progression in the archosaurs, and that quadrupedal members of the group were in general descended from bipedal ancestors. However, increasing knowledge of pre-Keuper thecodonts has weakened this assumption; the disproportionate development of the hind legs and the powerful tail may be interpreted as adaptations for an amphibious life (Charig, 1966;

Charig, Attridge, and Crompton, 1965; Charig, 1972). (*Mesosaurus* shows a parallel structure.) Certainly there was a strong trend toward bipedalism in advanced thecodonts, leading to bipedal dinosaurs, to birds and to pterosaurs, but various thecodonts were definitely quadrupeds, and rather surely quadrupedal progression in crocodilians and very probably in sauropod dinosaurs is primitive.[1]

Primitive thecodont characters. Hughes, as mentioned above, reviewed the postcranial features expected in primitive archosaurs, and Reig in 1970 gave an excellent account of primitive archosaur structure, which I summarize below.

The maxilla excluded from the external naris by the premaxilla; no septomaxilla; an antorbital fenestra of moderate size; postfrontal and postparietal present but no supratemporal or tabular; parietal foramen at best small (and generally lost); two temporal openings; the quadrate extends upward to be socketed beneath the squamosal; the lateral temporal opening with a "straight" posterior margin slanting backward ventrally and bounded by a union of squamosal and quadratojugal; the jaw articulation behind the level of the posterior margin of the lateral fenestra. The basal articulation of the palate moveable, and an interpterygoid vacuity persistent; palatal teeth reduced (and soon lost); an external mandibular fenestra almost always present; teeth subthecodont. The vertebrae never notochordal, and generally no more than mildly amphicoelous. Ribs double headed, the tuberculum arising from the transverse process, which becomes prominent in the dorsal region; the capitulum anteriorly arising low down in the centrum, but rising posteriorly to close in on the tuberculum and to move onto the base of the transverse process. A powerful tail.

The coracoid a simple single element, with a rounded border. The pubis always turned downward more than in the oldest reptiles, but primitively with retention of a considerable area of puboischiadic junction. The acetabulum closed. Lack of strong inturning of femoral head, suggesting that the proximal limb segments were still directed somewhat laterally rather than in a plane parallel to the body. As in primitive reptiles generally, the front legs rather shorter than the hind. The gait quadrupedal. The tibia shorter than the femur, the hind foot short, the toes perhaps somewhat spreading. Astragalus and calca-

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[1] Ceratopsians are rather surely secondary quadrupeds, and this, I believe, was probably the case with other ornithischian quadrupeds.

neum both well developed, the primitive nature of the joint between leg and foot uncertain.

Advanced thecodont characters. Within the order Thecodontia there are obviously many advances from the primitive structural situation, and since the thecodonts are by definition the stem group from which the various dinosaur types, the crocodilians, pterosaurs, and bird ancestors have been derived, we would expect a wide variety of diverse patterns in the order, were it fully known. As yet we have no clear indication of lines leading toward pre-avians, pterosaurs, or ornithischians; but saurischian dinosaurs are merely logical outgrowths of patterns obvious amongst thecodonts, and there are numerous indications of the development of crocodilians and pre-crocodilians among Triassic archosaurs. Some of the advanced or aberrant trends seen among thecodonts leading toward and to true saurischians or crocodilians may be listed.

Variations in snout length; entry of maxilla into narial border; backward movement of external nares dorsally; variations in development of antorbital vacuity; reduction of upper temporal opening; modification of lateral temporal opening, by forward angulation of quadratojugal and quadrate; forward movement of jaw articulation; loss of palatal teeth; loss of mobility of basipterygoid articulation; closure of palatal vacuities; modification of teeth from the simple primitive pattern to a less predaceous type; general loss of intercentra behind the axis; increase in sacrals; development of proximal accessory processes on ribs; increased down-turning of pubis and loss of continuity of puboischiadic plate; increasing length and slenderness of limbs; increased disproportion of hind limb over fore; excess of length of tibia over femur; elongation of metatarsals; trend toward an avian type of hind foot. A few of these "advances" are specializations, but many represent a trend in progressive forms toward a saurischian condition. Certain characters are indicative of conditions leading toward and to the Crocodilia, including reduction of antorbital vacuities, further modification of the lateral temporal region to produce the crocodilian type of otic notch, development of a secondary palate, posteroventral development of coracoid, lengthening of proximal carpals, and exclusion of pubis from the acetabulum.

Below, I review briefly the known genera of non-phytosaurian thecodonts and Triassic "pre-crocodiles," arranging most of them in provisional family groups and higher categories.

Proterosuchidae. If one wishes to sort out a basic group of

Thecodontia as a suborder Proterosuchia, it is *Proterosuchus* (of which *Chasmatosaurus* Haughton [1924a] is the better known synonym)[1] to which one turns for a primitive form. *Proterosuchus* has long been known from the early Triassic *Lystrosaurus* Zone of South Africa (Broom, 1903); a good account of the skull is that of Broili and Schroeder (1934), and Cruickshank (1972) has just described an excellent skeleton. The genus is also present in India (where fragmentary remains were early described as *Ankistrodon* and *Epicampodon* [Huene, 1942]), and in China (Young, 1936, 1958, 1963). *Elaphrosuchus* (Broom, 1946; Brink, 1955) is a close South African relative. Except for the overhang of the premaxilla and the somewhat excessive length of the snout, *Proterosuchus* is almost a diagrammatic primitive archosaur, and in the retention of dorsal intercentra is even even more primitive than other proterosuchian types. It lacks, however, the almost universal archosaur external mandibular fenestra (present, however, in *Elaphrosuchus*). Presumably related to *Proterosuchus*, but known only from very incomplete material, are *Chasmatosuchus* (Huene, 1940) from the early Triassic of Russia and, notably, *Archosaurus* (Tatarinov, 1960) from the late Permian of that region — the oldest known archosaur.

Proterochampsidae. I have recently discussed this family (Romer, 1971c, 1972a). *Chanaresuchus* is an adequately known form; *Gualosuchus*, also from the Chañares beds, is similar. *Cerritosaurus* from the Santa Maria beds (Price, 1946), known only from the skull, is obviously closely related; possibly Huene's (1944) genera *Procerosuchus* and *Rhadinosuchus* (cf. Hoffstetter, 1955) represent postcranial material of the same form. *Proterochampsa* (Reig, 1959; Sill, 1967) from Ischigualasto, has been described from relatively poor material, but is certainly a close relative. *Proterochampsa* was claimed by Reig and Sill to be a pre-crocodilian, but thought by Walker (1968) to be a pre-phytosaur; Walker (1968, 1970) suggests *Cerritosaurus* as a possible pre-crocodilian (although he is puzzled by the nostril position). There is, however, no real indication of crocodilian relationships in any member of the family, and only dorsal migration of the nostrils is positively suggestive of phytosaur relationship (see below). The proterochampsids are long-snouted amphibious forms which have advanced little beyond

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[1] Recent rediscovery of the lost type of *Proterosuchus* has definitely confirmed this long-questioned synonymy (Cruickshank, 1972).

the proterosuchian grade of organization and may well be placed in the Proterosuchia.

Erythrosuchidae. Apart from the genus *Proterosuchus* the only well known form which it is universally agreed pertains to the Proterosuchia is *Erythrosuchus,* from the Cynognathus beds of the Karroo, first described by Broom (1906), but more exhaustively treated by Huene (1911; cf. Brink, 1955). *Erythrosuchus* in a number of regards is as primitive as *Proterosuchus,* but a bit more advanced in, for example, loss of dorsal intercentra and loss of palatal teeth. Although the skull and postcranial skeleton of this reptile are incompletely known, we are obviously dealing here with quite a different sort of animal. The skull is short and massively built, the jaw articulation is still placed well posteriorly, and the lateral temporal opening is primitively built. The body is short and heavily built, the limbs short and stout. The dentition is carnivorous in type; dicynodonts were the obvious prey.

In recent years several genera, imperfectly known, have been described from the early Triassic of Russia. Tatarinov (1961) believes them to be generically identical with *Erythrosuchus,* including *Dongusia* (Huene, 1940, founded on a single vertebra), *Garjainia* (Otschev, 1958) and *Vjushkovia* (Huene, 1960). Included here also by some writers are genera that I discuss below under the rubric Prestosuchidae.

Prestosuchidae (Rauisuchidae). As knowledge of Middle Triassic thecodonts increased, it gradually became apparent that there continued throughout much of the Triassic period a series of relatively primitive thecodonts of large size, with large skulls, short legs, and a persistently quadrupedal posture. This was early realized by Huene, who tended to confuse such forms with larger members of the aetosauroid group, but nevertheless erected the family Rauisuchidae for certain thecodonts of this sort. The first able discussion of such a group was that of Reig (1961); Young (1964) expressed similar views, and the evidence for the existence of such a group is increasing. *Rauisuchus* (Huene, 1944) is poorly known and doubts as to its position have been expressed; in consequence, the term Prestosuchidae (Charig, 1957), based on a better known Santa Maria genus *Prestosuchus* (Huene, 1944), is preferable. *Saurosuchus* from Ischigualasto, first described by Reig (1959) and now being restudied by Sill, is reasonably placed in the same group, as is the fragmentary *Luperosuchus* skull from the Chañares beds (Romer, 1971a). A beast of similar nature, if not referable to the Erythrosuchidae, is *Shansisuchus* of China (Young, 1964). The headless thecodont skeleton from the Cacheuta basin of Argentina, first described by Rusconi (1951) and incongruously associated by him with the skull of a flat-headed labyrinthodont, is obviously in the same general category and has been named *Cuyosuchus* by Reig (1961). Quite surely a member of the group is *Ticinosuchus* (Krebs, 1965), the only good skeleton of a thecodont from the Middle Triassic of Europe. *Hoplitosaurus* [*Hoplitosuchus*] (Huene, 1944) is represented by poor material from the Santa Maria beds, but probably belongs in this family. So very likely do *Mandasuchus* (Charig, 1957), *Stagonosuchus* (Huene, 1938), and *Pallisteria* (now being described by Charig), represented by incomplete materials from the Manda beds of East Africa, as well as *Fenhosuchus* (Young, 1964) from China. *Spondylosoma* from the Santa Maria (discussed below) may belong here (Charig, 1957).

Putting together data from the various genera mentioned, we may characterize the prestosuchids as being the largest thecodonts of (roughly) Middle Triassic times. In the massively built skull the premaxilla sends a strong flange upward posterior to the naris, broadly excluding the maxilla from that opening. In *Saurosuchus* and, apparently, in *Luperosuchus*, a slit is present here between premaxilla and maxilla, and in the skull of *Shansisuchus*, as restored by Young, this slit appears to have developed into a good-sized vacuity. The jaw articulation is apparently nearly directly below the plane of the posterior margin of the lateral temporal fenestra, which is of a primitive nature, with little or no trend for development of an otic notch. The palate is primitive, with a mobile basal articulation, but palatal teeth have been lost. The vertebrae are short throughout the presacral column. The limb girdles are relatively primitive, with some retention of a puboischiadic plate, although the pubis is well turned ventrally. The limbs are short, although the hind limbs are somewhat longer than the fore; the femur is distinctly longer than the tibia, the humerus longer than the radius. The pose was quadrupedal; the main joint between limb and hind foot lay between astragalus and calcaneum. The foot was plantigrade, with the toes short and spreading, and little or no digital reduction. Large dorsal osteoderms were present.

This attempt at definition is to some degree composite, but will apply, as far as known, to the forms already mentioned. The prestosuchids, as here assembled, may be a rather heterogeneous group. It seems certain that they are of proterosuchian, and presumably erythrosuchid, derivation, and some of the genera noted above may actually prove to be members of the Erythrosuchidae; certainly they should be included in the Proterosuchia.

Huene (1944) points out, as does Krebs (1966), that the prestosuchid type of foot is of the sort that could have made the *"Cheirotherium"* footprints abundant in the early Triassic (Soergel, 1925), and not improbably all footprints of this sort were due to prestosuchids or their erythrosuchid ancestors.

Were the prestosuchids a sterile group? They surely have nothing to do with the ancestry of ornithischians, crocodilians, pterosaurs and birds, or theropod dinosaurs. Under the once popular hypothesis that sauropods were of bipedal ancestry, relationship with these forms too would be ruled out. But Charig *et al.* (1965) have presented a strong case for a continuous quadrupedal ancestry for the sauropods. The picture is still a cloudy one; but it is not impossible that it may one day prove that the erythrosuchid-prestosuchid line plodded on, with change, through the Triassic to become ancestors of the sauropods.

Phytosauridae (Belodontidae). The phytosaurs, or Parasuchia, were the first thecodonts to be at all well known, and they have retained prominence in the order. This is mainly due to the fact that they are confined (with one possible exception) to the late Triassic redbeds of Europe, North America, India, and China and it is from these beds in Europe and North America that, until recently, nearly all thecodont material was derived. More than 30 genera have been described, and despite work by Gregory (1962), Westphal (1963) and, finally by Gregory and Westphal combined (1969), the generic situation is still none too clear. Their general structure, in which there is relatively little variation, can be clearly seen in such works as those of McGregor (1906), Camp (1930), and Colbert (1947). Their general proportions (and probable habits) were similar to those of crocodilians of later periods. The body is low-slung, the limbs short (with, as in thecodonts generally, the front limbs shorter than the hind), the gait, when out of the water, definitely quadrupedal. The limb girdles were persistently primitive in nature (except for an anterior incisure in the coracoids) and the puboischium still retains much of its primitive platelike condition. Heavy armor was developed. The palate was persistently primitive, but the anterior portion of the skull was greatly specialized; there was great snout elongation, but with breathing facilitated by movement of the nares far back along the skull roof.

The phytosaurs flourished greatly in the northern continents during the late Triassic, only to be superseded by the crocodilians, already evolving at that time. Despite our considerable knowledge of late Triassic faunas in South Africa and Argentina, no positive evidence of the presence of phytosaurs is known in the "Gondwanaland" regions except for peninsular India. Isolated dermal plates from Madagascar have been compared with those of phytosaurs (Guth, 1963; Westphal, 1970), but they may equally well pertain to prestosuchids. The discovery by Jaekel (1910) of a phytosaur, *Mesorhinus*, in the early Triassic Bunter has been disturbing, and doubts have been cast upon its age and phytosaurian nature (Gregory, 1962). But recent work appears to have confirmed the stratigraphy, and in view of the wide radiation of archosaurian types which we now see to have taken place well before the close of the Triassic, the appearance of a possibly primitive phytosaur by the end of Bunter times seems reasonable.

Aetosauridae (Stagonolepidae). The aetosaurs are a well-defined group; *Aetosaurus* from the German Keuper (Fraas, 1877) has long been well known, and Walker (1961) has recently given an excellent description of *Stagonolepis* from the Elgin Triassic. Other late members of the family which appear to be relatively unspecialized are *Neoaetosauroides* (Bonaparte, 1969a, 1972) from the Los Colorados of Argentina and, apparently, *Stegomus* (Jepsen, 1948; Walker, 1961) from the Newark series. Earlier is *Aetosauroides* from Ischigualasto, with which *Argentinosuchus*, described also by Casamiquela (1960, 1961, 1967), may be synonymous (Bonaparte, 1972). In the American late Triassic are large aetosaurs with exaggerated armor — *Typothorax* [*Episcoposaurus*, ?*Acompsosaurus*] and *Desmatosuchus* (Sawin, 1947; Gregory, 1953). The diagnostic features of the aetosaurs are obvious — nearly complete armor sheathing; a short-legged quadrupedal gait; a relatively primitive pelvic structure; a toothless, rather piglike snout; large nares; deeply incised antorbital vacuities; retention of at least some basipterygoid movement; teeth modified from the general thecodont pattern. The lateral temporal opening is of interest. It is merely a small triangular affair, behind which the quadratojugal extends broadly upward and markedly forward, to come close to a contact with the postorbital. This situation suggests that in this regard the temporal region has gone through an evolutionary process similar to that which I have suggested for *Gracilisuchus* (Romer, 1972b).

There are no known intermediates between aetosaurids and other thecodonts, although the group cannot be traced back of the stratigraphic level of the Ischigualasto beds. The heavy armor suggests some possible relationship to other types in which armor is present (pre-crocodilians, phytosaurs, ornithosuchids) but no close relationship is apparent. The "advanced" nature of the lateral temporal region suggests some relationship to forms in which the original, essentially quadrilateral shape of the lateral fenestra had become modified; but this feature may have evolved in parallel fashion. The strictly quadrupedal nature of aetosaurids suggests that they branched off from other thecodonts at a very early stage, possibly directly from proterosuchian ancestors. But evidence is lacking.

The aetosaurs are generally included in the Pseudosuchia. But it is, I think, preferable to restrict this term to forms of advanced nature, tending toward and to a bipedal condition, and consider, as Reig (1970) has done, that these aberrant forms constitute a separate suborder Aetosauria.

Euparkeriidae. Euparkeria [*Browniella*] of the Cynognathus zone of South Africa (Broom, 1913), recently thoroughly restudied by Ewer (1965), is one of the most interesting of thecodonts. As pointed out by Hughes (1963) and Reig (1970) as well as Ewer, *Euparkeria* retains a large number of primitive proterosuchian characters — palatal teeth and dorsal intercentra, for example. But, on the other hand, this lightly built little reptile is a reasonable ancestor for the true pseudosuchians of more advanced nature which flourished throughout the later stages of the Triassic. Early authors invariably placed *Euparkeria* among the pseudosuchians. Hughes, Ewer, and Reig would include it in a "horizontal" type of classification in the basic proterosuchian group. This is perfectly acceptable; but I tend to class it as a primitive but true pseudosuchian, associating it with the more advanced forms to which it, or its close relatives, gave rise.

No further form has been placed with certainty in the Euparkeriidae. Young (1964) would assign here *Wangisuchus* from the Sinokannemeyeria beds of China. The remains are fragmentary, but indicate the presence of a long-legged pseudosuchian at an early Triassic stage, and the assignment may well be correct.

Ornithosuchidae. Ornithosuchus from the Elgin beds (with which Walker believes *Dasygnathus* to be synonymous) has been excellently redescribed by Walker (1964). Recently

(1972b) I have described a small early ornithosuchid, *Gracilisuchus*, from the Chañares beds of Argentina; Bonaparte (1969a) has described as an ornithosuchid *Riojasuchus* from the Los Colorados, and an Ischigualasto genus, *Venaticosuchus* (Bonaparte, 1972).

As best seen in little *Gracilisuchus* and the larger and later *Ornithosuchus*, we are dealing with gracefully built archosaurs, in which the slender hind legs and long slender hind toes suggest that these forms were at least partially bipedal. The skull is rather advanced in nature with a large and deeply recessed antorbital vacuity. It has a palate in which motility on the braincase has been lost and the pterygoids reach the midline; the posterior border of the lateral temporal fenestra is pronouncedly V-shaped. Notable is the presence of stout paired armor plates firmly sheathing the dorsal surface of the vertebrae. Walker has ably argued for considering *Ornithosuchus* as a primitive carnosaurian saurischian dinosaur. I have elsewhere, however, expressed doubts about this (as do Bonaparte, 1969b; Reig, 1970) and currently tend to believe that the ornithosuchids are more properly to be considered as one of several probable lineages amongst advanced thecodonts which were approaching the theropod level of organization, but were not direct theropod ancestors. *Ornithosuchus* itself is too late in time to be ancestral to essentially contemporary theropods; further, I think it is doubtful that the characteristic dorsal plating, acquired early in the Triassic, would be abandoned.

Various other genera have been suggested as members of this group. Walker, on the assumption that *Ornithosuchus* is a true dinosaur, suggested that the late Triassic carnosaurs *Teratosaurus* and *Sinosaurus* were members of this family; this seems very doubtful. *Parringtonia* (Huene, 1939) of the Manda is known only from very fragmentary material, but in what we know of it, it is comparable with the nearly contemporaneous *Gracilisuchus*. A form which may belong here is *Dyoplax* from the Keuper (Fraas, 1867). This is known mainly from a poorly preserved skull and a series of paired dorsal dermal plates. Because of the plates, it has frequently been assigned to the aetosaurid group. But there is no evidence of other armor; the plates are comparable to those of ornithosuchids; and significantly, the cervical ribs are of exactly the specialized overlapping type seen in *Gracilisuchus*.

Scleromochlidae. Far removed from most other pseudosuchians is tiny *Scleromochlus*, known only from bones and bone impressions in nodules from Elgin; first described by Smith Woodward in 1907, it was later restudied (with a restoration) by Huene (1914a). The trunk and neck are short; in contrast, the legs are extremely long — even the front legs, despite the fact that there is the usual disparity in length between front and hind legs. Huene's skull restoration is mainly hypothetical, as is that of the feet (except for the definite close apposition of the four long metatarsals). It is tantalizing — but at present useless — to speculate as to the possible relationships of this little reptile to the ancestry of the birds or the pterosaurs.

It is not impossible that *Lagerpeton* (Romer, 1971b) is related; it is almost equally small, lightly built, and very long-legged.

Miscellaneous pseudosuchians. Among pseudosuchians, in a narrow sense of that term — that is, thecodonts progressing toward or to a bipedal condition — we have discussed the Ornithosuchidae and the very different form *Scleromochlus.* These are clearly defined types, meriting distinction at the family level. In addition, however, are a number of forms which do not belong to either of these families, but show varied advances over the primitive thecodonts toward bipedality and may well represent a series of separate families. Family names have been given to such forms in several instances, but at the moment it seems inadvisable to recognize such families, and *pro tem* they may be simply listed as Pseudosuchia *incertae sedis.*

Erpetosuchus [*Herpetosuchus*], known only from a single specimen from Elgin (Newton, 1894; Walker, 1970), is quite distinctive. The antorbital fenestra is highly developed; the teeth are restricted to the anterior part of the jaws. Most notable is the temporal region; the lateral temporal opening is reduced to a ventral triangle, which is quite unrelated to the crocodilian type of modification but rather to the type of emphasis on the forward-turned V-shaped modification seen in major development in *Gracilisuchus.*

Lewisuchus, although represented only by a fraction of a skull and incomplete skeleton (Romer, 1972c), is distinctive. It is primitive in such features as a persistently moveable basipterygoid articulation and a lateral temporal opening of primitive nature; it is nevertheless well advanced in a bipedal direction and is perhaps tending toward the coelurosaurs. *Teleocrater* from the Manda, which Charig (1957) suggests as a possible coelurosaur ancestor, may be related.

Lagosuchus from the Chañares beds (Romer, 1971b), known from little but the hind leg, appears to be an advanced pseudosuchian of some sort.

Triassolestes from the Ischigualasto beds was thought by Reig (1963, 1970) to be a dinosaur. There is no proof of this, and placing this form in the Thecodontia seems more reasonable. Bonaparte (1972) states that nearly complete skeletal remains are known. Bonaparte notes that there are elongate proximal carpals and hence he is inclined to ally it with *Sphenosuchus* and other pre-crocodilians. But there are no further postcranial similarities to the crocodiles, and the skull is quite uncrocodilian in build.

Hesperosuchus (Colbert, 1952) is poorly known cranially, but is obviously a somewhat advanced pseudosuchian not closely related to the genera already mentioned. Bonaparte (1969a, 1972) and Walker (1970) believe it to be related to *Pseudhesperosuchus*, and to pre-crocodilians.

Saltoposuchus (Huene, 1921) is shown by Huene in restoration as if completely known; as may be seen, however, from Huene's text, this pseudosuchian is quite inadequately known and its relationships essentially indeterminate. It has dorsal armor but apparently not of ornithosuchid type. Walker (1970) suggests crocodilian relationships, but does so without adequate reason for this assignment.

Strigosuchus and *Dibothrosuchus* are names given by Simmons (1965) to poorly known forms from the late Triassic of China which are presumably pseudosuchians of some sort.

Thecodontia incertae sedis. There exists a variety of named Triassic genera, represented mainly by highly incomplete materials, which are probably thecodont in nature but cannot be satisfactorily placed in any specific group. Thus, for example, *Seemannia* (Huene, 1958) and *Crenelosaurus* (Ortlam, 1967) have been (regrettably) based on isolated teeth from the Bunter, and Rusconi (1947b) has given the name *Ocoyuntaia* to a tooth from the Cacheuta beds of Argentina. This last author (1947a) has given the name *Typothorax*? *punctulatus* to a good-sized dermal plate from the Cacheuta region; very likely tooth and plate pertain to prestosuchids. Welles (1947) has described as *Arizonasaurus* an archosaurian maxilla from the Moenkopi Formation of Arizona; with this he tentatively associated other materials, some possibly archosaurian, one definitely not. *Clarencea* (Brink, 1959) was founded on an imperfect skull, apparently of peculiar type, from the late Triassic of South Africa; it is probably a thecodont, but of uncertain relationships.

Ctenosauriscus [*Ctenosaurus*] from the Bunter (Huene, 1914c) consists of a vertebral column with tall spines; it has often been compared with pelycosaurs, but Krebs (1969) points out that it is archosaurian in nature, not pelycosaurian; not as yet fully described is a comparable vertebra, termed *Hypselorhachis* (Charig, *in* Harland *et al.* 1967), from the Manda beds. A trend toward spine elongation is not uncommon in archosaurs, as seen in the dinosaurs *Spinosuchus* from the late Triassic of Texas and *Spinosaurus* from the Egyptian Cretaceous.

Huene (1944; cf. Bonaparte, 1972) applied the generic name *Spondylosoma* to an assortment of bones, mainly fragmentary, from the Brazilian Santa Maria beds, and assigned the genus to the Saurischia. There is no guarantee that all the assortment belong to one type of animal (certainly not to one individual), and it is not improbable that we are dealing with thecodont material. Huene has on several occasions described fragmentary materials from the Muschelkalk which he belived to be coelurosaurian or pelycosaurian; considering their age, they may equally well pertain to thecodonts.

Elachistosuchus (Janensch, 1949) was described as a thecodont, but is now recognized to be a rhynchocephalian (Walker, 1966). *Anisodontosaurus* (Welles, 1947) from the Moenkopi is sometimes classed among the thecodonts but there is no evidence to warrant this.

I feel incompetent to discuss the probable systematic position of *Podopteryx*, based on a partial skeleton from the Mesozoic of Siberia which appears to have had membranes between the hind legs and tail and which Sharov (1971) assigns to the Pseudosuchia, or of *Longisquama*, with long scaly "plumes" projecting from its back which Sharov (1970) also considers a pseudosuchian.

Primitive crocodile relatives are frequently confused with thecodonts, are difficult in some cases to separate from them, and may be discussed here.

Protosuchidae (Stegomosuchidae). Apart from forms in which crocodilian characters are less marked or of doubtful significance, we find in the later Triassic of most continents forms that are unquestionably members of the Crocodilia, although primitive in some features. Typical skull features are seen in the African genera *Notochampsa,* and the closely related if not identical *Erythrochampsa* (Broom, 1904, 1927; Haughton, 1924a, 1924b), and *Orthosuchus* (Nash, 1968). *Protosuchus* (Colbert and Mook, 1951) is represented by a nearly complete skeleton, and a reinterpretation of the skull roof (Walker, 1968, 1970) shows excellent agreement with the African genera. Walker (1968) has restudied the difficult material of *Stegomosuchus* from the Newark series, and believes this previously problematical genus to belong to this group. *Platyognathus* from China (Young, 1944; Simmons, 1965), although imperfectly known, seems to follow the same pattern and hardly merits the erection of a separate family for its inclusion. *Microchampsa* (Young, 1951; Simmons, 1965) is a small form represented only by vertebrae and armor plating, but as far as can be seen is reasonably placed here.

As far as the material permits, all these protosuchids show a long series of crocodilian characters: postcranially, elongation of the coracoid, elongation of proximal carpals, exclusion (or near exclusion) of the pubis from the acetabulum, and good development of dermal armor; in the skull, a flattened table, presence of supraorbital bones, small antorbital fenestrae, considerable development of a secondary palate; and, most notably, the forward movement of the upper end of the quadrate (and quadratojugal), deep to the surface, to form the typical crocodilian otic notch, closed behind in more advanced members of the order.

Although "priority," as Walker points out, would insist on the use of Stegomosuchidae as the family name, common sense and usage speak for retention of Protosuchidae. The family certainly stands in an ancestral position to the more familiar crocodilians and is reasonably regarded as forming a primitive suborder (or infraorder) of the Crocodilia as the Protosuchia.

Sphenosuchidae (Pedeticosauridae). Apart from the forms just discussed, which are quite surely primitive crocodilians, there are a number of other Triassic genera which exhibit crocodilian features in less positive fashion. Best known and most important here is *Sphenosuchus* (Haughton, 1915, 1924b; Huene, 1925; Broom, 1927; Walker, 1970) from the Upper Triassic of South Africa. The skull shows the forward inclination of the quadrate expected in a crocodile ancestor; the quadratojugal is reduced (rather prematurely); the antorbital vacuity is small; the postfrontal is lost; the basipterygoid articulation is fused; there is some development of a secondary palate; the postcranial skeleton is incomplete, but the coracoid is crocodilian, and Walker, *in litteris*, tells me of further features that indicate crocodilian relationships.

With this genus Walker associates *Pedeticosaurus*, likewise from the late Triassic of South Africa (Van Hoepen, 1915; Haughton, 1924b). This is known only from a single imperfect skeleton, in which the incompletely preserved lateral temporal opening resembles that of *Sphenosuchus*. A further clue as to relationships lies in the fact that in both genera there is an enlarged mandibular tooth at about the level of the premaxillary-maxillary suture. *Hemiprotosuchus* (Bonaparte, 1969a, 1972) from the Los Colorados of Argentina has a similar skull, and like the last two genera has an enlarged lower "canine." For this family Walker uses the term Pedeticosauridae; it seems unfortunate to base the family on this poorly known form rather than on the much better known *Sphenosuchus*.

Walker (1970) and Bonaparte (1969a, 1972) have suggested crocodiloid relationships for several other Triassic genera such as *Hesperosuchus*, *Saltoposuchus*, and *Triassolestes*. As noted earlier, there seems to be little evidence for such assignment of these genera. A much better case can be made out for *Pseudhesperosuchus* (Bonaparte, 1969a, 1972) from the Los Colorados beds, because of the presence of an elongate coracoid and elongate proximal carpals. The skull, however, is not at all crocodilian.

To treat forms that have crocodiloid tendencies, but are not advanced to the typical protosuchian level, Walker (1970) divides the order, which he terms the Crocodylomorpha, into two suborders, one, Crocodilia, including proper crocodiles plus Protosuchia, and a second suborder, Paracrocodylia, in which are placed *Sphenosuchus* and *Pedeticosaurus* and their supposed allies, plus *Baurosuchus* and *Hallopus*. Discussion of these last two forms is beyond the scope of the present review, but provisionally I think we may treat other forms that are trending from the typical thecodont pattern toward that of the crocodiles as members of the Protosuchia in an expanded use of that term.

A summary of the above discussion may be made in the form of a tentative outline of classification of thecodonts and primitive crocodilians:

Order Thecodontia
  Suborder Proterosuchia
    Family Proterosuchidae (Chasmatosauridae): *Archosaurus*, *Elaphrosuchus*, *Chasmatosuchus*, *Proterosuchus* [*Ankistrodon*, *Epicampodon*, *Chasmatosaurus*].
    Family Proterochampsidae: *Cerritosaurus*, *Gualosuchus*, *Chanaresuchus Proterochampsa*, ?*Procerosuchus*, ?*Rhadinosuchus*.

Family Erythrosuchidae: *Erythrosuchus* [*Dongusia*, *Garjainia*, *Vjushkovia*].

Family Prestosuchidae (Rauisuchidae): *Prestosuchus*, *Rauisuchus*, *Saurosuchus*, *Luperosuchus*, *Ticinosuchus*, *Mandasuchus*, *Cuyosuchus*, *Shansisuchus*, *Hoplitosaurus* [*Hoplitosuchus*], *Fenhosuchus*, *Stagonosuchus*, *Pallisteria*, ?*Spondylosoma*.

Suborder Parasuchia (Phytosauria)

Family Phytosauridae (Belodontidae): *Mesorhinus* of probably early Triassic age and various Upper Triassic genera.

Suborder Aetosauria

Family Aetosauridae (Stagonolepidae): *Aetosaurus*, *Aetosauroides* [?*Argentinosuchus*], *Desmatosuchus*, *Neoaetosauroides*, *Stagonolepis*, *Stegomus*, *Typothorax* [*Episcoposaurus*, ?*Acompsosaurus*].

Suborder Pseudosuchia

Family Euparkeriidae: *Euparkeria* [*Browniella*], ?*Wangisuchus*.

Family Ornithosuchidae: *Gracilisuchus*, *Venaticosuchus*, *Riojasuchus*, ?*Parringtonia*, *Ornithosuchus* [?*Dasygnathus*, *Dasygnathoides*], ?*Dyoplax*.

Family Scleromochlidae: *Scleromochlus*, ?*Lagerpeton*.

Pseudosuchia, presumably representing a number of distinct families: *Lagosuchus*, *Hesperosuchus*, *Lewisuchus*, *Saltoposuchus*, *Strigosuchus*, *Dibothrosuchus*, *Teleocrater*, *Erpetosuchus* [*Herpetosuchus*], *Triassolestes*.

Possible Thecodontia, *incertae sedis: Seemannia*, *Ctenosauriscus* [*Ctenosaurus*], *Spondylosoma*, *Arizonasaurus*, *Ocoyuntaia*, "*Typothorax punctulatus*," *Crenelosaurus*, *Hypselorhachis*, *Podopteryx*, *Clarencea*.

Order Crocodilia

Suborder Protosuchia

Family Protosuchidae (Stegomosuchidae): *Protosuchus* [*Archaeosuchus*], *Notochampsa*, *Erythrochampsa*, *Orthosuchus*, ?*Platyognathus*, *Stegomosuchus*, ?*Microchampsa*.

Family Sphenosuchidae (Pedeticosauridae): *Sphenosuchus*, ?*Pedeticosaurus*, *Hemiprotosuchus*.

Protosuchia?, *incertae sedis: Pseudhesperosuchus*.

POSTSCRIPT

While this paper was in page proof, I received a copy of an excellent paper by Bonaparte describing reptiles, mainly thecodonts, from the Upper Triassic Los Colorados Formation of Argentina. It is mainly devoted to thecodonts. It will be noted that his paper went to press before he had received my recent papers on Chañares thecodonts in this series. For the most part our conclusions are in essential agreement. He gives an account of the skeleton of *Riojasuchus* which he assigns to the family Ornithosuchidae, as well as *Venaticosuchus* and possibly *Parringtonia.* Of *Pseudhesperosuchus,* previously known only from a preliminary description, he gives an account of the skull and much of the postcranial skeleton. He definitely assigns this genus to the Sphenosuchidae (which he retains in the Pseudosuchia), as he does *Hesperosuchus,* whereas I have considered *Pseudhesperosuchus* as doubtfully allied to the Sphenosuchidae and have kept *Hesperosuchus* in the Pseudosuchia in a narrower sense and see no reason to ally these two forms. The description of the skull of *Hemiprotosuchus* shows clearly that it is a primitive "crocodiloid," but whereas I included it in the Sphenosuchidae, Bonaparte would place it in the somewhat more more advanced family Protosuchidae.

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BREVIORA

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THE CHAÑARES (ARGENTINA) TRIASSIC REPTILE FAUNA. XVII. THE CHANARES GOMPHODONTS

Alfred Sherwood Romer

Abstract. Much of the gomphodont material in the Chañares collections appears to pertain to two closely related but distinct species, *Massetognathus pascuali* and *Massetognathus teruggii.* An especially large skull is described as *Massetognathus major,* sp. nov. Two skulls represent a distinct form, *Megagomphodon oligodens,* gen. et sp. nov., differing mainly in its smaller but more numerous cheek teeth.

As noted previously, a large proportion of the reptilian remains from the Chañares beds pertain to the peculiar gomphodont side branch of the Cynodontia, abundant in all Middle Triassic terrestrial faunas. Although much of the 1964–65 collection from these beds was, because of political complications, long delayed in shipment, the one box that reached the laboratory promptly contained a number of gomphodont skulls, on the basis of which I described two species as *Massetognathus pascuali* and *Massetognathus teruggii* (Romer, 1967). The skull materials then available sorted out clearly into two size groups, differing in skull length by about 40 percent. This figure was too great to be due to sex differences, and since there were in this sample of the collection no intermediates in size between the two groups, erection of two species seemed fully justified.

Today, with the full collection available, a much larger array of gomphodont skull material lies before me, and a re-study of the situation is called for. In many instances in vertebrate paleontology, specific diagnoses have been made on supposed size differences when only a few specimens were known, only to be proved invalid when more abundant material became available. Might that not be the case here? Two large specimens prove to be of a distinct type (described below) but most appear to pertain to *Massetognathus* and show a wide variation in size. They are here tabulated according to skull length measured to the condyles. Owing to imperfections in the material or incomplete preparation, this measurement was available only in a fraction of the cranial specimens, but in a number of other cases this basal length could be calculated fairly accurately from other measurements.

Table I. *Massetognathus* CRANIAL SPECIMENS GROUPED BY BASAL LENGTH, IN MM.

61– 70 mm	1
71– 80 mm	11
81– 90 mm	16
91–100 mm	13
101–110 mm	8
111–120 mm	6
121–130 mm	4
131–140 mm	5
141–150 mm	2
151–160 mm	1
161–170 mm	4
200–210 mm	1

In any population of living reptiles or any adequate sample of a fossil form, the size distribution is a characteristic one; the great proportion of the specimens represent young adults, but in addition there are present a few forms of somewhat greater size, presumably older individuals in which further growth had occurred. To some degree our distribution is of the type that suggests a single species, with the greater part of the specimens concentrated in the size range attributed in my earlier paper to *M. pascuali*, the holotype skull of which measured 87 mm in length. But in two regards the collection does not agree with the assumption that we are dealing with a single species. (1) In a typical one-species population only a very few "elderly" individuals are present far above the "young adult" size; here nearly half of the specimens extend onward toward sizes far exceeding that of the young adults. (2) Even excluding the single extra-large skull tabulated, these larger specimens run upward to a skull size about double that of "young adults" of *M. pascuali* — a situation quite out of the range of possibility of size increase in any known reptile population. It seems certain that in these larger specimens we are dealing with representatives of a second species, *M. teruggii*, less abundant than

M. pascuali, but of larger size — the holotype skull of *M. teruggii* measuring 125 mm in basal length.

Confirmation of this conclusion is given by a consideration of the "molar" dentition. In many cases the lower jaws are firmly occluded with the upper, so that (in default of difficult preparation) the tooth surfaces are not clearly seen. However, the "molars" are visible in surface view in a number of specimens of both the smaller, *M. pascuali*, and of the larger, *M. teruggii*, types. In the *M. pascuali* specimens the typical "molars" have an anteroposterior width which averages close to 3 mm; those of *M. teruggii* average 3.75 mm. Further, Mr. John Hillman, who has studied gomphodont dentitions intensively, pointed out to me that in the *teruggii* specimens the "molars" are also proportionately broader mediolaterally than in the smaller *M. pascuali* specimens.

It is highly improbable that this increase in individual molar size could occur during the lifetime of an individual. There is almost no evidence of any vertical replacement of these very deep-rooted teeth in the adult. There is evidence here, as in other gomphodonts, of a trend for suppression of one or two of the smaller anterior "molars" during the lifetime of an individual, and for the addition of one or more teeth at the posterior end of the series. But there is no indication of development of the complex type of tooth replacement found in the manatee, by which a whole series of "molars" might be replaced by larger successors pushing forward from the back end of the series. If such replacement were to occur, we would expect the new teeth added at the back of the series to increase in size. For the most part the "molars" in the back part of the series are larger than those anteriorly placed. But Mr. Hillman, who has made careful measurements of the *Massetognathus* dentitions, tells me that in a number of instances the last one or two teeth in the series are smaller, rather than larger, than those anterior to them.

Apart from the two species of *Massetognathus* discussed above, the Chañares gomphodont series certainly includes other variants. As discussed below, two specimens appear to represent a form generically distinct from *Massetognathus*. And in addition, the specimens assigned to that genus are quite surely not all assignable to *M. pascuali* and *M. teruggii*. As mentioned above, the *M. teruggii* type has a skull length of 125 mm. We would reasonably expect a number of older individuals to exceed this figure to a modest degree, up to about 160 mm or so — that is,

Figure 1. The holotype skull of *Massetognathus major* in dorsal view. × 2/5.

to a skull length of as much as 30 percent in excess of a "young adult." But the finding of four specimens in the 160–170 mm bracket is disturbing, and a skull of over 200 mm in length — two-thirds again as large as the type — gives us an impossible situation. We have here, quite certainly, a third, large species.

Massetognathus major sp. nov.

Holotype: La Plata Museum, No. 64-XI-14-15, (field no. 55). From the Chañares formation, about 4 km southeast of the mouth of the Rio Chañares, La Rioja Province, Argentina.

Diagnosis. Generally comparable to other species of *Massetognathus*, but orbits extend relatively far forward, antorbital region narrower than in other species; cheek tooth rows less divergent posteriorly; size large, the holotype with a basilar skull length of 205 mm.

The species is based primarily on a single skull (Figs. 1, 2) far larger than any other assigned to this genus. The specimen

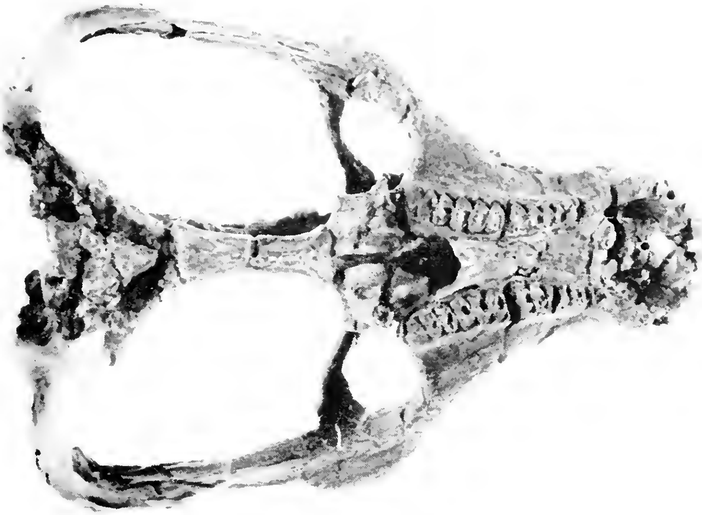

Figure 2. The holotype skull of *Massetognathus major* in ventral view. × 2/5.

was found exposed with the palatal surfaces upward, and in a somewhat weathered condition, so that the cheek teeth do not show the crown pattern well, and the posterior part of the skull is imperfectly preserved. In most regards the skull agrees well with the previously described species of *Massetognathus*. Distinctive, however, is the relative narrowness of the snout and a consequently lesser development of the broad shelf which, in ventral view, extends far out on either side of the cheek tooth series. The series of cheek teeth are but little curved, and diverge but little posteriorly. The orbits, instead of being essentially subcircular in outline, extend forward in triangular fashion, with the apex of the triangle lying at the entrance to the lacrimal duct. In relation, presumably, to large size, the sagittal crest is well developed, the ridges bounding the temporal openings fusing medially a short distance back of the postorbital bar, with complete obliteration of the parietal foramen. Thirteen cheek teeth are present on either maxilla; the most anterior are rela-

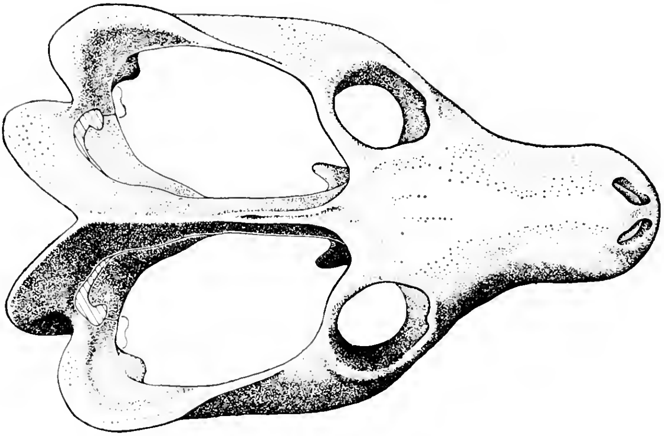

Figure 3. The skull of *Megagomphodon oligodens* in dorsal view. This figure and figs. 4–6 are composites, based on the holotype and MCZ 4138. × 2/5.

tively smaller in size, as compared with those farther back, than is the case in either *M. pascuali* or *M. teruggii*.

Megagomphodon oligodens gen. et sp. nov.

Holotype: La Plata Museum No. 64-XI-14-16, (field no. 65). Chañares formation, La Rioja Province, about 6 km ENE of the mouth of the Rio Chañares.

Diagnosis. A relatively large traversodontid gomphodont, with a basal skull length on the order of 180 mm. Cheek teeth relatively small, especially anteriorly, and about 17–18 in number. Skull relatively slender, the width across the orbital region being but about two thirds the total skull length.

In the collection two skulls, the holotype and MCZ 4138, represent a gomphodont type clearly distinct from *Massetognathus.* Incomplete jaws, but no postcranial materials, are associated with both. Neither is too well preserved; the holotype has fairly well preserved cheek teeth, but is imperfect posteriorly; the posterior part of the braincase is preserved in MCZ 4138, but teeth are represented only by their roots. My description is based on a combination of features present in one skull or the other, and my illustrations (Figs. 3–5) are likewise composite. On neither skull are the sutures well shown, and I have in consequence omitted most of them in my figures.

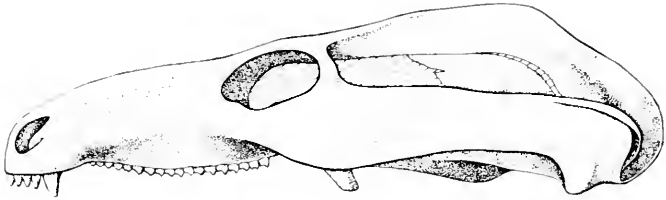

Figure 4. The skull of *Megagomphodon oligodens* in lateral view. × 2/5.

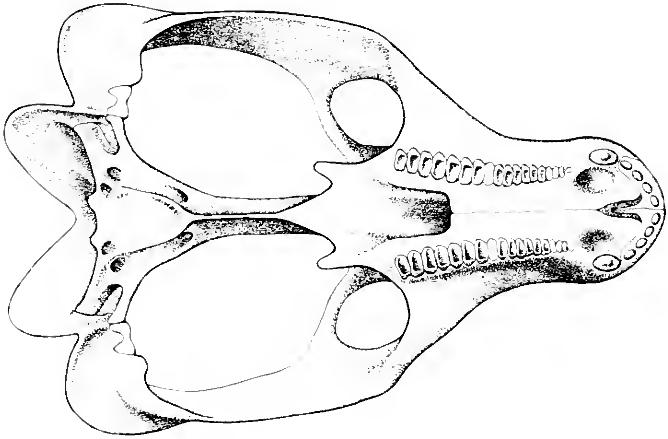

Figure 5. The skull of *Megagomphodon oligodens* in ventral view. × 2/5.

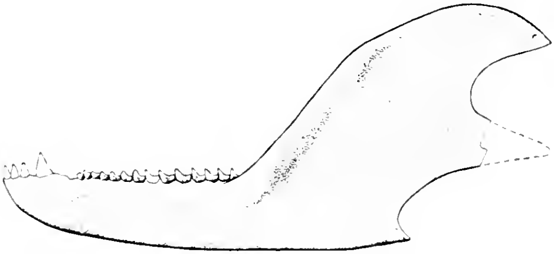

Figure 6. The dentary of *Megagomphodon oligodens* in lateral view. × 2/5.

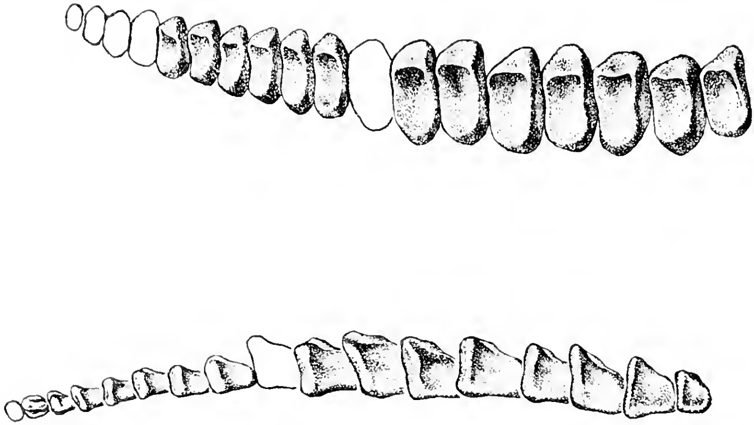

Figure 7. Left upper and lower cheek teeth of *Megagomphodon oligodens.* × 3/2.

The skull is somewht more slender than in *Massetognathus.* The "muzzle" is notably narrow, with a constriction back of the canine region, and expansion in width does not take place until well back toward the subcircular orbits. In correlation with large size, the sagittal crest is well developed, with the two crests becoming closely apposed not far back of the level of the postorbital bar.

Dentaries are preserved in both specimens (Fig. 6). The "angular" region is well developed, and in MCZ 4138 has a backwardly pointed tip. As in all traversodonts the ascending ramus is highly developed, and extends far back dorsally. In most specimens of Chañares gomphodonts in which the bone is well preserved, the posterior end of the ramus is rounded; in both specimens of the present form this process is sharp-tipped posteriorly. On the inner surface of the dentary there is a longitudinal recess, typical of advanced cynodonts, for the reception of the supporting bar formed by surangular + angular + prearticular.

The most distinctive feature of this genus is the nature of the cheek teeth (Figs. 5, 7). These are numerous, and in the holotype, where the dentition is nearly completely preserved, there appear to be 17 or 18 "molars" in both upper and lower jaws. This is, of course, a definitely higher count than in *Massetognathus.* On the other hand, the individual teeth are definitely smaller than in that genus. The length of the entire row of upper cheek teeth is about a third of the skull length in this form and in *Massetognathus* as well; but since the number of teeth in *Megagomphodon* is greater, the anteroposterior dimensions of individual teeth is relatively small; the average anteroposterior length of an individual tooth in *Massetognathus* is about 3 percent of the skull length, in *Megagomphodon* only about 2 percent. The *Megagomphodon* teeth are also relatively small in transverse measurement; the broadest teeth in this genus measure only about 4 percent of skull length, whereas this width in *Massetognathus* is approximately 5 percent.

Except for the reduced tooth size, *Megagomphodon* is obviously not distantly related to *Massetognathus* and this genus may perhaps have been derived from such a form as *M. major*.

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Romer, A. S. 1967. The Chañares (Argentina) Triassic reptile fauna. III. Two new gomphodonts, *Massetognathus pascuali* and *M. teruggii*. Breviora, Mus. Comp. Zool., No. 264: 1–25.

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XYLOREDO, A NEW TEREDINID-LIKE ABYSSAL WOOD-BORER (MOLLUSCA, PHOLADIDAE, XYLOPHAGAINAE)

RUTH D. TURNER

ABSTRACT. *Xyloredo*, a new genus of Xylophagainae characterized by having a long burrow with a calcareous lining, is described. Three new species belonging to this genus are also described, *Xyloredo nooi* and *X. ingolfia* from the Atlantic and *X. naceli* from the Pacific. The systematic position of the genus, its superficial resemblance to the Teredinidae, and the factors controlling the distribution of the species are discussed.

INTRODUCTION

The Xylophagainae are benthic, mainly deep-sea wood-borers. Their distribution is dependent on the presence of woody plant material and their dispersal on the free-swimming larval stage. From available evidence it appears that wood in the deep sea is scarce and its distribution patchy. Bruun (1959) reported on the remnants of plant material collected by the R/V GALATHEA during a circumnavigation of the globe. J. Knudsen (1961) reported on the *Xylophaga* collected on that cruise and also discussed the presence of plant debris in the deep sea, summarizing the results of earlier expeditions. An analysis of the data in these reports shows that 56 of the 180 successful bottom stations made by the GALATHEA in depths between 400 and 7290 meters yielded plant material. Only 22 of these hauls had woody material of sufficient size (e.g., over 10 grams) to support borers, but species of *Xylophaga* were taken at only 11 stations.

On the basis of material now available, the ranges of many of the species in this subfamily appear to be limited. The known ranges may be a reflection of the limited number of dredging stations but may also be because 1) the dispersal efficiency of the larvae is poor (J. Knudsen, 1961) and 2) wood in the deep sea is not only scarce but is found in "islands" of plant debris, usually in deep trenches near land, particularly in the regions of large rivers (Bruun, 1959). In order to better understand the distribution of these borers, we need to know more about their life history, particularly the length of time the larvae spend in the plankton and their behavior at the time of settlement.

Most *Xylophaga* are obtained by dredging, though a few species occurring in high latitudes can be found in shallow water, some even just subtidally in old wrecks or piling (Tomlin, 1920; Dons, 1929a, 1929b, 1940). In 1961 H. Turner attached a series of wood panels to the mooring line of a buoy set out by the Woods Hole Oceanographic Institution at 39°30′N; 69°40′W (on the Gay Head, Martha's Vineyard-Bermuda transect) in 3000 meters. When the panels were retrieved in October 1961, the bottom one was found to have been heavily attacked by *Xylophaga* (approximately 100 per square centimeter). This was the first time that "new" wood had been submerged to such a depth sufficiently rapidly so that there was no possibility of the larvae settling on the way down. Unfortunately, the specimens were too young for positive identification and no additional panels have been exposed at this site. About the same time the United States Navy began testing the performance of various materials, including wood, in the deep sea (DePalma, 1969; Muraoka, 1964–1967). These tests at depths of 1000 to 2000 meters have added greatly to our knowledge of the Xylophagainae and resulted in the discovery of a new genus, represented by three new species. Species in this new genus (*Xyloredo*, p. 3) are remarkably close to the teredinids in superficial appearance, as they produce long, often tortuous tunnels which have a calcareous lining; the valves, as in all Xylophagainae, are teredinid-like. The lack of pallets for closing the burrow and of apophyses for the attachment of the foot muscle, and the presence of a mesoplax, definitely place them in the Pholadidae, subfamily Xylophagainae.

Though mentioned in the literature (R. Turner, 1966a, 1969), this new genus was not named or described. Specimens of *Xyloredo nooi* (p. 5), the first new species to be received, were taken from tests put out by the U. S. Naval Oceanographic Office in the Tongue of the Ocean, Bahama Islands, in 1737 meters (DePalma, 1969). At this site, panels set in contact with the bottom were completely riddled, while those 15 meters off the bottom were entirely free of borers. Wood panels submerged by the U. S. Naval Civil Engineering Laboratory south of San Miguel Island off Port Hueneme, California, in 2072.6

meters were the source of the second new species, *Xyloredo naceli* (p. 9). At this site, panels 15 centimeters off the bottom were much more severely attacked by two species of xylophagaids than those only one meter up on the rack (Muraoka, 1966b). Tipper (1968), working with *Xylophaga washingtona* Bartsch off the Oregon coast, found that the number of borer penetrations dropped most markedly within the first 6 centimeters above the bottom. These findings suggest that the larvae probably remain close to the bottom throughout their free-swimming stage and that, except in areas where there are strong bottom currents, they probably are not widely dispersed (R. Turner, 1966b, 1968).

Xyloredo ingolfia (p. 7), the third new species belonging to this genus, came from a piece of wood dredged in 1896 by the INGOLF Expedition south of Eyrabakki, Iceland, from 1783 meters. This species appears to be more closely related to the California species than to the one from the Tongue of the Ocean.

As with many species of molluscan wood-borers, it is difficult to determine which characters of the species of *Xyloredo* will prove most stable and useful for taxonomic purposes until large series from several localities, representing all growth stages, are available for study. As intimated above, wood-borers from great depths are difficult to obtain, and such series may not be available for many years. In fact, the publication of the taxa included in this report has been delayed for five years while efforts were made to obtain additional material. Hopefully, knowledge of the existence of these remarkable Xylophagainae will stimulate personnel on dredging cruises and deep submersible dives to collect and preserve woody plant material. In addition to borers, dredged wood is a rich source of many species of benthic invertebrates.

Xyloredo[1], new genus

Type species. *Xyloredo nooi* Turner, new species.

Description. Valves typical of subfamily Xylophagainae and virtually indistinguishable from valves of *Xylophaga*; apophyses lacking; chondrophore, internal ligament, umbonal-ventral sulcus and ridge, and ventral condyle well developed. Mesoplax

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[1] A compound word, combining *Xylo-* *from* *Xylophaga* and *-redo* from *Teredo*, indicating the teredinid-like appearance of these Xylophagainae.

small, flat, triangular and only lightly calcified. Burrow, depending on size and age of specimen, 5 to 30 times length of valves. Posterior two-thirds of burrow with calcareous lining marked with distinct rings and covered by thin, outer periostracal layer which extends anteriorly as border (Plate 1, fig. 2). Periostracal covering of valves extending posteriorly as sheath that is continuous with heavy periostracal band on anterior end of tube. Mantle fold attached to anterior end of tube, point of addition of both periostracum and calcium. Burrow lining in very young specimens either entirely periostracal or lightly calcified.

Combined incurrent and excurrent canals extend length of tube and attach to calcareous lining at anterior end of siphons. Siphons short, separate and apparently margined with few cirri.

Visceral mass similar to *Xylophaga* (Purchon, 1941; Turner and Johnson, 1971), contained completely between valves. Ctenidium of single demibranch nearly covering sides of visceral mass. Mouth broad and slitlike; labial palps inconspicuous. Esophagus short, wide, and flattened; stomach large, subglobular, with large crystalline style sac opening into it at posterior end. Style sac bent forward so that lower end protrudes slightly through visceral mass posteroventral to foot. Caecum large, U-shaped, and located mainly on the right side.

Remarks. The general description of the anatomy of *Xyloredo* given above was derived from a study of the remains of specimens of all three species. Unfortunately none was sufficiently well preserved for detailed dissection or sectioning.

Xyloredo differs from *Xylophaga* by having: 1) a long, teredinid-like burrow with a calcareous lining, 2) a thin periostracal sheath extending from the valves to the heavier periostracal border of the tube, and 3) extended incurrent and excurrent canals. The siphons of *Xyloredo* are short and separate, and when the animal is removed from its burrow it resembles a shipworm without its pallets.

Unlike the Teredinidae, *Xyloredo* has short, broad ctenidia, and all of the visceral mass is contained between the valves; a mesoplax is present but pallets and apophyses are lacking. In addition, the calcareous tube of *Xyloredo* is thin, regularly ringed, and covered externally with a shiny periostracum.

The superficial resemblance of *Xyloredo* to the Teredinidae is a result of convergence. The Xylophagainae are probably most closely related to the Jouannetinae, a subfamily of rockboring pholads, which also lack apophyses and have the pedal retractor muscle inserted in the typical bivalve position anterior to the posterior adductor muscle.

The discovery of this teredinid-like genus of Pholadidae necessitates a reexamination of fossil teredinids, especially those with ringed tubes. If valves are not present, or if the inner surface of the valves cannot be examined to ascertain whether apophyses are present, it may be impossible to distinguish fossil *Xyloredo* from the Teredinidae. It is, of course, possible that all fossil tubes with regular rings are *Xyloredo* or some closely related fossil genus. Many teredinid tubes are marked with rings, but not in the regular, evenly spaced fashion found in *Xyloredo.*

Fossil deposits produced in the deep sea are virtually unknown, so perhaps there is no need to be concerned about fossil *Xyloredo*. However, like *Neopilina*, it might well be that at one time their ancestors lived in shallower waters. It is possible that, as a result of competition with the more efficient Teredinidae, only the deep-water species survive.

Range. Species of *Xyloredo* are known in the Atlantic Ocean from off Iceland and from the Tongue of the Ocean, Bahama Islands. In the eastern Pacific they are known only from off San Miguel Island, near Port Hueneme, California. *Xyloredo* may well be world-wide in distribution in depths of over 1500 meters, but further dredging and testing are needed to prove this.

Xyloredo nooi[1], new species

Plates 1 and 2

Type locality. From test panels submerged in the Tongue of the Ocean (25°54′N; 77°49′W), off the north end of Andros Island, Bahama Islands, in 1737 meters, from 4 April 1962 to 17 February 1965 (DePalma, 1969).

Types. Holotype, Museum of Comparative Zoology 279631. Paratypes from the same and other panels exposed at the same locality, Museum of Comparative Zoology 279632, 279633, 279634, 279635, and the Universitetets Zoologiske Museum, Copenhagen.

Description. Shell globose, valves reaching 10 mm in length and 10.5 mm in height, thin, fragile; umbos prominent. Perio-

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[1] An acronym based on the initials of the Navy Oceanographic Office, Washington, D.C., which was responsible for the tests in the Tongue of the Ocean, Bahama Islands, from which the specimens were obtained.

stracum relatively thick, golden brown, glistening and covering entire valve. Beaked portion of anterior slope sculptured with numerous, finely denticulated ridges (24 ridges on holotype). Posterior portion of anterior slope narrow; ridges closely spaced, coarsely denticulated, usually thickened posteriorly and extending only about one-half distance to shallow umbonal-ventral sulcus. Disc sculptured with fine growth lines only. Posterior slope high, reflected near dorsal margin and sculptured with fine growth lines. Umbonal reflection thin, wide and adhering closely to surface of valves posteriorly, free anteriorly.

Inner surface of valves smooth and glistening. Umbonal-ventral ridge narrow, high, slightly to strongly segmented and not greatly enlarged at ventral condyle. Chondrophore and internal ligament prominent (Plate 2, fig. 5). Disc separated from posterior slope by pronounced groove extending from umbo to posterior ventral margin. Posterior adductor muscle scar large, elliptical, and divided; upper part (on reflected portion of posterior slope) with irregular impressions, lower part with chevron-shaped impressions. Anterior adductor muscle scar covering umbonal reflection. Siphonal retractor muscle scars not impressed. Pedal retractor muscle scar elongate, located about midway on anterior margin of posterior adductor muscle scar. Mesoplax small, consisting of two flat, broad, subtriangular plates lying on dorsal surface of anterior adductor muscle and composed largely of periostracum.

Burrow long, teredo-like, with thin, calcareous lining for about three-fourths its length. Tubular lining marked with distinct rings and covered with thin, yellow-brown periostracum which extends as border anteriorly (Plate 1, fig. 2). Portion of animal between valves and tube covered by smooth, golden-brown, periostracal sheath, continuous anteriorly with periostracum of valves and posteriorly with periostracal border of tube. Tubes of young specimens (up to 10 mm long) may be entirely periostracal. Burrow opening on surface of wood with white, slightly raised, often divided cone about 1 mm in diameter. Siphons short and separate. Protoconch unknown.

Valve measurements.	Length	Height	
	9.5 mm	10.0 mm	Holotype
	9.5	9.8	Paratype
	7.2	7.8	"
	6.7	6.9	"
	5.0	5.1	"

Remarks. This species is closely related to both *Xyloredo naceli* and *X. ingolfia* (see also *Remarks* under *ingolfia*). It differs from them in having a much thinner burrow lining, a high, reflected posterior slope on the valves, and a proportionately smaller, more highly placed and divided posterior adductor muscle scar. In addition, the periostracal sheath extending between the valves and the calcareous tube is smooth. On the basis of the material at hand, *nooi* appears to be a much larger species. Size in borers, however, is often not a reliable taxonomic character, and an understanding of the size range requires the examination of large series from varied substrata. Stenomorphic adults often result from over-crowding or from penetration of an unusually hard substance.

The panels from which specimens of *nooi* were removed had been in the water for over 2½ years and were so badly riddled that the white, calcareous tubes showed through the thin surface. The general appearance of the wood was the same as that of a panel riddled with teredinids. It was not until the borers were exposed and examined closely that their pholad affinities were recognized. Many of the specimens were dead and their burrows filled with mud, with only the calcareous tube and valves remaining.

Unfortunately, the panels were not preserved immediately upon removal from the water, so the borers were in poor condition. Therefore, little anatomical work could be done, though it was possible to determine that the visceral mass was contained between the valves and that there was a large, U-shaped, wood-storing caecum.

The bottom at the test site was a gray mud; the temperature was 4°C and the salinity 35 ‰ (DePalma, 1969).

Range and specimens examined. Known only from the type locality.

Xyloredo ingolfia[1], new species

Plates 3–5

Type locality. From wood dredged by the INGOLF Expedition at station 67, south of Eyrabakki, Iceland (61°30′N; 22°30′W), in 975 fathoms [1783 meters].

Types. Holotype, Museum of Comparative Zoology 279636. Paratypes from the same locality, Museum of Comparative

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[1] Named for the Danish INGOLF Expedition, which collected the wood from which the specimens were obtained.

Zoology 279637, and the Universitetets Zoologiske Museum, Copenhagen.

Description. Shell globose, valves reaching 2.5 mm in length and 2.0 mm in height, thin, fragile, with prominent umbos; thin, glistening, almost colorless periostracum covering disc and posterior slope. Beaked portion of anterior slope wide, extending more than one-half distance to ventral margin; sculptured with close-set and very finely denticulated ridges. Posterior portion of anterior slope about two-thirds width of beak, sculptured with close-set ridges which extend to very slightly impressed umbonal-ventral sulcus. Disc sculptured with well-marked growth lines. Posterior slope small, low and not clearly demarcated on outer surface of valve. Umbonal reflection thick, narrow, short and free except at posterior end.

Inner surface of valves smooth, slightly shiny to chalky (perhaps owing to long preservation). Umbonal-ventral ridge wide, flattened, often varying in width, irregularly segmented and not enlarged at ventral condyle. Chondrophore and internal ligament large. Disc not clearly separated from posterior slope. Posterior adductor muscle scar large, slightly raised, elliptical, extending nearly to ventral margin, with irregular, transverse impressions. Anterior adductor muscle scar covering umbonal reflection. Siphonal retractor muscle scars not impressed. Pedal retractor muscle scar small, elongate to oval and located just anterior to posterior adductor muscle scar. Mesoplax of two very small, narrow, subrectangular, flat, calcified plates lying on dorsal surface of anterior adductor muscle.

Burrow 10 to 15 times length of valves; calcareous tubular lining three-fourths length of burrow. Tube relatively heavy, marked with uniform, close-set, raised rings, and covered with light tan periostracum which extends anteriorly as border. Portion of animal between valves and tube covered by thin, irregularly ridged periostracal sheath. Burrow opening often with small, white cone about 0.5 mm in diameter. Siphons short; incurrent siphon slightly longer than excurrent. Protoconch large, medium golden-brown and sculptured with fine, concentric ridges.

Valve measurements.	Length	Height	
	2.5 mm	2.3 mm	Holotype
	2.5	2.0	Paratype
	2.1	2.0	"
	2.0	1.9	"
	1.5	1.4	"
	1.5	1.2	"

Remarks. This species is most closely related to *Xyloredo naceli* from the eastern Pacific. It differs in having a less well-developed posterior slope, a shallow, indistinct umbonal-ventral groove, a flattened umbonal-ventral ridge, and in having the valves longer than high. In addition, the periostracal sheath posterior to the valves is not pustulose as in *naceli*, and the calcareous tube is much heavier and has raised rings. It also differs from *naceli* in having a much larger protoconch, which is sculptured with fine, concentric ridges.

It differs from *X. nooi* in having the valves longer than high, in having a low, rounded posterior slope, in lacking the distinct groove on the inner surface separating the disc from the posterior slope, and in having the plates of the mesoplax subrectangular and well calcified.

The wood dredged by the INGOLF Expedition had been heavily attacked by large teredinids before sinking to 1783 meters. These were all dead, only the empty tubes remaining as evidence of their presence. Filling every available space between the teredinid burrows were pipe-organ-like tubes of *Xyloredo* going both across and with the grain of the wood. Many of these tubes were 40 mm long and 1.2 mm in diameter. Jensen (1912: 56), in discussing the distribution of *Idas* [= *Idasola*] *argenteus* Jeffreys, states: "The specimens of the INGOLF Expedition were taken south of Iceland (61°30′N.L.; 22°30′W.L.) at 975 fathoms, under similar conditions to the last; the trawl brought up two large pieces of pine-wood, which had been pierced through and through by *Teredo*; in some of the *Teredo* tunnels were in addition mud and worm-tubes, further worms and small bivalves, namely *Idas argenteus*." This is the same piece of wood, remnants of which were preserved in the Copenhagen Museum, from which specimens of *Xyloredo ingolfia* were taken. The small, straight tubes were probably thought to be young teredinids.

The bottom at station 67 was a brown-gray transition clay of a fine, clayey-sandy consistency (Boeggild, 1900); the temperature was 3°C and the salinity 35.18 ‰ (M. Knudsen, 1899).

Range and specimens examined. Known only from the type locality.

Xyloredo naceli[1], new species

Plate 6

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[1] An acronym based on the initials of the Naval Civil Engineering Laboratory, Port Hueneme, California, which was responsible for the tests from which the specimens were obtained.

Type locality. From the U. S. Naval Civil Engineering Laboratory Submersible Test Unit at test site I [STU I–4], about 30 miles south of San Miguel Island, off Port Hueneme, California (33°46′N; 120°46′W), in 6800 feet [2072.6 meters], submerged from June 1964 to July 1965.

Types. Holotype, Museum of Comparative Zoology 279638. Paratypes from the same locality, Museum of Comparative Zoology 279639.

Description. Shell globose, valves reaching 1.5 mm in length and 1.5 mm in height, thin, fragile; umbos prominent. Periostracum thin, pale yellow, covering disc and posterior slope. Beaked portion of anterior slope with 8–12 pronounced, widely spaced, finely denticulated ridges. Posterior portion of anterior slope narrow; ridges extending to umbonal-ventral sulcus and more coarsely denticulated. Umbonal-ventral sulcus narrow, slightly depressed. Disc and posterior slope sculptured with fine growth lines only. Umbonal reflection narrow, free except at posterior end.

Inner surface of valves smooth and glistening. Umbonal-ventral ridge narrow and indistinctly segmented. Chondrophore and internal ligament well developed. Disc separated from posterior slope by low ridge. Posterior adductor muscle scar elliptical, extending from dorsal margin nearly to ventral margin and with indistinct, irregular, transverse markings. Pedal and siphonal retractor muscle scars impressed. Mesoplax of two small, thin, triangular plates composed almost entirely of periostracum.

Burrow six times length of valves; calcareous tubular lining two-thirds length of burrow, thin, marked with distinct rings, and covered with glistening, nearly colorless periostracum, which extends anteriorly as border. Portion of animal between valves and anterior end of calcareous tube with finely pustulose, light tan periostracal sheath. Siphons short, of about equal length and apparently lacking cirri. Protoconch very small, smooth (Plate 6, fig. 5).

Valve measurements.	Length	Height	
	1.1 mm	1.2 mm	Holotype
	1.5	1.5	Paratype
	1.2	1.3	"
	1.0	1.0	"

Remarks. This species, of which only eight small specimens were found, appears to be most closely related to *Xyloredo in-*

golfia from off Iceland. It differs by having a much smaller protoconch (hence the larvae in the pediveliger stage must be about two-thirds the size of those of *ingolfia*). It also differs in that the umbonal-ventral sulcus is impressed and the height of the valves is the same as or greater than the length.

The bottom at the test site was a green mud; the temperature was 2.1°C, the salinity 34.52 °/₀₀, and the dissolved oxygen 1.26 ml/L (Muraoka, 1966b). This species has not been taken at test site II of the Naval Civil Engineering Laboratory, located north of San Miguel Island (34°06′N; 120°42′W), where the depth is 2340 feet [713.23 meters], the bottom temperature 7.2°C, the salinity 34.37 °/₀₀, and the dissolved oxygen 0.42 ml/L (Muraoka, 1965). Specimens of *Xylophaga washingtona* Bartsch were found at both sites. It would appear that temperature and/or dissolved oxygen may be factor(s) controlling the distribution of *Xyloredo naceli*. However, so little is known about the biology of the Xylophagainae that no definite statements can be made at this time.

Range and specimens examined. Known only from the type locality.

ACKNOWLEDGMENTS

The author is grateful to John DePalma, U. S. Navy Oceanographic Office, Washington, D.C.; James Muraoka, U. S. Naval Civil Engineering Laboratory, Port Hueneme, California; and Dr. Jorgen Knudsen, Universitetets Zoologiske Museum, Copenhagen, Denmark, for the test panels and dredged wood from which the specimens were obtained. Thanks are also extended to Prof. Kenneth J. Boss of the Mollusk Department, Museum of Comparative Zoology, and Nancy Knowlton, my assistant, who critically read the manuscript. The aid granted by the Office of Naval Research through Contract no. N00014-67-A-0298-0027 with Harvard University is particularly appreciated.

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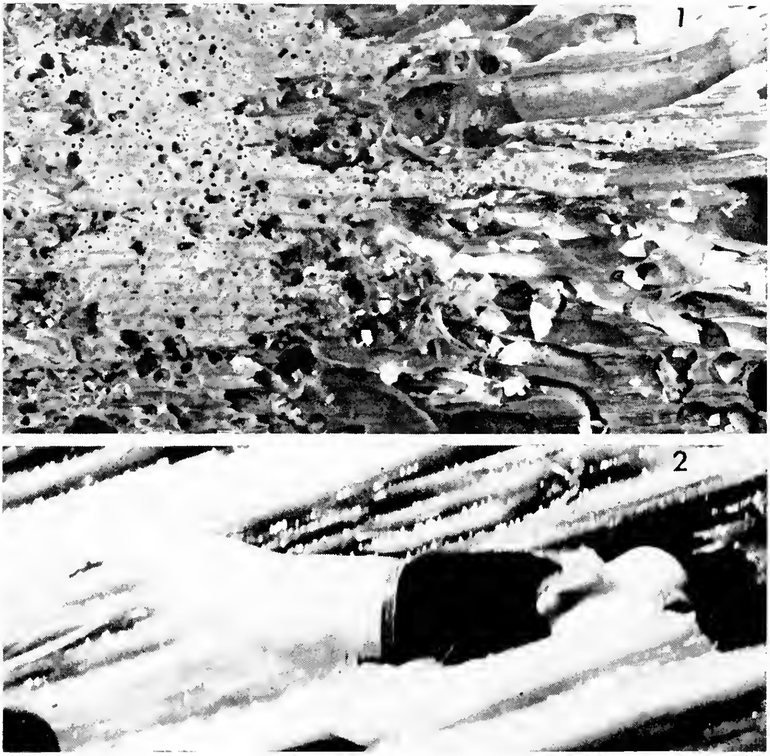


Plate 1

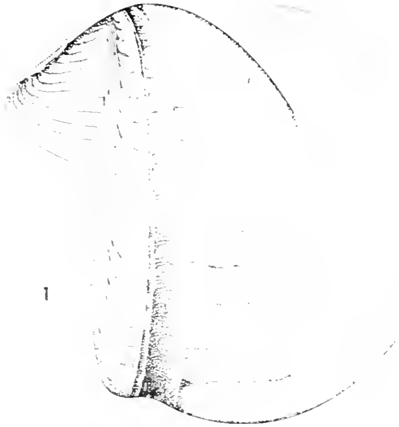
Xyloredo nooi Turner

Figure 1. Section of panel submerged in the Tongue of the Ocean, Bahama Islands, from April 4, 1962 to February 17, 1965 in 1737 meters (about 1/4 ×). Figure 2. Enlarged section of panel showing the calcareous lining of the burrow with anterior periostracal border, and dorsal view of apposed valves (about 4 ×).

Plate 2

Xyloredo nooi Turner

From panels submerged in the Tongue of the Ocean, off Andros Island, Bahama Islands. Figures 1–2. Holotype. Fig. 1. Outer view of left valve showing high, flaring posterior dorsal margin. Fig. 2. Inner view of right valve showing divided muscle scar, the deep groove separating the disc from the posterior slope, and the umbonal reflection. Figures 3–4. Outer and inner views of left valves of smaller specimens. Figure 5. Anterior view of apposed valves showing the chondrophore and internal ligament. Figure 6. Dorsal view of apposed valves showing mesoplax.



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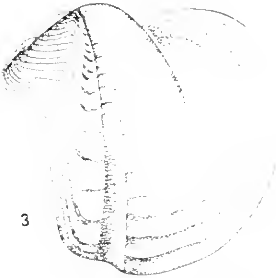

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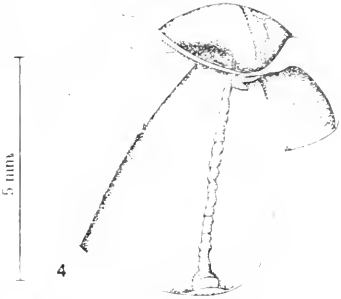

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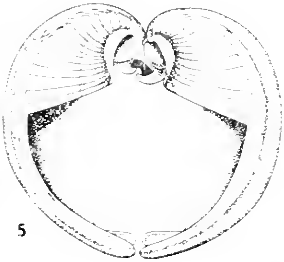

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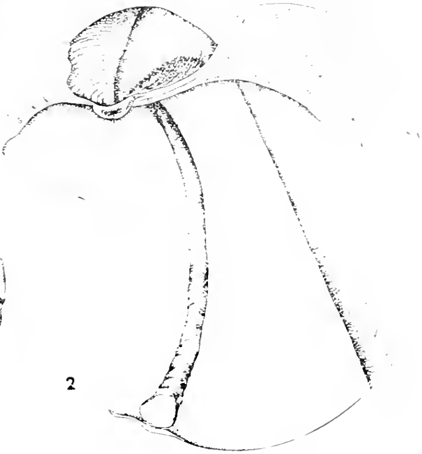

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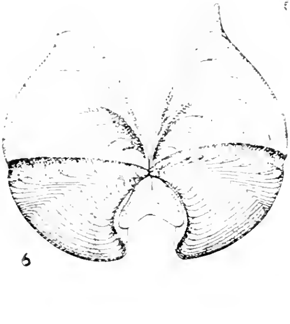

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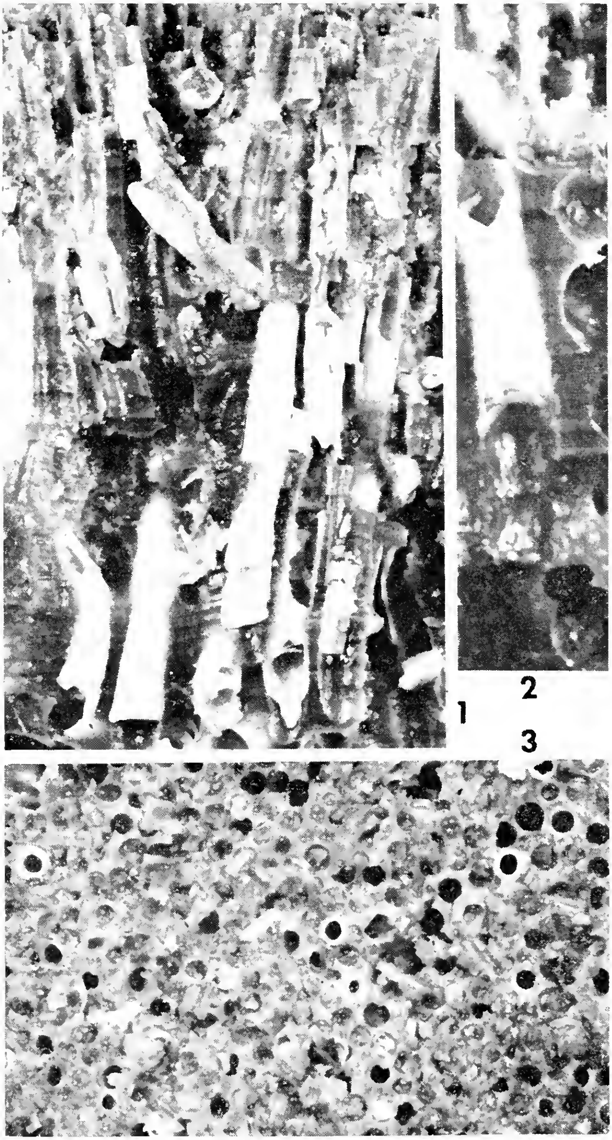

Plate 3

Xyloredo ingolfia Turner

Figure 1. Section through wood dredged at INGOLF-Expedition station 67, south of Eyrabakki, Iceland (61″30′N; 22°30′W) in 1783 meters, showing narrow, parallel tubes (5 ×). Figure 2. Enlarged section of burrow showing calcareous lining with anterior periostracal border (10 ×). Figure 3. Surface of wood showing entrances of burrows (5 ×).

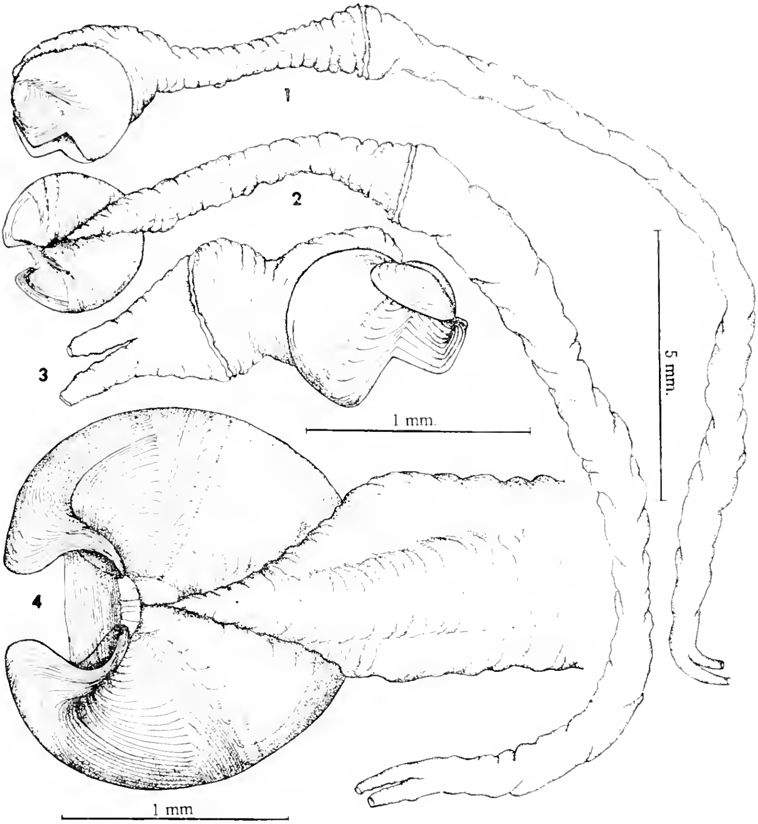

Plate 4

Xyloredo ingolfia Turner

From INGOLF-Expedition, station 67, south of Eyrabakki, Iceland.

Figures 1–2. (Holotype.) Lateral and dorsal views of entire animal showing the periostracal sheath, the extended anal and siphonal canals, and the short siphons. Figure 3. Lateral view of very young specimen showing large prodisoconch. Figure 4. Enlarged dorsal view of anterior end of entire specimen showing umbonal reflection, anterior adductor muscle, and small plates of the mesoplax in place.

Plate 5

Xyloredo ingolfia Turner

From INGOLF-Expedition, station 67, south of Eyrabakki, Iceland.

Figure 1. Outer view of left valve showing wide anterior slope and low, rounded posterior slope. Figure 2. Inner view of left valve showing large prodisoconch, strong umbonal-ventral ridge, reduced posterior slope, and lightly impressed muscle scars. Figure 3. Inner view of right valve. Figure 4. Inner view of left valve. Figure 5. Outer view of left valve with periostracal sheath attached.

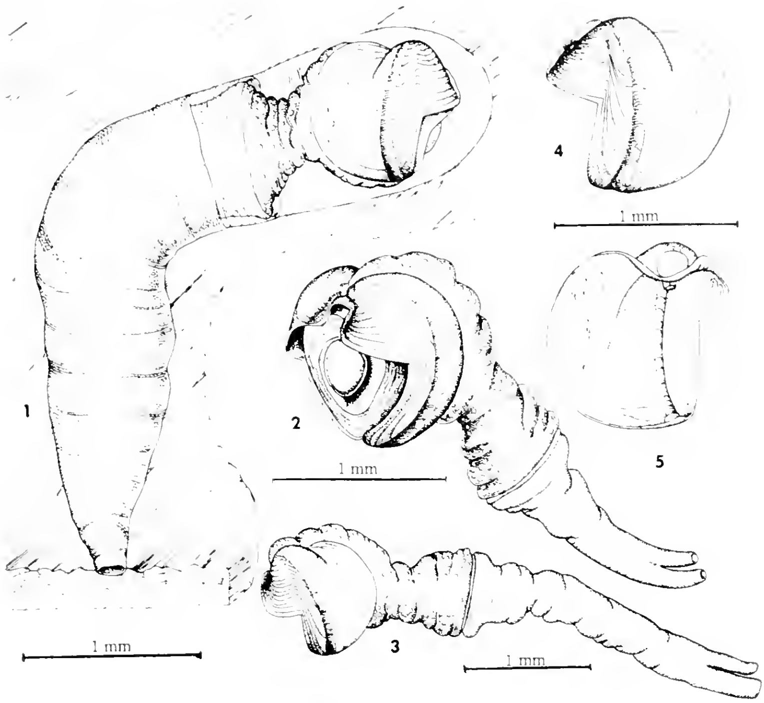

Plate 6

Xyloredo naceli Turner

From U. S. Naval Civil Engineering Laboratory test site I, south of San Miguel Island, Santa Barbara Islands, California.

Figure 1. Lateral view of specimen partially dissected from the wood showing the calcareous tube with the anterior periostracal margin and the papillose periostracal sheath covering the animal between the tube and the valves. Figure 2. Anterolateral view of entire specimen showing foot, mesoplax, and siphons. Figure 3. Lateral view of holotype. Figure 4. Outer view of left valve. Figure 5. Inner view of left valve showing muscle scars, chondrophore, umbonal-ventral ridge, and small prodisoconch.

BREVIORA

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PSEUDOBEACONIA, A PERLEIDIFORM FISH FROM THE TRIASSIC SANTA CLARA FORMATION, ARGENTINA

PETER HUTCHINSON[1]

ABSTRACT. Two species of the genus *Pseudobeaconia*, *P. bracaccinii* and *P. elegans*, from the Santa Clara Formation, Argentina, are described. The genus is an advanced member of the family Colobodontidae (subclass Chondrostei, order Perleidiformes), and is closely related to *Mendocinia* from the same locality. It is suggested that the success of the Perleidiformes is due, in part, to the evolution of a crushing dentition. The detailed structure of the unpaired fin rays indicates that control of the fin web area was possible in *Pseudobeaconia*, and probably in all Perleidiformes. The identification of *Pseudobeaconia* does not help the determination of the age of the Santa Clara Formation.

ABSTRACTO. Se describen dos especies del género *Pseudobeaconia*, *P. bracaccinii* y *P. elegans*, de la Formación de Santa Clara, Argentina. El género es un miembro avanzado de la familia Colobodontidae (subclase Chondrostei, orden Perleidiformes), y está íntimamente relacionado con *Mendocinia* de la misma localidad. Se sugiere que el éxito de los Perleidiformes se debe, en parte, a la evolución de una dentición molar. La estructura detallada de los rayos de las aletas impares indica que el control del área de la membrana de las aletas era posible en *Pseudobeaconia*, y probablemente en todos los Perleidiformes. La identificación de *Pseudobeaconia* no facilita la determinación de la edad de la Formación de Santa Clara.

INTRODUCTION

In 1944 three genera of fossil fish were described from the Santa Clara Formation, a series of shales, mudstones, and sandstones that outcrop between the provinces of San Juan and Mendoza, western Argentina (Bordas, 1944). Two of these genera were new, *Mendocinia* and *Pseudobeaconia*, while the

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[1] Gothic House, Drayton, Berks, England.

third was doubtfully identified as *Cleithrolepis.* More recently Schaeffer (1955) has redescribed *Mendocinia* and has shown that it is a member of the Perleidiformes. *Pseudobeaconia* remained relatively unknown, although it appeared in most classifications as a member of the Redfieldiiformes (*e.g.*, Gardiner, 1967a) because Bordas had described similarities between it and a redfieldiiform genus called *Beaconia* (= *Brookvalia*, Hutchinson, 1972) from the Triassic Hawkesbury Series of New South Wales (Wade, 1935).

The material described here was collected by an expedition from the Museo de La Plata and the Museum of Comparative Zoology, Harvard University, in 1964, and is derived from two localities in the Santa Clara Formation. The first is near the north end of the formation, near the Puesto of Santa Clara, at the east margin of the Precordillera in southern San Juan Province. This is the same locality that produced the fish described by Bordas in 1944. The second locality is north of the Quebrada de la Montaña, a short distance east of the boundary between the Santa Clara beds and the Villavicencio group (Romer, 1966).

There is little doubt that the specimens described here represent the two species of *Pseudobeaconia* described by Bordas in 1944. The reasons for this identification are given in the discussion below. *P. bracaccinii* occurs in both the localities mentioned above, while *P. elegans* occurs only in the former.

Pseudobeaconia is preserved in a matrix of dark mudstone or, more commonly, shale. The shales from the second locality usually contain bands of a light calcareous deposit. There may be up to ten such bands in a sample 10 mm thick. As well as fish, fragments of plant material are preserved in the shales. Preservation is extremely good and the fish have either been prepared with a fine needle or sometimes, when they occur in calcareous bands, dissolved in acetic acid to reveal natural moulds. All the specimens had been crushed to a thickness of, at most, 2 mm.

The Santa Clara Formation is difficult to date because it is limited to a block isolated by faulting during the Tertiary. Bordas (1944) is of the opinion that the Santa Clara Formation is contemporaneous with the Hawkesbury Sandstone of Brookvale, New South Wales. This conclusion is based on the supposed close relationship between *Pseudobeaconia* and *Beaconia*, a conclusion that is unfounded according to evidence presented here. Harrington (unpublished MS) notes that, near the locality described by Bordas, there are plant remains that include *Glossopteris, Walkonia, Pecopteris, Gondwanidium, Cordaites*, and *Dicranophyllum*, which are Permian in age. But, as noted above, the Santa Clara Formation is isolated from other sediments in the area, and there is no evidence that the flora listed by Harrington occurred within its boundaries. Schaeffer (1955: 3) has estimated the age of the beds of the Cacheuta basin (and by inference the Santa Clara Formation) to be Norian. This estimate is based on a similarity between floras of the Cacheuta and Upper Triassic sediments of the Northern Hemisphere. Lack of similar comparative data from the Middle Triassic means that this estimate can only be regarded as an indication of the youngest possible age of the Cacheuta beds.

A possible estimate of the age of the Santa Clara Formation depends on correlations made recently by Bonaparte and runs as follows. The Santa Clara Formation forms one of several outcrops that lie within the Cacheuta basin of deposition (Stipanicic, 1967: 3). Another of these outcrops contains the Potrerillos Formation from which a cynodont lower jaw, *Colbertosaurus*, has been recovered (Minoprio, 1954). *Colbertosaurus* is similar to *Pascualgnathus* from the Puesto Viejo Formation (Bonaparte, 1966a: 4–5). Thus the Potrerillos and Puesto Viejo formations can be considered to be very similar in age. The age of the Puesto Viejo formation is considered to be Scythian because it also contains a dicynodont *Kannemeyeria* (Bonaparte, 1966b: 266) and a cynodont *Cynognathus* (Bonaparte, 1969), both typical genera of the Lower Triassic South African fauna.

It should be emphasized that this estimate of Lower Triassic age for the Santa Clara Formation is tentative and open to two objections. Firstly, it is not certain that all the outcrops within the Cacheuta basin were once continuous. Secondly, the resemblance between *Colbertosaurus* and *Pascualgnathus* is not completely convincing, and has limited significance, according to Bonaparte (1966a: 5).

The identification of *Mendocinia* and *Pseudobeaconia* from Santa Clara adds nothing of significance to the debate on the possible age of the formation. Both genera are more advanced than *Perleidus* from the Lower Triassic of Madagascar, Greenland, and Spitsbergen but, because they are not directly descended from *Perleidus*, this does not necessarily indicate that the Santa Clara Formation is younger than Lower Triassic. Another member of the same perleidid radiation, *Meidiichthys*, from the Cynognathus zone of South Africa, demonstrates that advanced features such as an anteriorly inclined suspensorium evolved extremely rapidly, and the presence of such characters in forms from Santa Clara does not exclude the possibility that the Santa Clara Formation is Lower Triassic in age.

DESCRIPTION

Order Perleidiformes
Family COLOBODONTIDAE Stensio 1916
Pseudobeaconia Bordas 1944

Pseudobeaconia Bordas, 1944: 454.
Type species. Pseudobeaconia bracaccinii Bordas 1944

Diagnosis (emended). Skull short anteroposteriorly. Skull roof evenly curved to snout tip, upper jaw steeply inclined. Skull roof composed of two extrascapulars, a parietal, and a frontal. Lateral walls of skull roof composed of a dermopterotic and an accessory dermopterotic. Ventral end of the suspensorium inclined anteriorly so that the jaw articulation lies vertically below the posterior orbital edge. Opercular series composed of opercular, subopercular, and three or four branchiostegal rays. Opercular anterior in position so that its anterior edge lies in advance of the level of the posterior edge of the parietal. Subopercular larger than opercular. Triangular dermohyal and suborbital elements. Dermohyal small, extending ventrally along half the anterior edge of the opercular. Dermosphenotic short anteroposteriorly, in contact dorsally with both the posterior supraorbital and the dermopterotic. Dorsal orbital edge bordered by two supraorbital elements. Maxilla not greatly expanded posteriorly. Snout composed of paired nasals, antorbitals and (probably paired) toothed premaxillae, and a medial rostral and postrostral. Nasal bordering anterior orbital edge. Rostral large, bordering the anterior edge of the nostril. Nostril elliptical. Marginal teeth on maxilla and dentary conical and pointed, palatal teeth low and rounded.

Body fusiform, attaining a total length of up to 120 mm. Dorsoventral length of scales in flank region up to three times their anteroposterior length. Scales in the transverse row immediately behind the pectoral girdle twice as long anteroposteriorly as succeeding body scales. Scale ornament of between two and six ridges running concentrically along posterior and ventral borders. Scales in lateral line series with an indentation in their posterior borders. No hinge line at base of caudal lobe of body. Ridge scales present anterior to unpaired fins and on the dorsal side of the body midway between the skull and dorsal fin. Dorsal and anal fins posterior in position. Caudal fin hemiheterocercal. All fin rays jointed and usually bifurcated. Basal fulcra present anterior to all fins. Paired fin rays apparently lacking fringing fulcra. Proximal lepidotrichia of all fins at least three times as long as distal lepidotrichia. Proximal lepidotrichia of unpaired fins equal in number to endoskeletal supports, and expanded proximally, with insertions for depressor and erector muscles.

Pseudobeaconia bracaccinii Bordas 1944
Figures 1–5

Pseudobeaconia bracaccinii Bordas, 1944: 454-455, pl. 1.

Diagnosis (emended). Parietal just under half the length of the frontal. Opercular plate roughly rectangular, its anteroposterior length being under half its dorsoventral length. Ventral edge of opercular deeply convex. Posterior edge of maxilla lying anterior to the level of the posterior orbital edge. Anterior supraorbital extending anteriorly as far as the anterior end of frontal. Suprascapulars separated at midline. Dorsoventral length of supracleithrum twice that of cleithrum.

Body fusiform. Body length, from snout tip to the posterior tip of the caudal lobe of the body, three times the greatest depth of the body. Scale formula:

$$\frac{25}{13 \qquad 21 \qquad 35}$$

Length of the longest pectoral fin rays 1.5 times the length of the longest pelvic fin rays. Some paired fin rays bifurcated distally. Dorsal fin rays not bifurcated. Dorsal fin slightly in advance of anal fin. Dorsal lobe of caudal fin slightly longer than ventral lobe.

Holotype. Museo Argentino de Ciencias Naturales at Bernardino Rivadavia, Catalogue of Paleontology (Vertebrates) No. 14.868 (Bordas, 1944: pl. 1).

Additional material. Thirty-two specimens in the collection of the Museum of Comparative Zoology, Cambridge, Massachusetts.

Skull. The dermal bones of the skull are restored in Figure 1. The skull roof slopes evenly to the snout, and is composed of extrascapulars (which are divided [MCZ 12891]), parietals,

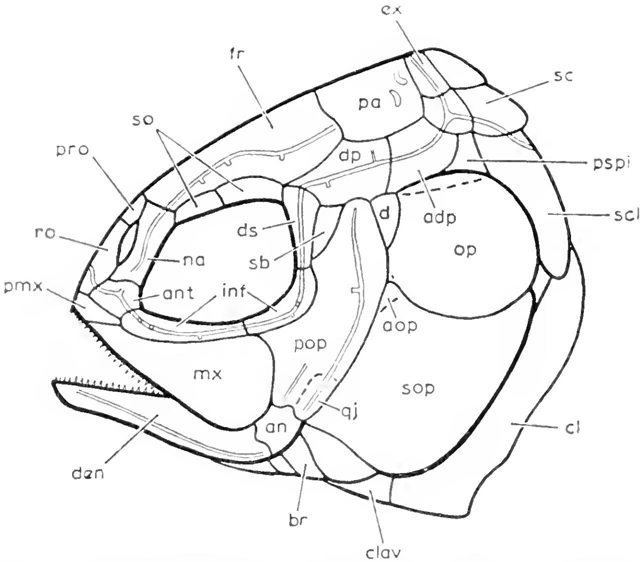

Figure 1. *Pseudobeaconia bracaccinii* Bordas. Restoration of skull and pectoral girdle, ornament omitted. × 5 approx.

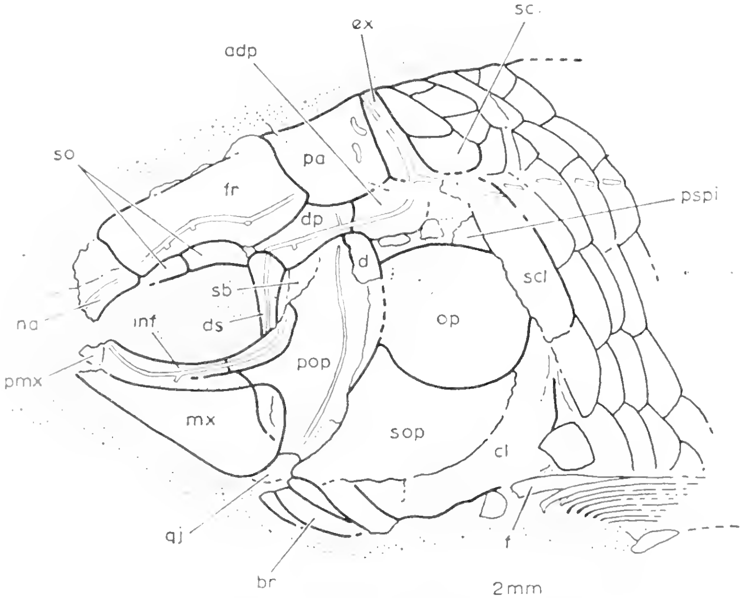

Figure 2. *Pseudobeaconia bracaccinii* Bordas. MCZ 12883. Left side of skull and pectoral girdle.

and frontals. The parietal is square; its anteroposterior length is just under half the length of the frontal. The frontal is deep and excavated above the orbit so that its widest part lies above the posterior edge of the orbit.

The lateral part of the skull roof is composed of two elements, a dermopterotic and an accessory dermopterotic, which are separated from one another by a vertical suture that runs from a point midway along the ventral margin of the parietal (Fig. 2). In MCZ 12883, the dermopterotic appears to be shallow, but this is because the preopercular has been displaced and overlaps its ventral part. The full depth of the dermopterotic is seen in MCZ 12894. The dermopterotic meets the posterodorsal border of the dermosphenotic, and may also have point contact with the posterior supraorbital element. A postspiracular lies posterior to the accessory dermopterotic and meets the ventral border of the extrascapular series. In lateral view the anterior part of the postspiracular is overlapped by the opercular, but in MCZ 12893 it is seen to extend anteriorly along the entire dorsal border of the opercular.

The opercular is circular, and the subopercular roughly oblong but with a curved posteroventral border. In most specimens the ventral part of the subopercular is crushed against the pectoral girdle, but its outline is clearly seen in MCZ 12898, where it has been slightly displaced. Its dorsoventral length is slightly longer than that of the opercular. There are only three or four rather broad branchiostegal rays. The preopercular is high, and meets the ventral edge of the dermopterotic. Its ventral part is inclined forwards so that the lower jaw articulation lies almost directly below the posterior edge of the orbit. The preopercular has a short infraorbital process. In MCZ 12883 (Fig. 2) an element lies between the posterior edge of the maxilla and the anteroventral corner of the subopercular. This is not a fragment of the preopercular, for in MCZ 12900 there is a notch on the median surface of the ventral end of the preopercular which indicates the position of a separate element (Fig. 1). It is likely, therefore, that a quadratojugal is present. There is no sign of any sensory canal on the quadratojugal. The dorsal end of the preopercular is constricted between triangular dermohyal (MCZ 12893, 12891) and suborbital elements (MCZ 12883). In MCZ 12893, which includes a natural mould of the median surface of the cheek, there is a small triangular accessory opercular at the anterodorsal corner of the subopercular. This element is not visible in lateral view, as it is completely overlain by the subopercular.

The dorsal orbital edge is bordered by two supraorbitals. There is some variation in the relative lengths of these elements; in MCZ 12898 and probably also in MCZ 12883 (Fig. 2) the posterior element is slightly longer than the anterior element, whereas in MCZ 12891 (Fig. 3A), the posterior element is slightly shorter than the anterior one. The posterior orbital edge is bordered by a narrow dermosphenotic, which has an expanded dorsal end, and the ventral orbital edge by two infraorbitals. The anterior infraorbital is expanded anteriorly, while the posterior infraorbital is expanded midway along its length.

In MCZ 12883 (Fig. 2), the maxilla has been displaced so that its posterior part is overlapped by the preopercular. The preopercular is so thin in this region, however, that the outline of the maxilla is clearly seen as a ridge. The upper jaw margin is steeply inclined, but lies at right angles to the anterior edge of the subopercular. The maxillary teeth are pointed (MCZ 12894, 12895, 12898, and 12901), and appear to be present only along the anterior half of the maxillary border. There are about 20 teeth in the upper jaw row.

The snout is best preserved in MCZ 12893, 12891 (Fig. 3A), and 12894 (Fig. 3B). The nasal borders the anterior orbital edge and is in contact dorsally with both the frontal and

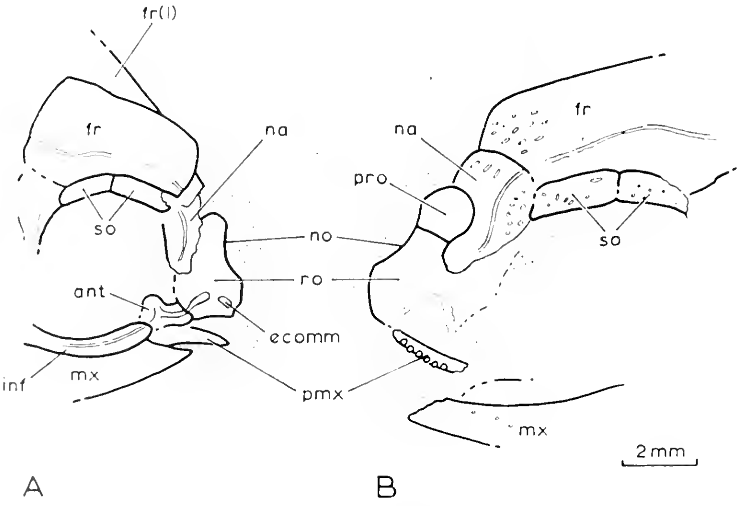

Figure 3. *Pseudobeaconia braeaccinii* Bordas. A. MCZ **12891**. Snout regon, right side unless otherwise indicated. B. MCZ **12894**. Snout region, left side.

the anterior supraorbital. The ventral part of the snout is composed of paired antorbitals, which border the anteroventral corner of the orbit, and premaxillaries, which bear up to six teeth (MCZ 12894, Fig. 3B). It is not known for certain whether the premaxillaries are paired or fused. The anterior part of the snout is composed of medial rostral and postrostral elements. The rostral bears the ethmoid commissure and extends dorsally so that it borders the anterior margin of the nostril (Fig. 3), while the postrostral is a small bone which just borders the anterodorsal corner of the nostril. The suture between the rostral and postrostral elements is indistinct in MCZ 12891, but clearly seen in MCZ 12894 (Fig. 3B).

The lower jaw is best preserved in MCZ 12893.

Most of the dermal bones of the skull are smooth. Tubercles are present, however, on the anterior ends of the frontal and anterior supraorbital, on the nasal, and on the infraorbital part of the maxilla. Low ridges are seen on the opercular and subopercular elements and near the edges of the branchiostegal rays (Fig. 4).

The sensory canals of the head are enclosed in massive tubes which open to the surface through well-defined pores (MCZ 12883, Fig. 2). In addition, there is a vertical pit line on the ventral part of the preopercular, while short, curved, middle and posterior pit lines are present on the parietal.

All the skulls of *P. bracaccinii* are crushed and few details of the internal anatomy are displayed. In MCZ 12897, however, part of the palate is visible and about ten low and rounded palatal tusks can be seen. In MCZ 12897 two branchial arch elements are seen, lying against the anterior edge of the cleithrum; they are flattened and their posterior edges bear numerous toothlike projections that are less than 0.1 mm long.

Pectoral girdle. The suprascapulars are D-shaped and do not meet at the midline as they are separated by a pair of scales that meet the posterior edges of the dorsal extrascapular elements (MCZ 12883, Fig. 2; MCZ 12891). The infraorbital sensory canal crosses the anteroventral corner of the suprascapular (MCZ 12893). The supracleithrum, which extends ventrally to a point close to the ventral edge of the opercular, has an excavated dorsal end. This excavation does not appear to fit directly onto the ventral edge of the suprascapular, for in several specimens it terminates at a level nearer the midline than does the suprascapular edge (MCZ 12893, 12891, and 12894). It is possible, therefore, that the dorsal end of the pectoral girdle is buttressed, in part at least, against the posterolateral wall of the braincase. The dorsoventral length of the

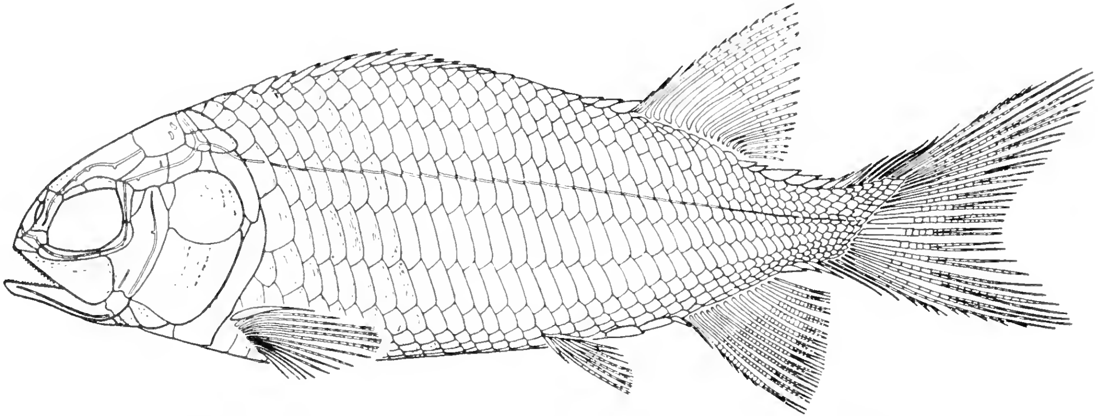

Figure 4. *Pseudobeaconia bracaccinii* Bordas. Restoration, ornament on posterior scales omitted. × 2.5 approx.

cleithrum is twice as long as that of the supracleithrum. The cleithrum has a broad ventral plate, and its anterior border bears an ornament of sinuous rugae. Small clavicles are present (MCZ 12893, 12899, 12901).

Paired fins. The paired fins are restored in Figure 4. In both, the rays are jointed so that the proximal lepidotrichia are up to six times as long as the distal ones, while the longest rays are bifurcated at their extreme distal ends (MCZ 12893, 12906). Fringing fulcra were not observed and are probably absent, but in both fins a stout basal fulcral scale participates in the leading edge. The pectoral fin is composed of 13 rays, which have between 4 and 12 joints. In well-preserved specimens (for example MCZ 12883, Fig. 2), the bases of the anterior rays are inserted in a more dorsal position than are those of the posterior rays. The pelvic fin lies two-thirds of the way between the pectoral and anal fins. It is composed of seven rays, which have between four and eight joints.

Unpaired fins. The unpaired fins are restored in Figure 4. In all, the rays are jointed, so that the proximal lepidotrichia are from three to eight times as long as the distal ones. The rays of the anal and caudal fins are bifurcated, and in all the unpaired fins the leading rays bear fringing fulcra. The dorsal fin is composed of 16 rays, which have between three and nine joints, and is preceded by three basal fulcra. The anal fin is composed of 14 rays, which have between 9 and 22 joints, and is preceded by a single basal fulcral scale. The dorsal and anal fins are similar in shape, but the former is larger and is slightly more anterior in position than the anal fin. The caudal fin is hemiheterocercal and the rays of its dorsal lobe are slightly longer than those of its ventral lobe. It is composed of 21 rays, which have between 15 and 24 joints. The four rays, which have their origins on the dorsal side of the caudal lobe of the body, do not bifurcate. There are about six basal fulcral scales on the dorsal side of the caudal lobe of the body; their exact number is difficult to determine because anteriorly they become very similar in form to the ridge scales, which extend posteriorly from the posterior edge of the dorsal fin.

In MCZ 12892 and 12905 some details of the articulation of the anal fin rays are seen, and in MCZ 12912 (Fig. 5) similar details are seen in the dorsal fin. In both fins the number of radials equals the number of rays. In the dorsal fin the proximal lepidotrichia have expanded proximal ends but, whereas the posterior lepidotrichia are almost straight, the anterior ele-

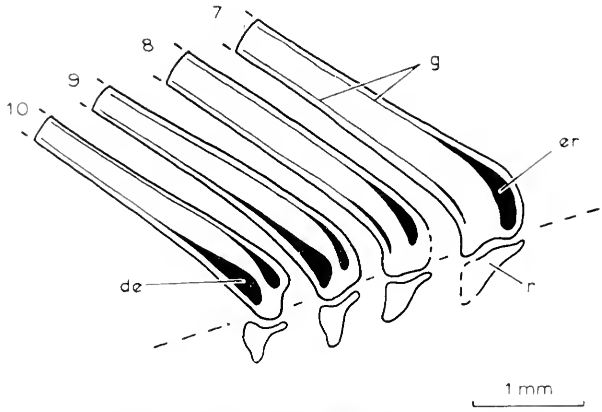

Figure 5. *Pseudobeaconia bracaccinii* Bordas. MCZ 12912. Proximal lepidotrichia and distal radials of dorsal fin rays 7-10. Right side.

ments become progressively more curved. Two grooves extend along the entire length of each fin ray, running close to the anterior and posterior edges. At their proximal ends, these grooves open into broad depressions so that there is an anterior and a posterior depression on each side of the base of every fin ray. As one passes anteriorly along the dorsal fin ray series, the anterior depressions become progressively larger, while the posterior depressions become progressively smaller (Fig. 5). The probable significance of these features is discussed below.

Squamation. The scales are restored in Figure 4. There are 35 transverse scale rows between the anterior transverse scale row and the row in front of the anterior caudal fin ray. The positions of the pelvic, dorsal, and anal fins relative to the scale rows is given in the formula:

$$\frac{25}{13 \qquad 21 \qquad 35}$$

(See Westoll, 1944: 20. Note that, because there is no clear hinge line in *Pseudobeaconia*, the last figure given in Westoll's formula is not used here.) The scales in the transverse row immediately behind the pectoral girdle are considerably longer anteroposteriorly than are the scales in any other row. Each scale in the lateral line series has a slight indentation in its posterior border, coinciding with the lateral line canal. The outlines of all the other scales are smooth. There is no hinge line between the scales of the body and those of the caudal lobe. Ornament is limited to between 2 and 6 ridges that run concentrically along the posterior and ventral borders of each scale.

Ridge scales occur in front of the unpaired fins and also on the dorsal side of the body between the skull and the dorsal fin.

Pseudobeaconia elegans Bordas, 1944
Figures 6–8

Pseudobeaconia elegans Bordas, 1944: 456, pl. 1.

Diagnosis (emended). Parietal just over half the length of the frontal. Opercular plate D-shaped, its anteroposterior length being over half its dorsoventral length. Ventral edge of the opercular slightly convex. Posterior edge of the maxilla lying posterior to the level of the posterior orbital edge. Anterior supraorbital extending anteriorly beyond the anterior end of the frontal. Suprascapulars meeting in the midline. Dorsoventral length of supracleithrum equal to that of the cleithrum.

Body fusiform. Body length, from snout tip to the posterior tip of the caudal lobe of body, 3.5 times the greatest depth of the body. Scale formula:

$$\frac{23}{11 \qquad 20 \qquad 34}$$

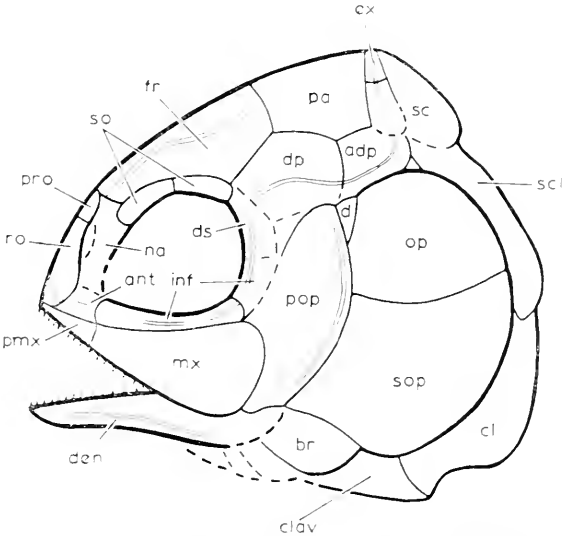

Figure 6. *Pseudobeaconia elegans* Bordas. Restoration of skull and pectoral girdle, ornament omitted. × 5 approx.

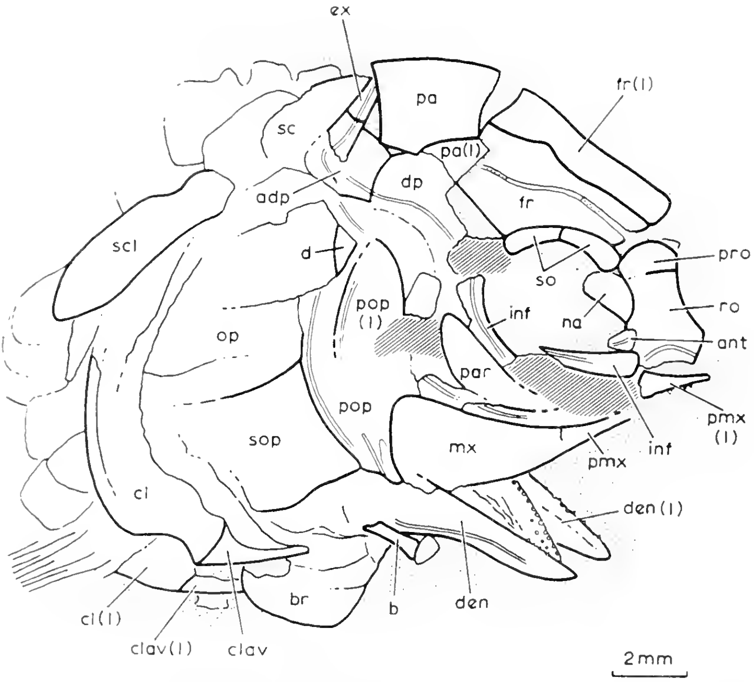

Figure 7. *Pseudobeaconia elegans* Bordas. MCZ 12892. Skull and pectoral girdle, right side unless otherwise indicated.

Length of the longest pectoral fin rays about 2.5 times the length of the longest pelvic fin rays. Paired fin rays probably not bifurcated. Dorsal fin rays bifurcated. Dorsal fin almost entirely in advance of anal fin. Caudal fin equilobate.

Holotype. Museo Argentino de Ciencias Naturales at Bernardino Rivadavia, Catalogue of Paleontology (Vertebrates) No. 14.689 (Bordas, 1944 : pl. 1).

Additional material. Four specimens in the collection of the Museum of Comparative Zoology, Cambridge, Massachusetts.

A full description of *P. elegans* is not necessary, as many of its features have already been observed in the type species *P. bracaccinii.*

Skull. The restoration of the dermal bones of the skull (Fig. 6) is based mainly on MCZ 12892 (Fig. 7). The anteroposterior length of the parietal is just over half the length of the frontal. The dermopterotic appears to be deeper than in *P. bracaccinii*, and the anterior supraorbital extends anteriorly beyond the anterior tip of the frontal. The opercular is less rounded than in *P. bracaccinii*, and has a straighter ventral edge, and the subopercular is relatively longer anteroposteriorly (MCZ 12893). As a result of these differences the opercular plate is D-shaped rather than rectangular, as in *P. bracaccinii*. The maxilla, although similar in shape to that of *P. bracaccinii*, extends posteriorly beyond the level of the posterior edge of the orbit.

Pectoral girdle. The suprascapulars are D-shaped and appear to meet in the midline. The supracleithrum extends ventrally beyond the ventral edge of the opercular. The dorsoventral length of the supracleithrum is the same as that of the cleithrum.

Paired fins. The paired fins are restored in Figure 8. Both are incompletely preserved. The rays are jointed so that the proximal lepidotrichia are up to eight times as long as the distal ones. Fringing fulcra are not preserved, and the rays appear not to be bifurcated. The pectoral fin is composed of at least seven rays that are extremely long, so that the fin is a fifth of the length of the entire fish (MCZ 12893). The pelvic fin is composed of at least seven rays that have up to four joints, and lies two-thirds of the way between the pectoral and anal fins.

Unpaired fins. The unpaired fins are restored in Figure 8. In all, the rays are jointed so that the proximal lepidotrichia are from five to eight times as long as the distal ones. The anterior rays of each fin bear fringing fulcra, and all the others are bifurcated. The dorsal fin is composed of 13 long rays that have between 11 and 14 joints, and is preceded by three basal fulcra. The anal fin is composed of 15 rays that have between 10 and 18 joints, and is preceded by two basal fulcra. The base of the dorsal fin lies almost entirely in advance of the level of the anterior end of the anal fin. The caudal fin is hemiheterocercal and equilobate. It is composed of 20 rays that have between 18 and 25 joints. There are about seven basal fulcral scales on the dorsal side of the caudal lobe of the body.

Squamation. The scales are restored in Figure 8. There are 34 transverse scale rows between the anterior transverse scale row and the row in front of the anterior caudal fin ray. The scale formula is:

$$\frac{23}{11 \qquad 20 \qquad 34}$$

The transverse scale rows are less steeply inclined than in *P.*

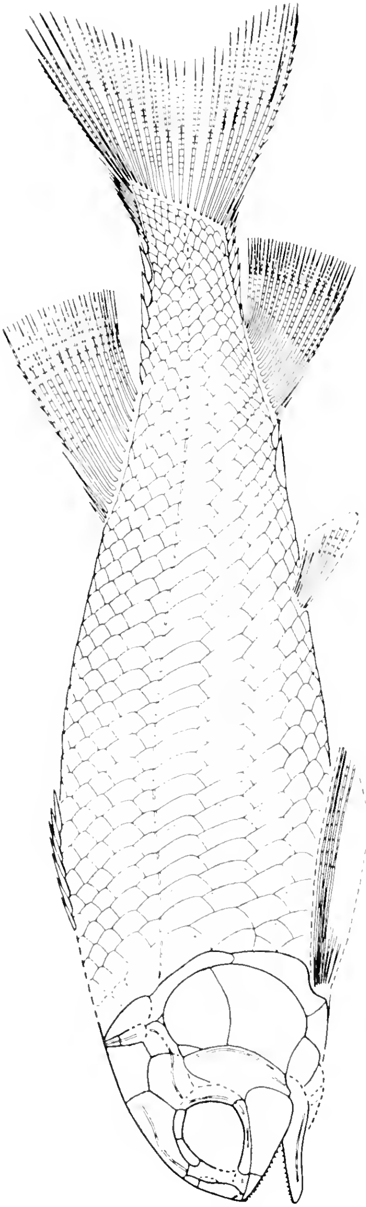

Figure 8. *Pseudobeaconia elegans* Bordas. Restoration, ornament on posterior scales omitted. × 2.5 approx.

bracaccinii, a feature to be expected in the squamation of a more fusiform body.

DISCUSSION

The Systematic Position of the Genus *Pseudobeaconia*

Before discussing the systematic position of *Pseudobeaconia*, it is necessary to state why the material described in this paper is considered to represent the genus described by Bordas in 1944. *Pseudobeaconia* is usually assigned to the order Redfieldiiformes (Gardiner, 1967b), whereas the specimens described here are clearly members of the Perleidiformes, as will be shown below.

The original diagnosis of *Pseudobeaconia* (Bordas, 1944: 454) is based on poorly preserved material and is therefore brief. The most important diagnostic features of the genus noted by him are: the absence of branchiostegal rays; the presence of a reduced tabular and postparietal; a dorsal fin divided into two parts, an anterior part near the head and a posterior part lying in the posterior part of the body; and finally, scales longer dorsoventrally than anteroposteriorly. These features are seen in the material described here, or can reasonably be considered as misinterpretations based on poorer material of the same taxa investigated in the present paper. The tabular and postparietal of Bordas correspond to the two extrascapular elements, and the anterior dorsal fin to the row of ridge scales that lie between the head and the dorsal fin. The supposed absence of branchiostegal rays is probably due to the poor preservation of Bordas' material. The similarities discussed so far would not allow certain identification of the present material with *Pseudobeaconia*. However, Bordas recognized two species of the genus: *P. bracaccinii*, which was characterized by a quadrangular opercular, a subopercular slightly longer dorsoventrally than anteroposteriorly, and a dorsal fin that was slightly anterior to the level of the anal fin; and *P. elegans*, which was characterized by a more delicate body shape, an opercular that was less quadrangular than in *P. bracaccinii*, and a dorsal fin that was more clearly anterior to the level of the anal fin (Bordas, 1944: 455, 456). These differences correspond exactly to the differences between the two species recognized in the present material (*cf.* Figs. 4 and 8), strongly suggesting that we are dealing with the same taxa. The material described here can therefore be ascribed to the genus *Pseudobeaconia* with a high degree of confidence. This conclusion is strongly supported by the fact that

Bordas' material and most of that described here have been collected from the same locality.

Returning to the systematic position of *Pseudobeaconia*, it is clear that the genus is not a redfieldiiform. Members of the Redfieldiiformes are characterized by a number of features, such as a dermosphenotic that borders the orbital edge, an R-shaped preopercular, an antorbital that borders the nostril edge, and an excess of rays over endoskeletal supports in the unpaired fins (Hutchinson, 1972), none of which are seen in *Pseudobeaconia*. On the contrary, consideration of the morphology of *Pseudobeaconia* leaves no doubt that it is a member of the Colobodontidae (= Perleididae), a perleidiform family well represented in both marine and freshwater Triassic deposits. With two exceptions, *Pseudobeaconia* has all the diagnostic characters of this family (*cf.* Schaeffer, 1955: 19). The exceptions are the presence of a suspensorium that slopes forwards, and a rostral that extends dorsally to take part in the nostril border. The first of these characters represents an advanced state of a trend well known in the family, while the second must be regarded as a specialization of the genus.

When compared to other members of the Colobodontidae, *Pseudobeaconia* appears to be similar to *Mendocinia* (Fig. 9B), which occurs in the same locality (Bordas, 1944; Schaeffer, 1955), but differs from that genus in having the following characteristics: subdivided extrascapulars; lateral part of skull roof composed of dermopterotic and accessory dermopterotic elements; ventral end of suspensorium inclined anteriorly; opercular anterior in position relative to skull roof elements; dermohyal small; two supraorbital elements; maxilla not greatly expanded posteriorly; rostral large and bordering anterior edge of nostril; scales with ornament of ridges; scales of lateral line series indented; unpaired fins with fringing fulcra.

Pseudobeaconia is also extremely similar to *Praesemionotus* from the Lower Triassic of Germany (Jörg, 1969). There are however, two characters mentioned in the diagnosis of *Praesemionotus* that do not appear in *Pseudobeaconia*. They are an interopercular and a narrow preopercular that separates the opercular series from the suborbital bones (Jörg, 1969: 89). The presence of these characters led to the classification of *Praesemionotus* in the order Parasemionotiformes. Jörg has recently revised this opinion (personal communication), and now believes that there is no interopercular, and that the preopercular extends over that part of the cheek previously described as being composed of both preopercular and suborbital bones. There is little doubt that *Praesemionotus* is a perleidiform, and that it should be referred to the family Colobodontidae.

In conclusion, therefore, *Pseudobeaconia* is in no way related to the redfieldiiform *Beaconia*. It represents the termination (as far as is known at present) of a line of colobodontid perleidiforms. Although its immediate ancestors are not known, they are likely to have been those that also gave rise to *Mendocinia* and *Praesemionotus*.

The Evolution of the Skull in the Perleidiformes

The evolution of the holostean feeding mechanism from the palaeoniscoid type is well known. The functional advantages of the former have been discussed by Schaeffer and Rosen (1961) and by Gardiner (1967b), and reviewed recently by Olson (1971). As Schaeffer and Rosen have noted (1961: 203), the modifications that occurred during the palaeoniscoid-holostean transition "permitted a considerable adaptive radiation in the feeding mechanism at the holostean level." However, during the Triassic period, two chondrostean orders, the Redfieldiiformes and the Perleidiformes, underwent a considerable adaptive radiation of their own, yet neither group achieved the holostean condition. The Redfieldiiformes owed their success in part to the evolution of a suctorial habit of feeding (Schaeffer, 1967; Hutchinson, 1972), and it remains to examine the Perleidiformes to see if there are equally obvious reasons for their success.

The skulls of four perleidiform genera are compared in Figure 9. They are not directly related to one another, but they are members of a radiation that must have had a beginning sometime during Upper Permian times. In an earlier radiation, haplolepid genera show parallel evolution of an almost vertical suspensorium from an oblique one (Westoll, 1944); in the perleidiforms the skull structure shows even more variation. Three main trends in their evolution can be traced: 1. The evolution of an anteroventrally inclined suspensorium from one that is posteroventrally inclined. 2. The shortening of the lower jaw from a length equal to 68 percent of the anteroposterior length of the skull (*Perleidus madagascariensis*) to one only 55 percent of the length of the skull (*Pseudobeaconia bracaccinii*). 3. The elevation of the anterior end of the upper jaw.

Associated with these changes are alterations in the shape of the maxillary-preopercular complex, and a shift of the level of the jaw articulation from a point well behind the orbit to a point below the orbit.

The advantage of a suspensorium that is anteroventrally inclined has been demonstrated by Schaeffer and Rosen; it allows greater posterior and lateral expansion of the orobranchial chamber (1961: 191). However, evolution of such a suspensorium does not necessarily involve significant shortening of the lower jaw (See, for example, the haplolepids [Westoll, 1944: fig. 44]), and the latter phenomenon in perleidids cannot therefore be regarded simply as a corollary of the former.

The advantage of a short lower jaw over a longer one is

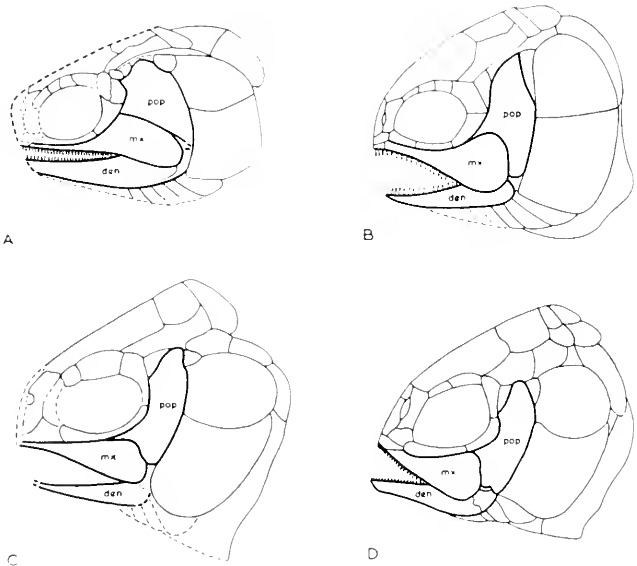

Figure 9. Restorations of the skulls and pectoral girdles of representatives of four perleidiform genera to show variation in shape of the preopercular, maxilla, and dentary. Ornament and sensory canals omitted. Not to scale.

A. *Perleidus madagascariensis.* Lower Triassic, Madagascar. From Lehman, 1952, fig. 85.

B. *Mendocinia brevis.* Lower Triassic, Argentina. From Schaeffer, 1955, fig. 4.

C. *Cleithrolepidina extoni.* Lower Triassic, Orange Free State. From Hutchinson, 1972, fig. 41.

D. *Pseudobeaconia bracaccinii.* Lower Triassic, Argentina.

that it can exert a greater force when adducted, assuming other factors such as the mass of the adductor muscle are constant. It may be concluded, therefore, that changes in the perleidid skull architecture are related, not only to the evolution of more efficient abduction of the orobranchial chamber, but also to the need to exert a powerful force on adduction of the lower jaw. It is not difficult to discover why this last requirement was of great adaptive significance to the perleidids. The group is characterized by the presence of low rounded teeth on the palate *(Perleidus, ?Colobodus,* and *Pseudobeaconia)* and on the lower jaw *(Perleidus, Colobodus,* and *Meridensa).* These teeth suggest that an important element of the perleidid diet consisted of food that required crushing, such as small molluscs and crustaceans.

The third trend in perleidid evolution, the gradual elevation of the anterior end of the upper jaw, is probably related to the evolution of shorter jaws. The disadvantage of short jaws is that the gape is reduced, but this appears to have been compensated for by elevation of the anterior end of the maxilla.

This brief analysis suggests that an important reason for perleidid success is that the evolution of short jaws and crushing teeth enabled them to feed, in part, on prey not accessible to other forms. This interpretation is not complete, however, for it does not explain the success of the Cleithrolepididae, which have rather slender lower jaws and few teeth (Fig 9C). Members of this family, although early offshoots from perleidid stock (Hutchinson, 1972), have an advanced type of suspensorium and laterally flattened bodies, and must have occupied a somewhat different niche to that of other perleidids.

The Structure of the Unpaired Fins in the Perleidiformes

The detailed structure of the unpaired fin rays in *Pseudobeaconia* shows that control of the fin web area was possible.

The unpaired fins of modern selachians are similar to those of chondrosteans in that each radial is associated with a large number of ceratotrichia (lepidotrichia in chondrosteans). In selachians, lateral movement of the fin web is effected by contraction of radial muscles that originate on the radials and that have broad insertions on either side of the proximal ends of the ceratotrichia. The area of the fin web cannot, however, be altered, and the fins cause considerable drag even when not being used to aid stability. The unpaired fins of *Acipenser* have essentially the same structure and restricted range of movements as have those of selachians (Alexander, 1967: 38), and the same is almost certainly true of the fossil chondrosteans in which the number of rays exceeds the number of radials.

In the unpaired fins of teleosts a discrete musculature, which originates on the radials, enables erection, depression, and lateral movement of each ray. Such a system is only possible because the numbers of rays and radials are equal.

Westoll (1944: 83) has suggested that control of the fin web area was possible in haplolepids because in the Haplolepididae the unpaired fin rays are small in number, stout, and beveled along their anterior edges to facilitate overlapping when the web is collapsed. In *Pseudobeaconia* there is even more evidence which suggests that in that genus, and possibly in all 'subholosteans' in which the unpaired fin rays and radials are equal in number, the fins were capable of almost as much mobility as is seen in teleosts.

The dorsal fin of *P. bracaccinii* has been described above (Fig. 5). The rays and radials are equal in number, a condition which suggests that a discrete musculature between the two was present. This is confirmed by the presence of an anterior and a posterior depression at the proximal end of each ray. The anterior depression is here interpreted as the point of insertion of an erector muscle, and the posterior depression as that of a depressor muscle. Anteriorly, the erector muscle insertions become progressively larger and the depressor insertions progressively smaller. Because of their position and greater length, the anterior rays are more affected by water forces that tend to collapse the fin. As a result, more effort is required to erect, and less to depress, these anterior rays, and these requirements are reflected by the variation in size of the erector and depressor muscle insertions. There is no sign of any depression which would indicate the presence of an inclinator muscle, but inclination of the fin is theoretically possible if the erector and depressor muscles of one side are contracted simultaneously. Such a mechanism does in fact occur in modern Siluriformes (Alexander, 1967: 40), but cannot be confirmed in *Pseudobeaconia* because the state of preservation of the joint between each lepidotrichium and radial does not allow an accurate assessment of the degrees of freedom of the ray.

The grooves that run along the anterior and posterior edges of the rays in *P. bracaccinii* (Fig. 5) probably helped to support the soft fin web tissues.

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ABREVIATIONS

aop	accessory opercular
adp	accessory dermopterotic
an	angular
ant	antorbital
b	branchial arch element
br	branchiostegal ray
cl	cleithrum
clav	clavicle
d	dermohyal
de	insertion of depressor muscle
den	dentary
dp	dermopterotic
ds	dermosphenotic
ecomm	ethmoid commissure
er	insertion of erector muscle
ex	extrascapular
f	fulcral scale
fr	frontal
g	groove
inf	infraorbital
(l)	left side
mx	maxilla
na	nasal
no	nostril border
op	opercular
pa	parietal
par	parasphenoid
pmx	premaxilla
po	postorbital
pop	preopercular
pro	postrostral
pspi	postspiracular
qj	quadratojugal
r	radial
ro	rostral
sb	suborbital
sc	suprascapular
scl	supracleithrum
so	supraorbital
sop	subopercular

B R E V I O R A

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THE EVOLUTION OF MAMMALIAN FROM REPTILIAN DENTITIONS

J. W. Osborn[1] and A. W. Crompton[2]

Abstract: A model to explain the evolution of a typical mammalian tooth replacement pattern is proposed. Osborn (1971) has described the early development of the teeth and replacement pattern in a typical modern reptile *(Lacerta vivipara).* The replacement of the postcanine teeth in an early Triassic mammal-like reptile, a cynodont, *Thrinaxodon liorhinus*, is basically the same as that of *Lacerta vivipara* except that the number of replacements closely approaches the mammalian condition. The rate of replacement has slowed down considerably and towards the back of the jaw only three teeth develop at each locus. Three different types of postcanine teeth can be recognized, an A type with a simple crown pattern towards the front of the row, an M type in the midsection with a more complex pattern, and a P type with the most complex pattern towards the back of the row. A P type is replaced by an M type and the latter by an A type. The progressive reduction in the complexity of the teeth produced at each locus in *Thrinaxodon* and in mammals (deciduous molar as compared with the premolar replacing it) is ascribed to the aging of the dental lamina. The typical mammalian pattern can be derived from that of *Thrinaxodon* by further reducing the rate of replacement.

INTRODUCTION

Two theories have been proposed to explain the evolution of mammalian dentitions, in which teeth are only replaced once (diphyodonty), from reptilian dentitions in which teeth are replaced throughout life (polyphyodonty). Bolk (1922) concluded that reptilian dentitions consist of two sets of alternat-

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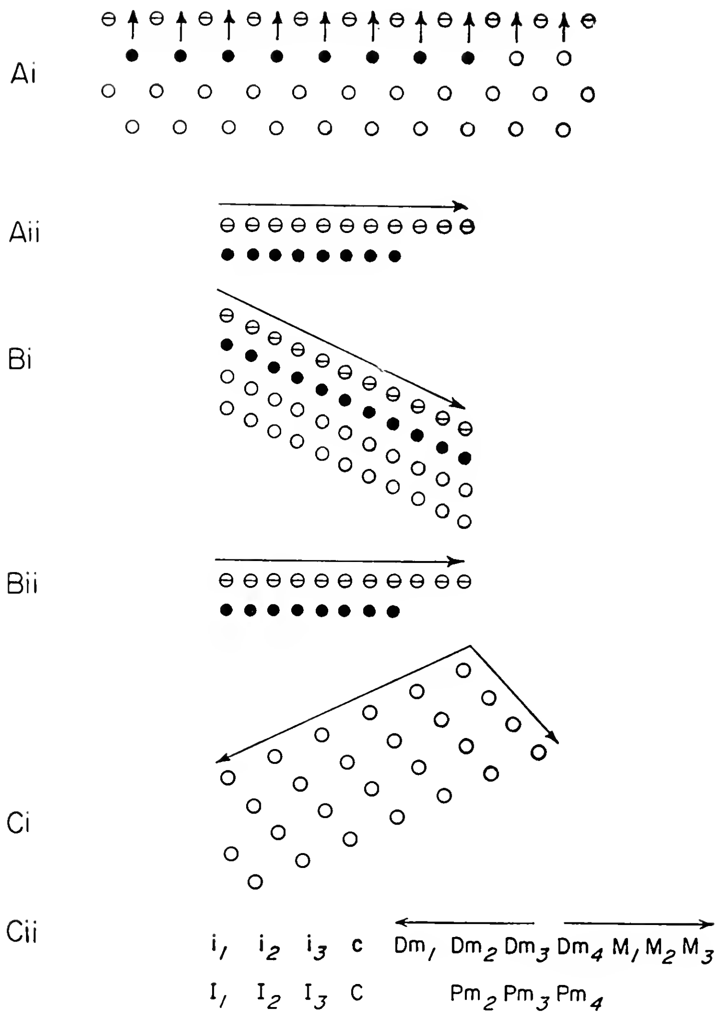


Figure 1. Ai represents Bolk's concept of the sets of alternating teeth present in a reptile. All members of a set develop at the same time. Aii shows what he considered to be the homologies between polyphyodont reptilian and diphyodont mammalian dentitions. Bi (reptile) and Bii (mammal) illustrate Edmund's (1960, 1962) concepts. He suggested that teeth develop in the sequence shown by the arrows. (Time is represented by a vertical axis.) Ci shows the actual sequence of tooth development in a primitive reptilian dentition (note alternation of teeth). Cii (arrows) shows the actual sequence in mammalian postcanine dentitions (Osborn, 1970). In all diagrams anterior is to the left and the mouth above.

ing teeth, each set being replaced alternately throughout life (Fig. 1Ai). He suggested that parts of a mammalian dentition is equivalent to one set that has become pushed together and that the replacing teeth are equivalent to the other alternating set (Fig. 1Aii). Edmund (1960, 1962) concluded that reptilian teeth are initiated in sequence from the front to the back of the jaw in rows which he called Zahnreihen (Fig. 1Bi). He suggested that the two mammalian dentitions are equivalent to two reptilian Zahnreihen (Fig. 1Bii).

It has recently been demonstrated (Osborn, 1971) that in an embryo reptile teeth are initiated in alternating sequences from the back to the front of the jaw (Fig. 1Ci), while in the postcanine dentitions of embryo mammals (Osborn, 1970), the first (most anterior) deciduous molar is always the last of the deciduous molars to develop and only the permanent molars develop in sequence from the front to the back of the jaw (Fig. 1Cii). We conclude that neither Bolk's nor Edmund's theory is acceptable because neither takes into account the sequences in which teeth actually develop.

One other feature clearly distinguishes between the dentitions of mammals and primitive reptiles: in mammalian dentitions, the postcanine teeth generally have different shapes (heterodonty) whose complexity reaches a peak somewhere within the permanent molar series; primitive reptilian teeth are generally all peg-shaped and alike (homodonty).

We are concerned in this paper with the phylogenetic process by which the heterodont, diphyodont dentitions of mammals evolved from those of the homodont, polyphyodont dentitions of primitive reptiles. In the absence of any recent animal which has a dentition even remotely intermediate between these two extremes, a solution to these problems must either be entirely speculative (Bolk, 1922; Edmund, 1960, 1962) or based on evidence from the fossil record. The gap between mammals and reptiles was bridged by the mammal-like reptiles of the Triassic. For our study we have chosen *Thrinaxodon*, whose tooth morphology and pattern of tooth replacement have already been investigated (Crompton, 1963; Parrington, 1936), but not in sufficient detail to answer the problems which we have posed.

POST-CANINE TEETH OF *THRINAXODON*

Preliminary Arrangement of Material

For the present investigation ten extremely well-preserved, as yet undescribed, *Thrinaxodon* jaws have been studied, together with four of those described by Crompton (1963), two of which were available to Parrington (1936). These have been labelled A to N. The investigation was confined to the lower postcanine teeth.

In order to arrange these specimens in a growth series, photographs, reproduced at the same magnification, were taken of the lingual sides of the jaws. Tracings were made of the jaw outlines of all the available material. These tracings were compared by superimposing one on another. It was necessary to speculate on the growth processes of the mandible to make accurate comparisons between the positions of the postcanine dentitions in jaws of different sizes. These speculations will be described later. On the basis of this study we arranged the specimens in a tentative growth sequence.

We speculated that the majority of growth in length of the jaw took place at the posterior end of the dentary where room was being made for the addition of postcanine teeth (Crompton, 1963) and that there was only a limited subperiosteal deposition of bone at the anterior end of the jaw (Fig. 2, *cf.* Fig. 7). From this we now concluded that successive replacement incisors remained in approximately the same anteroposterior position in relation to a hypothetical fixed marker, or that they erupted in only a slightly more anterior position than their predecessors. Successive canines might have become more posteriorly located

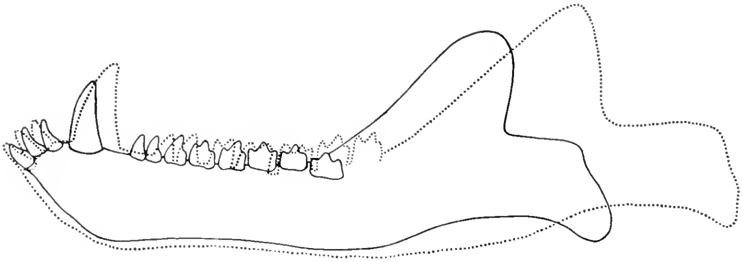


Figure 2. A diagram in which growth processes of the lower jaw of *Thrinaxodon* are postulated. Uninterrupted line = younger animal; interrupted line = older animal. The jaw has increased in length by the deposition of bone at the borders of the dentary. The anterior border of the coronoid process has been resorbed, making room for the addition of another postcanine in the older animal. There has been very little deposition of bone at the anterior end of the jaw. The most anterior of the postcanines in the younger animal has been lost in the older animal.

because we observed that the tip of a replacing canine was generally located posterior to the functional canine. However, we finally decided that as a canine erupted it moved into a more anterior position than would have been predicted from the position of its erupting tip (Fig. 7).

The tentative growth sequence established in this way was modified following a study of the shapes of the teeth and the positions of replacing teeth. For this purpose the sections of the prints containing the postcanine teeth were cut from full prints of the jaws. These small prints were rearranged until the best correspondence between adjacent dentitions was achieved, bearing in mind the original tentative arrangement based on jaw sizes.

Tooth Shape in *Thrinaxodon*

It appeared that the preliminary arrangement was in many cases inaccurate because frequently there was poor correspondence between what initially appeared to have been equivalent teeth in jaws which had been judged as being of comparable age (based on the similarity of their sizes). By comparing tooth shapes and by making estimates of the ages of teeth based on Crompton's (1963) observations, a definitive growth sequence was established. Before presenting this we will briefly describe the shapes of the teeth.

We finally established that *Thrinaxodon* possessed only three distinctive postcanine tooth types. It was because variations of each tooth type were present that Crompton (1963) did not recognise the division into three tooth types. We will refer to these as A = anterior, M = middle, and P = posterior. Between two and four A types (Figs. 3, 4) are always present at

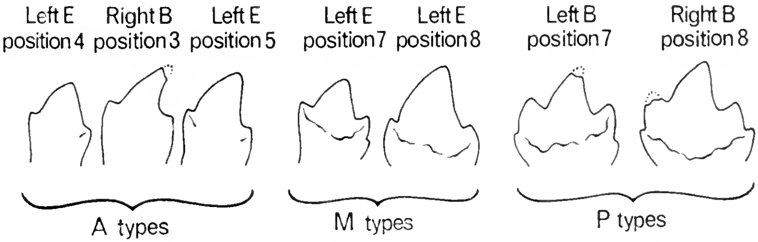
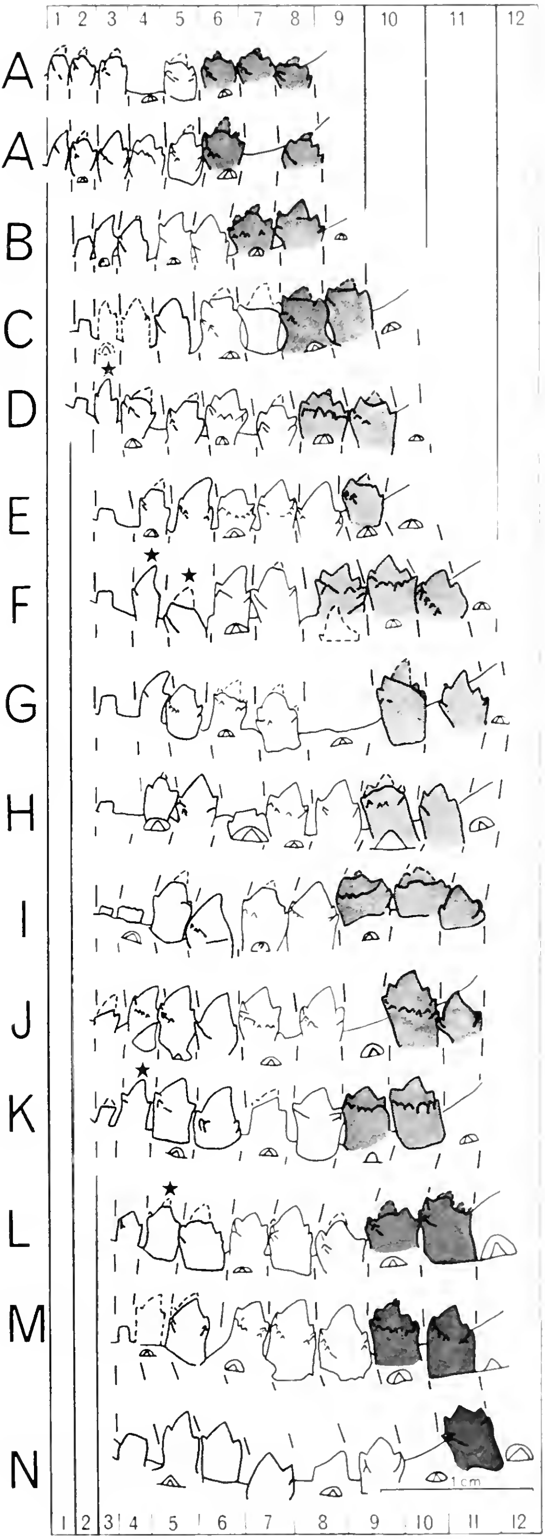


Figure 3. The three tooth types defined in this study. P = posterior, M = middle, A = anterior. More detailed descriptions of the postcanines in *Thrinaxodon* are given by Crompton (1963).

the front of the postcanine row. The crown is dominated by the main cusp and flanked by very small anterior and posterior accessory cusps. Lingual cingulum cusps are poorly developed or absent. Frequently the main cusp is markedly tilted posteriorly. The most anterior A type is often extremely small (Fig. 4). Either two or three M types (Figs. 3, 4) are always present in the middle of the postcanine row. The main cusp dominates the tooth but accessory cusps are usually situated much higher up its flanks than in the A type, reducing its apparent height when compared with the equivalent cusp on the A types. Cingulum cusps are generally well developed, producing a frill around the lingual surface of the tooth. The postcanine dentition terminates with either two or three P types (Figs. 3, 4) (dentition E contained only one). Included with these in the older animals may be found a "hybrid" MP type situated at the back of the dentition (*e.g.*, H, I, J, M in Fig. 4). These MP types will be considered with the P types because they are present at the back of the jaw. Their significance will be discussed later. In the P types the main cusp is very much reduced in height by large anterior and posterior accessory cusps situated high up on its flanks. Well-developed anterior and posterior cingulum cusps are usually placed at the ends of the tooth in such a way as considerably to increase its anteroposterior proportions when compared with A and M types. A well-developed array of lingual cingulum cusps gives the tooth what approximates to an occlusal surface although it did not occlude with the upper teeth. The occasional MP type has, as might be expected from the terminology, a shape intermediate between M and P types.

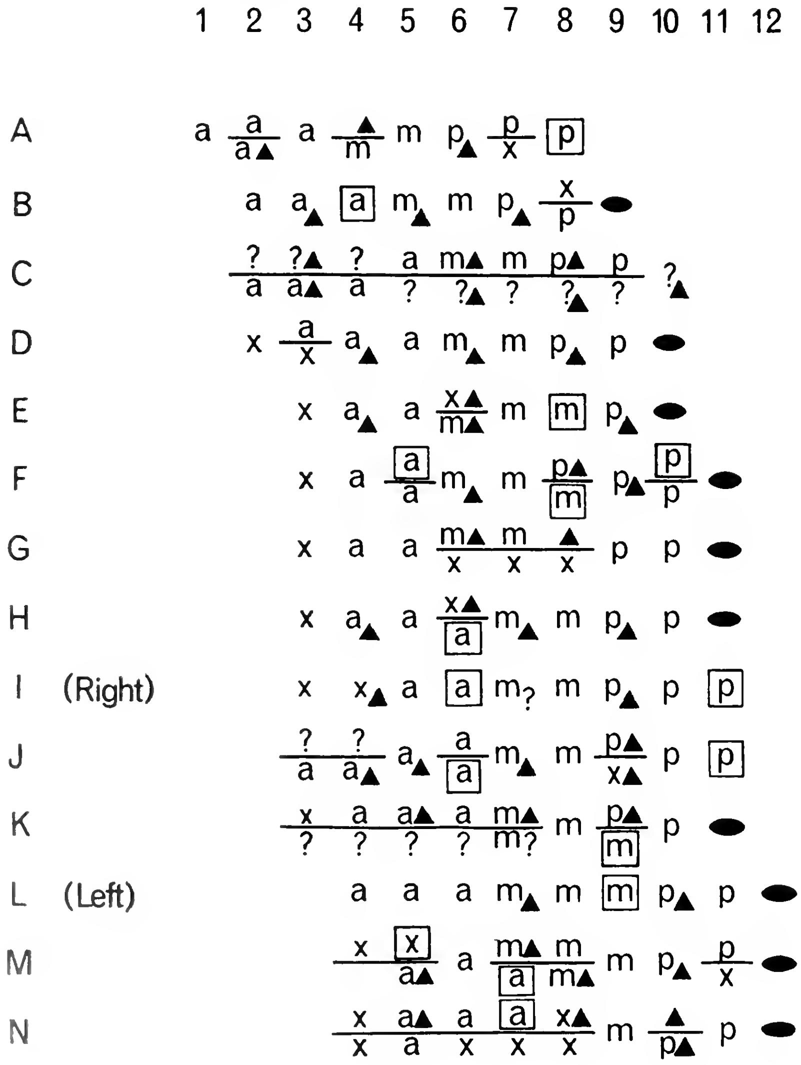
From the above definitions it can be visualised that the sizes of the anterior and posterior accessory cusps 1) increase from the front to the back of the dentition and 2) are directly related to the prominence of the lingual frill of cusps. In all the present material and in all well-preserved material which we have subsequently examined the postcanine dentition begins with between two and four A types which can be clearly distinguished from the succeeding two or three M types. These M types can be clearly distinguished from the P types which terminate the dentition.

Figure 4. Fifteen postcanine quadrants described in this study arranged in the suggested age sequence. The prints of the left jaws were reversed to simplify comparisons between dentitions. A and P types are shaded. Developing teeth are shown in the appropriate positions.


1 2 3 4 5 6 7 8 9 10 11 12
A
A
B
C
D
E
F
G
H
I
J
K
L
M
N
1 cm
1 2 3 4 5 6 7 8 9 10 11 12

The Definitive Arrangement of Specimens

We finally decided on the sequence of dentitions shown in Figure 4. This can be compared with Figure 5 in which each postcanine has been allotted a tooth form A, M, or P and Figure 6, which is a simplified version of Figure 5. Mandibular sizes are shown in Figure 7.



In support of this sequence the tooth types present in each dentition in positions 4 to 9 should be studied from Figures 4 and 5.

Position 4: The M type of dentition A is replaced in dentition B by an A type. This A type is replaced twice by further A types. Only a root is present in dentitions M and N.

Position 5: The M type of dentitions A and B is replaced in C by an A type, which is replaced once by another A type.

Position 6: The P type of dentition A is replaced in B by an M type. This tooth can be traced through to G being replaced in I by an A type, which can be recognised in the remaining dentitions.

Position 7: The P type of dentitions A and B is replaced in C by an M type, which can be recognised through to dentition L. On one side of dentition M and probably of N it has been replaced by an A type tooth.

Position 8: The P type in dentitions A to D is replaced in E by an M type. This M type can be recognised through to the last dentition. The small size of the P type in dentitions A, B, and C will be referred to later.

Position 9: In C a P type has erupted in the equivalent alveolus present in B. This P type can be recognised up to dentition K. In dentitions L, M, and N it has been replaced by an M type tooth.

Figure 5. The dentitions of all the specimens studied are represented in the form of an age sequence. Specimen identifications are to the left and tooth positions above. Where the teeth on left and right sides of a dentition differed the right side is represented above a line and the left side below the line. X represents a badly mutilated or lost tooth in an intact region of the jaw. The query marks represent teeth that were probably present in regions from which the jaw was missing. The triangles represent developing teeth, the ovals are the crypts which contained them. The origin of the material is as follows: A = TM 80; B = TM ?; C = TM 80B; D = BMNH R3731 = Crompton's specimen C = Parrington's specimen E; E = NM C354; F = SAM; G = NM C318; H = AMNH; I = SAM K377 = Crompton's specimen D; J = TM 180; K = BMNH R511 = Crompton's specimen F; L = TM 81; M = SAM ?; N = BMNH R511A = Crompton's specimen H = Parrington's specimen I. TM = Transvaal Museum; BMNH = British Museum (Natural History); SAM = South African Museum; NM = National Museum (Bloemfontein); AMNH = American Museum of Natural History.

In each of the above sequences it is important to recognise that correct aging of teeth has been observed. Consider position 7. The young P type in dentition A is old in B. The replacing M type in C is young (there is no replacing crypt). It is not until dentition H that a crypt is observed beneath this now aging M type tooth. On one side of dentition M (Fig. 5) and probably of N (Fig. 4) it is replaced by an erupting A type.

Tooth Replacement in *Thrinaxodon*

Before discussing the present data we must point out that it is by no means certain that all the animals studied belonged to a homogeneous population. The discrepancies between dentitions, particularly the smallness of the P types in position 8 of dentition A, position 9 of C, D, and E, position 10 of G, and position 11 of I and J could represent terminal stages in the growth series of animals of different sex or species. Nevertheless we will treat the data as if the animals belonged to a homogeneous population.

If the growth series presented here is correct then the pattern of tooth replacement in the heterodont postcanine dentition of *Thrinaxodon* conforms precisely with that described by Edmund (1960) for the majority of the homodont dentitions of nonmammalian vertebrates. This is shown in Figure 8B in which the numbering of the tooth positions corresponds to that in Figures 4, 5 and 6. By adding two further positions on the left (P_0 and P_{-1}) we calculate that it is possible to fit Crompton's (1963) very small specimen A, in which only the maxillary teeth are visible, into the series.

In most reptiles the actual number of tooth replacements at each tooth position is determined first by the longevity of the animal and second by the rate at which replacement teeth are initiated. Compared with other reptiles the rate of replacement of postcanine teeth in *Thrinaxodon* appears to have been so reduced in proportion to its longevity that posterior to position 6 at most only three teeth occupy each position. The number of replacement teeth in the anterior postcanine positions are limited in the following way. The replacing canines developed very close to the roots of the most anterior A types (Hopson, 1964). Hopson *(ibid.)* suggested that the presence of the developing canine prevented the development of replacements for these A types. The result was that even in the anterior postcanine positions, at most five teeth (position 4) erupted in any tooth posi-

		1	2	3	4	5	6	7	8	9	10	11	12
A	Right	a	a▲	a	m▲	m	p▲	p	$\boxed{p}$				
B	Left		a	a▲	$\boxed{a}$	m▲	m	p▲	p	⬬			
C	Right *1		a	a▲	a	a	m▲	m	p▲	p	⬬		
D	Right		x	a	a▲	a	m▲	m	p▲	p	⬬		
E	Left			x	a▲	a	m▲	m	$\boxed{m}$	p▲	⬬		
F	Left *2			x	a	a	m▲	m	$\boxed{m}$	p▲	$\boxed{mp}$	⬬	
G	Right			x	a	a	m▲	m	$\boxed{m}$	p	p	⬬	
H	Left			x	a▲	a	$\boxed{a}$	m▲	m	p▲	mp	⬬	
I	Right			x	x▲	a	$\boxed{a}$	m▲?	m	p▲	p	$\boxed{p}$	
J	Left *3			a	a▲	a▲	$\boxed{a}$	m▲	m	p▲	p	$\boxed{mp}$	
K	Right			x	a	a▲	a	m▲	m	p▲	p	⬬	
L	Left				a	a	a	m▲	m	$\boxed{m}$	p▲	p	⬬
M	Left *4				x	a▲	a	$\boxed{a}$	m▲	m	p▲	mp	⬬
N	Right *5				x	a▲	a	$\boxed{a}$	x▲	m	p▲	p	⬬

*1 2-4 left
*2 Position 10 right
*3 Position 9 right
*4 Position 11 right
*5 Position 10 left

Figure 6. The information in Fig. 4 is simplified in this diagram. Where a tooth is missing or unrecognisable on one side of the jaw the corresponding tooth on the intact side of the dentition is represented. In the few cases where the left and right dentitions of an animal are different the tooth form that more closely fits the predicted sequence is shown. A box indicates that the tooth was not yet fully erupted. A triangle represents an erupting tooth, an oval represents an alveolus.

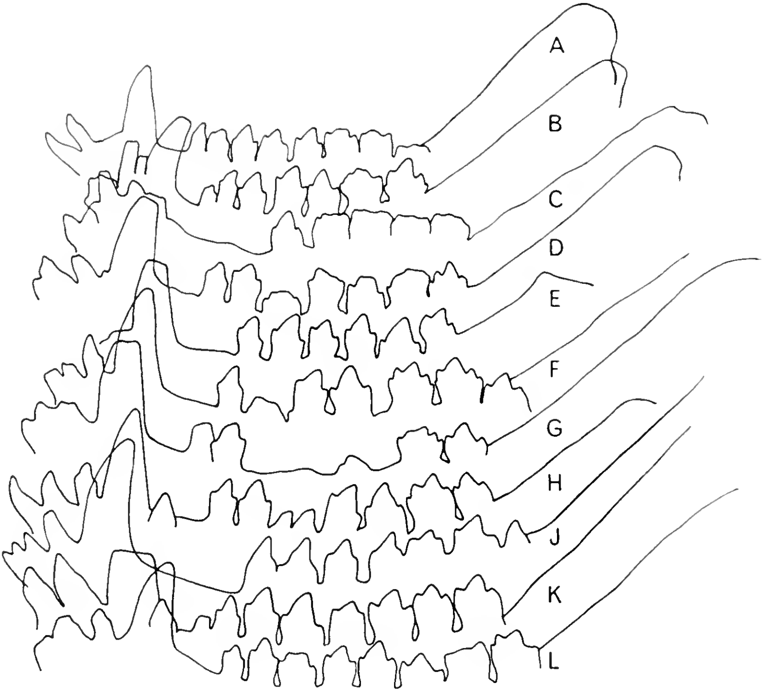


Figure 7. Tracings of the jaws and postcanine dentitions from one side of all specimens except I, M, and N for which suitable photographs were not available. The tracings have been arranged in accordance with the growth processes suggested in Fig. 1.

tion. Thus, although *Thrinaxodon* was strictly polyphyodont (because the dental lamina was active in budding new teeth through the life of the animal) the number of replacement teeth was severely limited when compared with most modern reptiles which have been studied.

The following argument suggests that *Thrinaxodon* may have been evolving towards a condition in which the activity of the dental lamina terminated during the life of the animal. This is the characteristic which distinguishes polyphyodont from other dentitions. In the anterior postcanine tooth positions the last replacement teeth were so small (position 3 in dentitions D to K; position 4 in dentitions L to N) that they can hardly have had any functional value. Thus, it can be argued that, despite its continued presence, the dental lamina in these positions no longer contributed significantly towards the maintenance of an efficient dentition. This is likely to be the first stage in the evolution of non-polyphyodont (*e.g.*, diphyodont) from polyphyodont dentitions.

The same type of process appears to have taken place at the back of the dentition. Instead of bulky P type teeth, very reduced hybrid MP types were erupting at the back of dentitions H, I, and J: once more, the dental lamina seems to be showing a reduced activity in the adult animal. In conclusion, although *Thrinaxodon* was undoubtedly polyphyodont, the adult animal shows a tendency toward producing small teeth of limited value at the front and back of the dentition. It is as if the dental lamina was becoming senescent during vigorous adult life, a feature which is not typical of a polyphyodont dentition. As described in the next section, this possibility may have important implications for determining the shapes of successional teeth.

Tooth Morphology in *Thrinaxodon*

It will be observed that in each tooth family there is a progressive simplification of cusp detail starting with the complex P type and ending with the very simple A types. This was accounted for by Crompton (1963) in the following way. Basing his argument on the concept of embryological fields (Butler, 1939), he proposed that several morphogenetic fields moved anteroposteriorly along the jaws of *Thrinaxodon*. In terms of the present observations he suggested that initially a "P type" field travelled slowly backwards through the jaw. Under its influence the first tooth in each tooth position developed into a P type. Following closely behind this was an "M type" field which induced the second tooth in each tooth position to develop into a M type. In turn this was followed by two or three A type fields. However, there is a more simple and biologically probable explanation for the present observations. We speculate that in each tooth position there was a gradual decrease in the morphogenetic capacity of the dental lamina and that this was an aging phenomenon. A newly differentiated "segment" of the dental lamina was capable of inducing the development of a complex P type tooth. This same "segment" of dental lamina now aged in such a way that the second tooth it produced was the less complex M type tooth. If time allowed, further aging resulted in its producing successively less complex A types. This

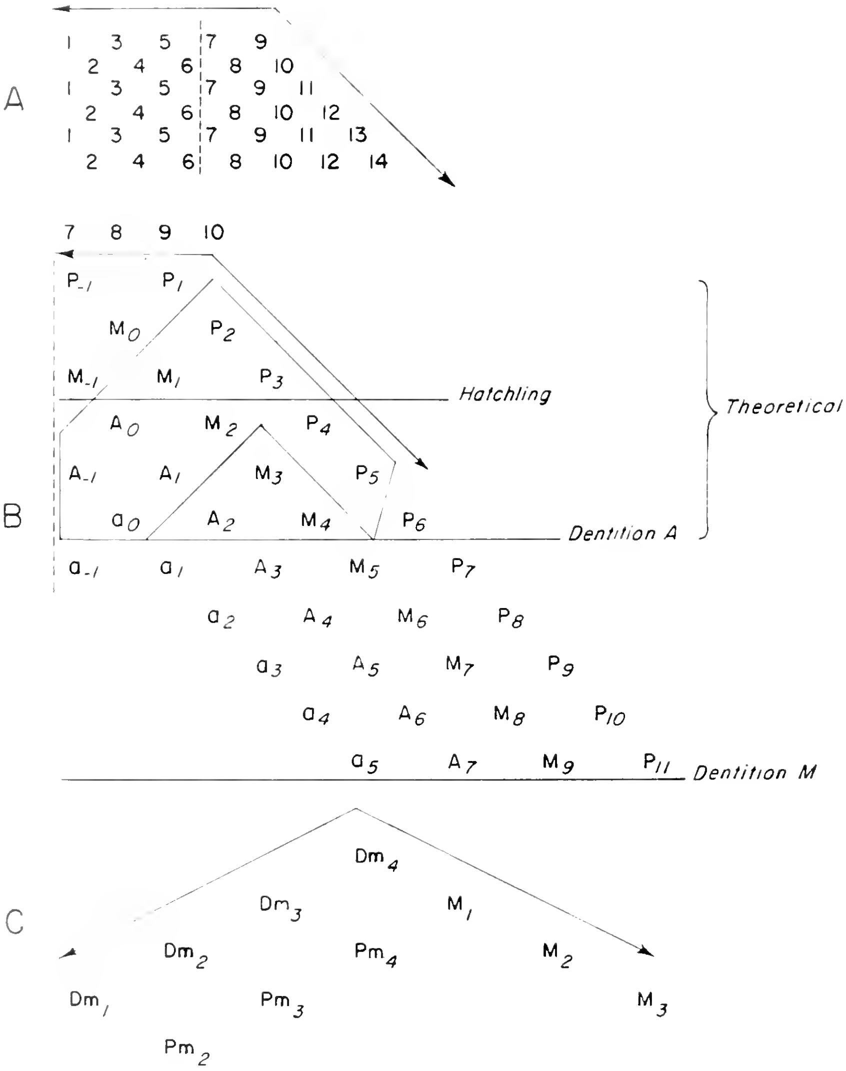


Figure 8. "A" shows the sequence in which teeth develop in a primitive reptile (Osborn, 1971). Teeth equivalent to those at the right of the interrupted line may have evolved into postcanines in *Thrinaxodon* (B). A mammalian dentition may be represented by the teeth enclosed within the box in B. Equivalent teeth are given mammalian nomenclatures in C.

same sequence of aging was reproduced sequentially in each segment of dental lamina as it extended backwards through the jaw into each new tooth position. In other words, heterodonty in the postcanine dentition of *Thrinaxodon* was achieved by a genetic process linked to the phenomena of aging rather than to the diametrically opposed phenomena of embryology (typified amongst other things by morphogenetic fields). Such a hypothesis could have considerable evolutionary significance, for it will be noted that if the postulated senescence of the dental lamina were to be accelerated, a stage would be reached at which the dental lamina was no longer capable of initiating a new tooth. Such a dentition ceases to be polyphyodont and suggests a possible origin for diphyodonty.

It is now necessary to allot a functional significance to the waning of the potential of the dental lamina to induce the development of cusps in the replacement teeth of *Thrinaxodon*. Newly hatched reptiles require a functional dentition. Thus even in the youngest animals strongly cusped teeth (relative to the size of the animal) are required at the back of the jaw where maximum power is developed. The teeth in positions 3 and 4 were probably at the back of the postcanine dentition in the new-born *Thrinaxodon* (Fig. 8B). Thus P types would initially have been present here and throughout life new P types would have erupted in sequence at the back of the jaw. But a neonatal *Thrinaxodon* jaw could only accommodate a relatively short and fragile P type tooth in position 4 in comparison to the size of the P type tooth which could be accommodated in an adult jaw. This same restricted space was available for the teeth which subsequently occupied position 4 in older animals. It is not difficult to visualise that it was an advantage to fill this space with a proportionately shorter but more robust M type tooth than a proportionately longer and more fragile P type. This same space was sufficient to accommodate an even more robust A type tooth in the adult animal. Thus, by reference to Figure 4, it can be seen that in position 6 the A type of dentition L has roughly the same length as the M type of dentition E and the P type of dentition A. However, the final A types in positions 3, 4, and 5 were very diminutive teeth which had little functional significance.

The most significant feature of the above hypothesis in relation to the ontogeny of postcanine teeth in *Thrinaxodon* is the suggestion that the successive tooth types in each tooth position were developed in relation to a form-determining stimulus which was repeated in every section of the dental lamina (or adjacent ectomesenchyme). No sequential stimulus travelling between adjacent segments of the dental lamina, such as that inherent in the embryological concept of a morphogenetic field, is required. The same difference in interpretation separates the hypotheses of Edmund (1960, 1962) and Osborn (1970, 1971) which have been put forward to explain the manner in which wave replacement of teeth develops in lower vertebrates. Edmund (1960, 1962) suggests that the timing of tooth initiation from the free margin of the dental lamina is co-ordinated by an impulse that travels backwards through the length of the jaw (*cf.* a morphogenetic gradient travelling backwards along the length of the jaw). By modifying Edmund's hypothesis Osborn (1970, 1971) explains wave replacement in terms of a control which is localised to each tooth position and which is repeated in every tooth position (*cf.* the P, M, and A types repeated in each tooth position). The absence of any evidence of a caudad impulse or a morphogenetic gradient (in postcanine dentitions) suggest that, in terms of biological possibilities, the more simple explanations offered here are more probable.

THE EVOLUTION OF MAMMALIAN DENTITIONS

It is now possible to speculate on the evolution of mammalian postcanine dentitions from polyphyodont dentitions (Fig. 8). We speculate that dental ontogeny in a primitive early reptile was like that described for a modern reptile (Osborn, 1971) which retains the archetypal pattern of tooth replacement observed in fossil reptiles (Fig. 8A). In this figure a canine might have evolved at position 6; therefore we are only concerned with positions 7 and beyond (the postcanine teeth). We speculate that in *Thrinaxodon* (Fig. 8B) postcanine development might have begun at about position 9. Anterior to this, just as in the primitive reptile, teeth could have developed alternately from back to front although there is no evidence for this. The tooth at position 8 developed later than that at positions 9 and 7, and owing to aging of the dental lamina, may therefore have been an M type rather than a P type. Behind position 9, teeth developed in sequence from front to back, just as in the primitive reptile. The first teeth at each tooth position were the complex P types. It can be seen that the sequence of tooth development in *Thrinaxodon* may have been similar to that in a primitive reptile.

We now speculate that a primitive mammalian postcanine dentition with four deciduous molars, four premolars, and three molars was equivalent to the teeth within the box in Figure 8B. Equivalent teeth have been given mammalian nomenclatures in Figure 8C. The sequence of development of deciduous molars and premolars is from back to front. This sequence matches data which show that Dm 4 is usually the first and Dm 1 is always the last to develop (Osborn, 1970). Furthermore these teeth decrease in complexity from back to front just as in the box shown in Figure 8B. The Dm 1 in mammals appears never to be replaced. This also is a trend which can be seen in the equivalent tooth position in *Thrinaxodon*. The most molariform teeth in mammals develop in sequence from front to back; again this agrees with the model in Figure 8B. Finally, the premolars are generally less complex than the deciduous molars and this too matches our model (Fig. 8B).

SUMMARY

In a primitive reptilian embryo the first tooth in each jaw quadrant develops at about the ninth tooth position from the front of the jaw. In front of this position teeth develop in the odd-numbered positions from the back to the front (9, 7, 5, 3, 1) to be followed by a similar sequence in the even-numbered positions (8, 6, 4, 2). Behind this position teeth develop in sequence from front to back (9, 10, 11, 12, etc.). Teeth continue to be replaced throughout life.

We have confirmed that the pattern of tooth replacement in the postcanine dentition of the mammal-like reptile, *Thrinaxodon*, was similar to that seen in primitive reptiles. We speculate that the sequence of tooth development in embryos was also similar to that in a primitive reptile. However, the rate of tooth replacement was so much slower that at most five, and usually fewer, replacement teeth were developed at each tooth position.

It has been shown (Osborn, 1971) that in primitive mammals either the fourth or third deciduous molar is the first to develop and the 1st deciduous molar is the last to develop (*i.e.*, development is from back to front as in primitive reptiles and *Thrinaxodon*). Behind the fourth deciduous molar, teeth develop in sequence from front to back (again as in the reptiles). Thus, by further slowing down the rate of tooth replacement in *Thrinaxodon*, we arrive at the peculiar sequence of tooth initiation which has been observed in primitive mammals.

In *Thrinaxodon* the first tooth to develop in each postcanine tooth position was the most complex, to be follwed by replacing teeth which were necessarily less complex. We speculate that this sequence was related to aging of the dental lamina, the epithelial ingrowth from which all teeth develop, and furthermore, that the same is true for mammals. This theory explains why both the deciduous molars and premolars become progressively less complex from back to front; it is the sequence in which they develop. Premolars are less complex than the teeth they replace (the deciduous molars) because they develop later. Permanent molars are complex because they are the first teeth to develop at their respective tooth positions.

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THE CAROLINA SALT MARSH SNAKE: A DISTINCT FORM OF *NATRIX SIPEDON*

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Abstract. Hybridization between two species and intergradation between races of one of them has long obscured the nomenclatural status of the water snakes of the *Natrix sipedon-fasciata* group in eastern North Carolina. A study of recently acquired material and the recognition that hybridization is occurring in several localities where fresh- and brackish-water habitats meet make possible a clarification of the confusing *engelsi* situation. Because the name *engelsi* was inadvertently applied to a snake of the wrong species, a taxonomic adjustment is made and the name *Natrix sipedon williamengelsi* is erected for the salt marsh snake that occurs on several of the islands of North Carolina's Outer Banks and along the mainland perimeter of Pamlico Sound and associated estuaries.

INTRODUCTION

The confusing status of the water snakes of the *Natrix sipedon* complex from the Outer Banks of North Carolina and the adjacent mainland has long intrigued both of us. Conant (1963: 29–32) summarized much of the data available at that time under the heading of "brackish-water populations." Lazell, as part of studies on the biota of the Banks, has recently accumulated considerable fresh material that helps to throw light on the situation. We have deemed it advisable to pool our knowledge and resolve the "*engelsi*" problem, which we review in some detail.

Three recognizable forms of the *Natrix sipedon-fasciata* group occur in eastern North Carolina. *Natrix sipedon* and *Natrix fasciata* are distinct species, based on their wide sympatry in the Mississippi Valley, along the Gulf Coast, and in northeastern North Carolina (Conant, *ibid.*). In the Carolinas *fasciata* is confined almost exclusively to freshwater habitats on the Coastal

Plain; *sipedon* occurs in the mountains and Piedmont, but it also invades the Coastal Plain north of Albemarle Sound, occurs on the peninsula between Albemarle and Pamlico Sounds, enters and is quite tolerant of brackish-water conditions bordering Pamlico and Core Sounds, and also occurs on the islands of the Outer Banks. In much of this general area it is differentiated at the subspecific level, thus providing the third form of the complex from eastern North Carolina.

That peculiar specimens of *Natrix sipedon* occur on the Outer Banks is a view scarcely novel with us. Barbour (1943) described *Natrix sipedon engelsi* on the basis of a single individual taken from Mullet Pond on the Shackleford Banks. Mullet Pond, which was formerly a bay on the north shore of the island (Engels, 1952: 704), now has no connection with salt water and is fresh; it supported a dense stand of cattails *(Typha)* and there was very little open water when a field party of the American Society of Ichthyologists and Herpetologists visited it on 5 September 1964. The snake Barbour used for his type (MCZ 46688) unfortunately is identifiable as *Natrix fasciata.* We have examined this specimen both independently and together, and we agree that from all diagnostic morphological characters it is a *fasciata.* The name *engelsi,* therefore, should be relegated to the synonymy of *fasciata,* a view previously suggested by Conant (1961: 19).

The history of the description of *engelsi* is of considerable interest, and we quote from a letter that Dr. William L. Engels sent to the senior author under the date of 27 February 1962: "Dr. Barbour spent a few days in Chapel Hill in May 1942 . . . . Dr. Coker brought him around to me. I was just finishing the manuscript for my report on the Ocracoke fauna, and I showed him the king snake I had from there which was certainly a peculiar looking, chocolate-colored individual. I also showed him the only other live snake I had, the rat snake from Shackleford Banks. He immediately got quite excited, came back the next day and stared at those snakes some more, and wanted me to sit down immediately to describe them as new. I was about to go into the Air Force, did not have any comparative material, and at any rate was totally lacking in experience in systematic herpetology. The end of it was that I sent him the snakes and went myself into service. He wrote me proposing that either my name should be given to one of them or that my name should be put on the descriptions as joint author. I agreed to the latter, and that ended our collaboration. I deliberately did not show him the water snakes — I thought that was a little project I could keep for myself, for after the war (they did strike me as being unusually dark). But Dr. Coker did not know this. He did know that Dr. Barbour had become quite excited about 'the new herpeto fauna' which I 'had discovered' — the quotes are Barbour's words. So, having come into possession of a *Natrix* from the Mullet Pond on Shackelford, while I was in Egypt, he sent it to Barbour. That became the type of *N. s. engelsi*."

The practice of describing new taxa from single specimens, although always potentially risky, was widespread 30 years ago. Consideration should also be given to the fact that Barbour was an alpha taxonomist; he seldom examined large series of specimens, and he was accustomed to describing new species from islands of the West Indies. It is understandable that he could engender strong enthusiasm about unusual insular specimens. His type of *engelsi*, a very dark snake in which black pigment obscures many of the pattern details, is now known to be a representative of a deme inhabiting Mullet Pond that shows strong evidence of hybridization between *sipedon* and *fasciata*. As is noted below, some of the snakes of this population are morphologically indistinguishable from *sipedon*, others could be identified as *fasciata*, and others combine characters of both. This phenomenon is not unique to the Shackleford Banks. It also occurs at other places where fresh- and saltwater habitats meet and in a few localities within the Fall Line zone of both the Carolinas and Georgia (Conant, 1963).

In an effort to end the confusion that has thwarted a real understanding of the *Natrix sipedon-fasciata* complex of the region for three decades, we take pleasure in describing:

NATRIX SIPEDON WILLIAMENGELSI n. ssp.

Holotype. MCZ 129298, a young adult male, collected by Paul Elias, 14 June 1971, along Island Creek on Ocracoke Island, Hyde Co., North Carolina.

Paratypes. (All from North Carolina.) CORE BANKS, *Carteret Co.*: North Carolina State Museum (NCSM) 11796, MCZ 131993, Cape Lookout. HATTERAS ISLAND, *Dare Co.*: United States National Museum (USNM) 72573; MCZ 130278–79, Hatteras Village. OCRACOKE ISLAND, *Hyde Co.*: MCZ 129290, Horse Pen Creek; MCZ 129299, 129302, Island Creek; MCZ 129242, between Island Creek and Pamlico Sound; MCZ 131990–91, Ocracoke Village; MCZ 131988, Quork Hammock; MCZ 129288, 129300, Quorks Point Creek; MCZ 129249, Old Hammock Creek; MCZ 129250, Pony Pasture Creek; NCSM 11798, 1 mi. W of The Knoll; NCSM 11797, Try Yard Creek. PORTSMOUTH ISLAND, *Carteret Co.*: MCZ 129251–74, 129289, Portsmouth Village. MAINLAND: *Carteret Co.*: NCSM 8003, 11 mi. S of Merrimon; MCZ 131992, SW part of Cedar Island. *Hyde Co.*: American Museum of Natural History (AMNH) 88076, Rose Bay Creek. *Pamlico Co.*: AMNH 88075, Oyster Creek near Lowland.

Diagnosis. A strongly melanistic race of *Natrix sipedon* in which: (1) the dorsum in adults is essentially black with the interspaces between the crossbands and blotches so dark that pattern details often can be discerned only if the specimen is immersed in liquid; (2) the venter posterior to midbody is predominantly black; (3) there are no reddish- or brown-centered ventral crescents or half-moons posterior to the 50th ventral; and (4) the light scales between the dark crossbands average one and one-half (maximum three) on the neck at the level of the second dorsal scale row.

Description of the type. MCZ 129298 is a young adult male 725 mm in total length; the tail is complete and measures 168 mm. There are 138 ventrals, 72 subcaudals, and a maximum of 23 dorsal scale rows. The anal is divided and both hemipenes are everted. The general coloration is black with dull gray interspaces between the black bands and blotches. The interspaces vary, at the level of the second dorsal row, from one to two scales in width; most are about a scale and one-half. The dark dorsal bands are continuous, from ventral edge to ventral edge across the anterior part of the body; they are replaced posteriorly by alternating lateral bars and middorsal blotches, as in the nominate race. The entire snake is so dark that the pattern is most clearly observed under liquid.

The ventrals are virtually uniformly black at the posterior end of the body, but are lightly spotted with white; the white spots are larger and much more prominent on the anterior third of the body. There are no reddish- or brown-centered ventral crescents posterior to ventral 48.

Variation. We have examined 50 specimens of this race (26 males and 24 females). Of these, the senior author examined three alive, the junior author more than 20 alive or freshly killed on the road. The very dark coloration of *williamengelsi* is little affected by preservation, and there is far less variation than in the nominate race. All specimens are black or dark brownish black with very narrow, lighter, grayer interspaces between the dark bands. The bands are so wide relative to the interspaces that most individuals appear uniformly black in the field. One specimen (MCZ 131990) from Ocracoke Village was aberrantly red. The areas normally white or gray, ventrally and laterally, were rose or rusty. There were, however, no red-centered crescents posterior to ventral 44.

Many specimens show an indication of the pale vertical bar that crosses the angle of the jaws as illustrated in Conant (1963, fig. 6E). This is frequent in *Natrix sipedon* from southern coastal localities, and usually quite different from the pale longitudinal stripe of *Natrix fasciata* (Conant, 1963, fig. 6F).

Most specimens have red- or brown-centered ventral crescentic markings on the anterior venter; the most posterior of these vary in position from ventral six to ventral 48. Very young specimens, such as MCZ 129252–74, from Portsmouth, Portsmouth Island, have no red- or brown-centered ventral crescents at all.

Scale characters are of little use in distinguishing *Natrix fasciata* from *Natrix sipedon sipedon* (Conant, 1963: 11–15), and they are of no value in separating *williamengelsi* from the nominate race of *sipedon*. Overall variation in *williamengelsi* is as follows: ventrals 129–143, mean 138 (females 133 to 143, mean 138; males 129 to 143, mean 137); subcaudals 57–84, mean 70 (females 57–70, mean 64; males 62 to 84, mean 75); maximum number of dorsal scale rows in both sexes 21–23 (among the 50 specimens, only six vary from 23 — three have 22 and three have 21).

Size. Our largest specimen (MCZ 129290, a female from near Horse Pen Creek in the "Up Trent" region of Ocracoke Hammock, collected 16 June 1971, by Numi C. Spitzer) measured 1224± mm (48 in.) in life. This snake is illustrated in Figure 1. The smallest specimen examined is 139 mm in total length. This snake (a male) is the runt of a litter of 24 the rest of which vary from 193 mm to 216 mm (mean 204 mm). These are young of a female (MCZ 129251) from Portsmouth, Portsmouth Bank, that measures 1040 mm, total length, and has a stump tail 125 mm long.

Comparisons. Melanism occurs sporadically in several parts of the range of the nominate subspecies *(sipedon)*. Occasional individuals of that widely distributed complex may be as dark dorsally as typical specimens of *williamengelsi*, and some large adults may be almost plain black or very dark brown. Ventrally, however, there is great variation in such dark snakes. In some, the under surface may be virtually plain black, but in others there may be bold black half-moons with or without deep red centers, a longitudinal midventral stripe of white, yellow, orange, or red may be present, or the entire belly may be dusted with gray or black, etc. Among the many thousands of specimens of *N. s. sipedon* that we (collectively) have examined, we have never encountered a melanistic population that combines all four diagnostic characteristics of *williamengelsi.* Melanism in other populations is local or restricted to a few individuals, usually large adults.

INTERGRADATION

Intergradation between *williamengelsi* and nominate *sipedon* is extensive. The fresh- and brackish-water marshes of Pea Island, which is the northern end of Hatteras Island, and on Bodie Island, just north of Oregon Inlet, have yielded a considerable number of specimens from intergradient populations. Among 13 from the Bodie Island marshes, five appear to be typical *sipedon,* four are indistinguishable from *williamengelsi,* and four are intermediate.

Among 27 specimens from Pea Island, eight show the pattern characteristics of *sipedon,* six those of *williamengelsi,* and the other 13 are intermediate. We have 11 additional specimens from the zone of intergradation between *sipedon* and *williamengelsi.* A specimen from east of Manteo, Roanoke Island, is virtually typical *N. s. sipedon*; another from the same locality is close to *williamengelsi.* Of two from Waves, Hatteras Island, one is intermediate, the other virtually *williamengelsi.* A specimen taken eight miles north of Avon, Hatteras Island, has all the characteristics of *williamengelsi.* Another, from 4.3 miles north of Buxton, Hatteras Island, is typical of *N. s. sipedon.* From the Buxton area, the southernmost limit of the zone of intergradation, one specimen appears to be typical of *sipedon,* two are typical of *williamengelsi,* and two are intermediate. Two specimens from Hatteras Island, without precise data, but presumably from north of Hatteras Village, are *N. s. sipedon* in most characters. A specimen from Creed's Hill, Frisco, within the Buxton Woods region but well west of Buxton proper, is intermediate.

We consider the following preserved specimens (all from Dare Co., North Carolina, except as indicated) to be intergrades between *Natrix sipedon sipedon* and *N. s. williamengelsi*: BODIE

ISLAND: AMNH 108839, 108842–50; Duke University collection (DU) 288. HATTERAS ISLAND: MCZ 129294, 8 mi. N of Avon; DU 227, 229, and MCZ 129296, Buxton; MCZ 129293, 4.3 mi. N of Buxton; NCSM 11800, Cape Hatteras; DU 228, Creed's Hill; USNM 72571–72, NE of Hatteras Village; DU 242, and MCZ 129301, Waves. PEA ISLAND: AMNH 108835, 108837–38, 108840–41, 108851–64 and MCZ 129309–10; DU 231, 1/4 mi. S of Oregon Inlet; DU 226, 230, 2 mi. S of Oregon Inlet; MCZ 129295, 4 mi. N of Rodanthe. ROANOKE ISLAND: Carnegie Museum (CM) 23074, E of Manteo; DU 120, 2 mi. SE of Manteo. MAINLAND: *Hyde Co.*: AMNH 89149, Engelhard.

Another specimen of *Natrix sipedon sipedon* is now available from the peninsula between Pamlico and Albermarle Sounds, an area in which members of this taxon apparently are quite uncommon. This is NCSM 11475 from Slades Creek, near Sladesville, Hyde County. The only other specimen of the nominate race reported from the peninsula is AMNH 43427 from Lake Phelps (Conant, 1963: 26).

HYBRIDIZATION

Hybridization with *Natrix fasciata* is also a major feature of *N. s. williamengelsi* biology. An apparently typical but exceptionally dark female *Natrix fasciata*, from Ponzer, on the Hyde County mainland (AMNH 88077), produced a litter (AMNH 88078–101) that exhibits a variety of characteristics ranging from those of the mother *(fasciata)* to those of typical *N. s. williamengelsi*. The pale marking passing through the angle of the jaws matches the vertical bar of *Natrix sipedon* in some, whereas in others it is comparable with the longitudinal stripe of *Natrix fasciata*. The dorsal markings vary from the posteriorly staggered middorsal and lateral bars of *sipedon* to the bands that are continuous throughout the length of the body in *fasciata*. All members of this litter are very dark. (See Conant, 1963: 30, for further details.) The mother, as noted, is a very dark *N. fasciata*; we do not know the relevance of visual cues in mate selection in these forms of *Natrix*; perhaps they are important.

A hybrid swarm occurs at Mullet Pond, on the Shackleford Banks, in a freshwater ecosystem of largely mainland ecological affinities. Among 22 specimens from Mullet Pond, four (including MCZ 46688, the type of *"engelsi"*) are morphologically typical of *Natrix fasciata*, three are more or less typical of *wil-*

liamengelsi, and the others, including young from three litters and totalling 15 specimens, are intermediate. Snakes from Mullet Pond, Shackleford Banks, are: AMNH 75800–04 + 13 untagged; DU 10, 234; California State University, Long Beach (CSULB) 263–64.

Apart from the Ponzer litter and Mullet Pond specimens, we have examined one other snake from the North Carolina mainland which is apparently a hybrid. It is NCSM 11799 from Lennoxville Point, 3 miles east of Beaufort, Carteret County.

We are of the opinion that much of the apparent introgression manifest along the shores of Pamlico Sound and associated bodies of water is a direct consequence of the massive disturbance of habitats by the great cyclonic storms that sweep ashore rather frequently in eastern North Carolina. To visit the marshes after a hurricane, as Lazell did, following Ginger in early October, 1971, is to see convincing evidence that salt water can be driven far inland by winds and tides. Conversely, as the result of torrential rains, vast quantities of fresh water move seaward after each tempest has passed, carrying many animals and plants of the freshwater biota with them on debris borne by the flood. Some of these organisms certainly must make landfalls in the salt marshes. Mayr, Linsley, and Usinger pointed out long ago (1953: 102) that hybridization between related species may occur in localities where the natural ecological balance has been badly disturbed by human interference. Conant (1963: 16–23) marshalled evidence indicating introgression between *sipedon* and *fasciata* along the Fall Line in the Carolinas where mankind has been active. Surely hurricanes are equally disturbing to the ecological balance, at least in some localities.

The distribution of specimens examined is shown in Figure 2. We have made no attempt to show localities for *Natrix fasciata*. which probably occurs in virtually every body of fresh water on the adjacent mainland. Some specimens on which we report patterns and scale counts are not included on our lists. A few snakes were discarded because of their poor condition, and one escaped near where it was collected.

ECOLOGY

Natrix sipedon williamengelsi is closely associated with marsh grasses of the genus *Spartina* and the rush, *Juncus*, wherever these form salt and brackish marshes. On Ocracoke Island, *williamengelsi* is common in salt marshes adjacent to Pamlico Sound, along the tidal creeks that carry brackish water among the dunes, and also in the fresh water of land-locked ecosystems such as that which occurs at Island Creek. The density of the water where some of the snakes were collected varied from that of the Sound proper, 1.018, to Island Creek at .999. The density at five collecting stations sampled in May and June, 1971, ranged from 1.007 to 1.015; the average density was 1.013.

The relation of density to salinity is dependent on temperature. The water samples taken at the times the snakes were collected varied from 25° to 29°C; the average was 27°C. Salinities of seven habitats sampled (including the Sound, Island Creek, and the above five) varied, therefore, from 2.7 to 24 grams per kilogram; the average was 20.5 g/kg.

In the laboratory, specimens of *N. s. williamengelsi* fed voraciously on the minnow, *Fundulus heteroclitus*, the frogs, *Hyla cinerea*, *Hyla squirella*, and *Rana pipiens*, and the toad, *Bufo fowleri*. All of these are abundant on Ocracoke. We have the impression that these snakes will eat almost any fish or amphibian small enough to swallow, as is also the case with the nominate race. Even after a full week of water starvation, our captives would not drink salt water, but they eagerly drank fresh water. Pettus (1963) obtained similar results with Gulf Coast salt marsh snakes, *Natrix fasciata clarki*.

N. s. williamengelsi is a favorite prey of marsh hawks, *Circus cyaneus*, and is no doubt taken by other raptors. The numerous species of egrets and herons that frequent the Carolina salt marshes in all probability eat these snakes regularly, but we have not observed this. Many specimens have mangled or abbreviated tails that suggest predation by birds or the crabs that are common in the habitat.

The junior author, on field trips over several years, has found *N. s. williamengelsi* abundant from May to September in the optimal habitats south of Cape Point, Hatteras Island, on the Outer Banks. In the Buxton Woods area, north and west of Cape Point, *Agkistrodon piscivorus* is common, but it is not known from the Banks to the southward, at least to Cape Lookout. *Natrix sipedon* is scarce in the Buxton Woods area, where it may fall prey to the cottonmouth.

The only other water snake known from the Outer Banks is *Natrix taxispilota*; it is confined to fresh water in the Buxton Woods area, and is scarce.

It should be pointed out that a large part of the range of *N. s. williamengelsi* is within National Park borders. The blanket protection provided for all animals includes this snake. Collecting is illegal within the Cape Hatteras National Seashore, except by specifically designated Park Service employees.

ACKNOWLEDGMENTS

We are indebted to staff members of the Cape Hatteras National Seashore Recreational Area for their cooperation with the junior author during his field work, especially to Clay Gifford, Park Naturalist; David Fletcher, Ranger; and John A. Musick, Collaborator. Specimens were lent from several study collections by, respectively, Charles M. Bogert and Richard G. Zweifel of the American Museum of Natural History, Neil D. Richmond of the Carnegie Museum, Joseph R. Bailey of Duke University, Richard B. Loomis of California State University, Long Beach, Ernest E. Williams of the Museum of Comparative Zoology, and William M. Palmer of the North Carolina State Museum. William L. Engels and John B. Funderburg loaned us material from their private collections and permitted us to deposit it in the North Carolina State Museum and the American Museum of Natural History, respectively.

The senior author is grateful to Dr. Bailey for making it possible to visit the Shackleford Banks. Harold A. Dundee furnished useful information, and Hobart M. Smith has read the manuscript and made a number of helpful suggestions.

The junior author was actively aided in the field by James Woessner, John R. Alexander, Paul Elias, Edward James, Peter Rabinowitz, Numi C. Spitzer, and Dr. Musick. Meristics, measurements, and other data were assembled by Norma Rothman, Constance A. Rinaldo, and Miss Spitzer. Mrs. Rothman obtained many specimens for the senior author's studies on the genus *Natrix* in conjunction with her own field work in North Carolina.

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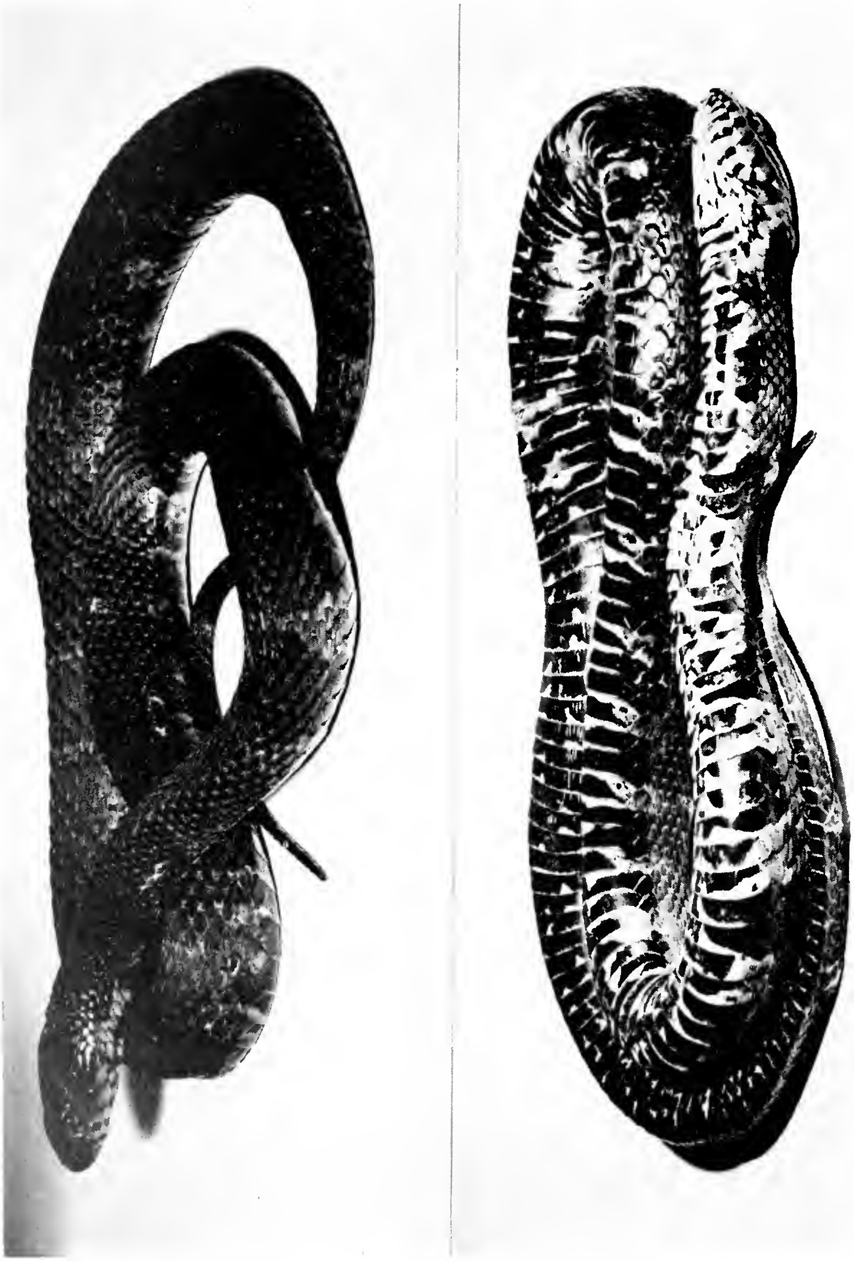

Figure 1. Carolina Salt Marsh Snake, *Natrix sipedon williamengelsi* (MCZ 129290). A large adult female from near Horse Pen Creek in the "Up Trent" region of Ocracoke Hammock, Ocracoke Island, Hyde Co., North Carolina. Total length 1224 mm. Upper: Dorsal view. Lower: Ventral view. Photos by Isabelle Hunt Conant.

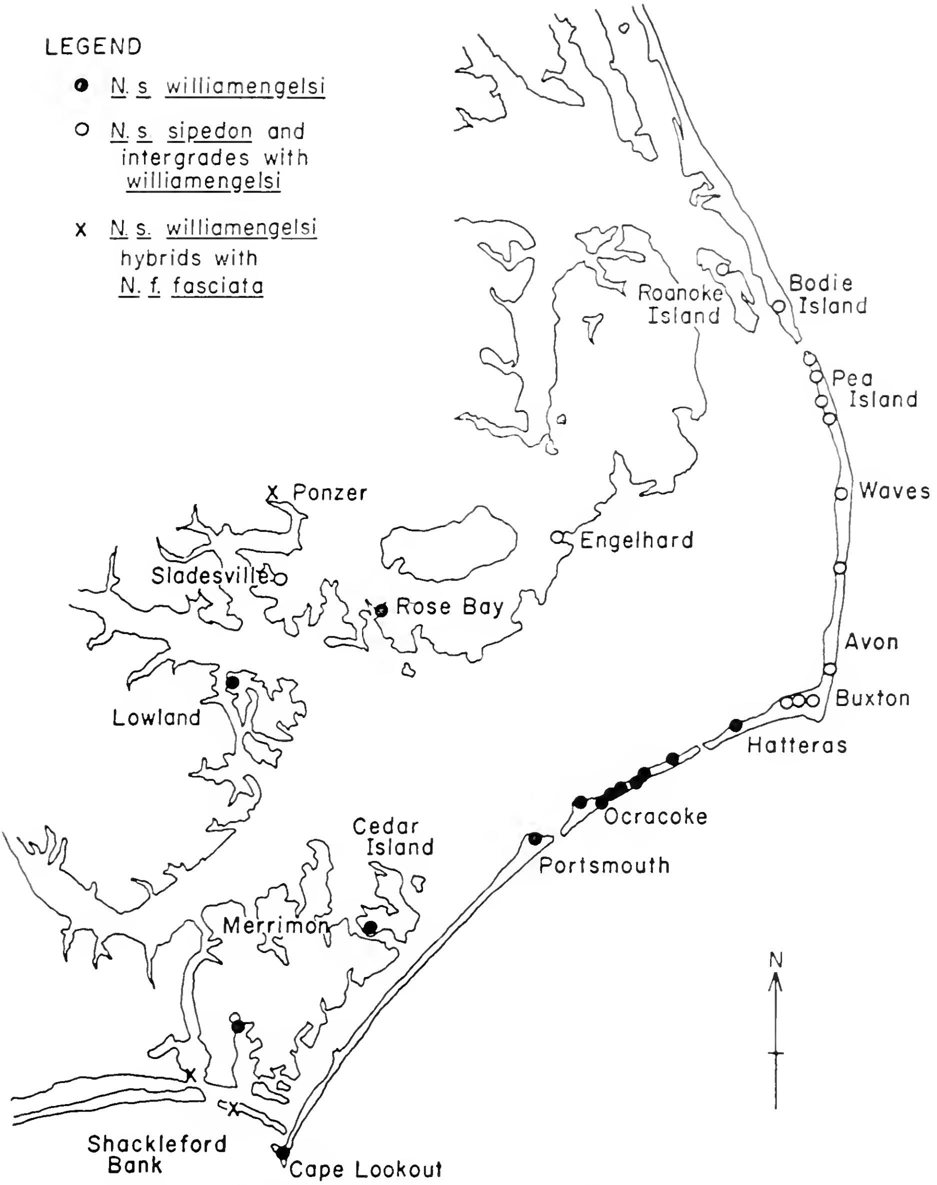

Figure 2. Map showing distribution of *Natrix sipedon williamengelsi* and intergrades between it and *N. s. sipedon* and hybrids between *williamengelsi* and *N. fasciata fasciata*.

B R E V I O R A

Museum of Comparative Zoology

Cambridge, Mass. March 6, 1973 Number 401

THE CHAÑARES (ARGENTINA) TRIASSIC REPTILE FAUNA. XVIII. *PROBELESODON MINOR*, A NEW SPECIES OF CARNIVOROUS CYNODONT; FAMILY PROBAINOGNATHIDAE NOV.

Alfred Sherwood Romer

Abstract. A small species of *Probelesodon*, similar to *P. lewisi* but of smaller size, is described as *Probelesodon minor* sp. nov.

Because of its advanced nature, particularly in the development of a squamosal socket for lower jaw articulation, it seems advisable to remove *Probainognathus* from the Chiniquodontidae and to erect for it the monotypic new family Probainognathidae.

Probelesodon minor sp. nov.

Holotype: La Plata Museum 64-XI-14-18 (field no. 138 pt.). A skull and jaws (Figs. 1, 2). From the Chañares Formation, about 4 km north of the mouth of the Rio Chañares, La Rioja Province, Argentina.

Diagnosis. A small species of *Probelesodon*, about half the size of *P. lewisi*, known skulls having a basal length of about 70 mm.

In earlier papers on the carnivorous cynodonts from the Chañares (Romer, 1969, 1970), two forms were clearly distinguishable, a large form described as *Probelesodon lewisi*, and a small, more advanced form described as *Probainognathus jenseni*. At the time of publication, preparation of this carnivorous series had not been completed and it was assumed that all the small skulls pertained to *Probainognathus*. With further preparation by Head Preparator Arnold D. Lewis, it became obvious that this is not the case. Several small skulls and jaws are clearly of the *Probelesodon* type. All are apparently mature, and do not represent growth stages; all are about half the size of the "typical" specimens of *Probelesodon lewisi*, and show a size difference too great to be sexual dimorphism. It is obvious

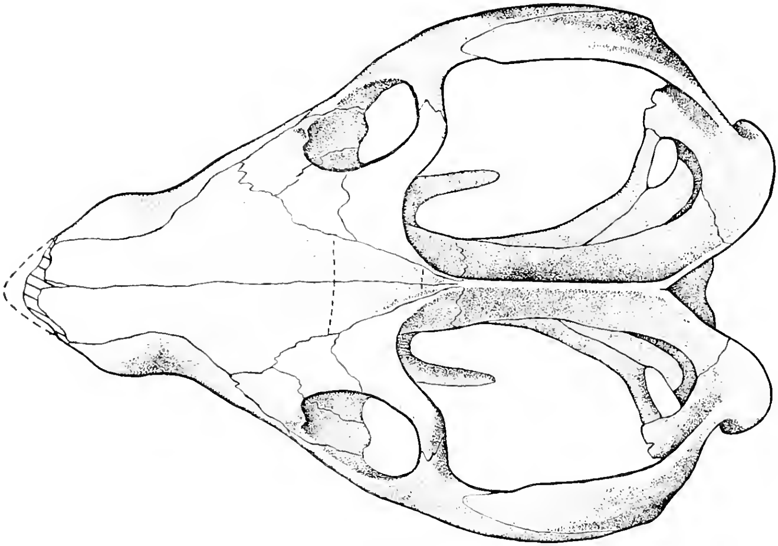

Figure 1. *Probelesodon minor,* holotype skull in dorsal view, × 3/2.

that we have a second, small, species of *Probelesodon* which is herewith described.

In addition to the holotype the new species is represented by: MCZ 4100, a skull and jaws; MCZ 4099, partial skull and jaws; MCZ 3777, jaws and some postcranial scraps; MCZ 4102, incomplete jaws; MCZ 4163, postcranial materials.

The holotype skull is incomplete in the premaxillary area, but total length was approximately 78 mm from snout to the level of the posterior end of the squamosal arch, 68 mm to the condyle. The lower jaw length is 64 mm. In MCZ 4100 the comparable figures are 73, 70, and probably 62 mm (the jaw is incomplete posteriorly). The materials of MCZ 4099, MCZ 3777, and MCZ 4102 are comparable in size. The postcranial material of MCZ 3777 (to be described in the next paper in this series) is comparable in nature to equivalent elements in *P. lewisi* except for smaller size, and the postcranial elements of MCZ 4163 are similar.

In all major features the skull and jaws are comparable to those in *P. lewisi;* skull proportions are closely comparable and the sutural pattern is similar, except that in *P. minor* the lacrimal and prefrontal are somewhat more expanded dorsally at the

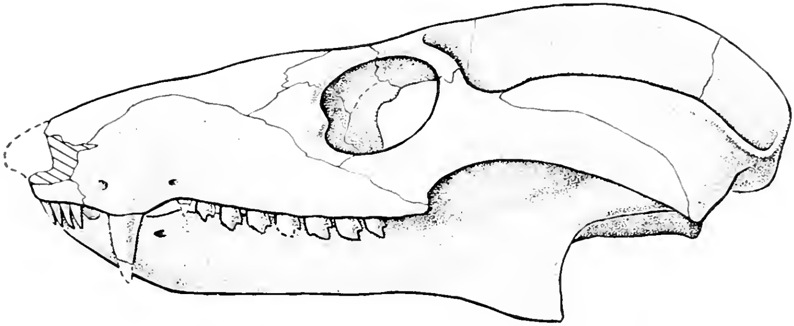

Figure 2. *Probelesodon minor*, holotype skull in lateral view, × 3/2.

expense of the nasal. The secondary palate, as in *P. lewisi*, extends remarkably far back, exceeding in development even the contemporary *Probainognathus*. As in *Probainognathus jenseni* the posteroventral flanges of the pterygoid are highly developed; also as in that species the posterior end of the lower jaw lies very close to the inner surface of the squamosal, and there was presumably a ligamentous connection, although no development of a "glenoid" articular surface.

As in *P. lewisi* there were four premaxillary "incisors," and there are, in the type and MCZ 4100, eight postcanine cheek teeth. As in *P. lewisi* these teeth are somewhat "hooked" — curved backwards at their tips. Three "incisors" are present in the lower jaw, and seven "cheek" teeth behind the prominent canine.

I have earlier suggested that *Probelesodon lewisi* was ancestral to the larger *Belesodon* of the Brazilian Santa Maria beds. Closely related to the latter was the smaller, contemporary, *Chiniquodon*. Not improbably *P. minor* may have been ancestral to *Chiniquodon*, a form of similar structure but of considerably larger size.

PROBAINOGNATHIDAE Fam. Nov.

The carnivorous cynodonts from the Chañares Formation, *Probainognathus* and *Probelesodon*, are both obviously advanced forms, with an elongate secondary palate and other progressive features. Similarly advanced are the Santa Maria forms, *Chiniquodon* and *Belesodon*, for which Huene (1944) erected the family Chiniquodontidae. In the past, I have included both

Chañares genera in that family. That this assignment is correct for *Probelesodon* seems certain, for that genus is obviously closely related to the Santa Maria forms. The position of *Probainognathus*, however, calls for further consideration. Like the proper chiniquodonts, *Probainognathus* is quite surely descended from the primitive galesaurid cynodonts of the early Triassic. But the progress has been in a somewhat different direction. The chiniquodonts proper are even more advanced in palatal construction than *Probainognathus*, but are apparently somewhat aberrant in dentition and in certain postcranial features to be described in a future number of this series of publications. *Probainognathus*, on the contrary, appears to be taking a direct course toward a mammalian condition and shows a very marked progressive situation in the development of a "glenoid" socket in the squamosal for lower jaw articulation. On the whole, it is perhaps best to separate *Probainognathus* as the type of a new family Probainognathidae, characterized by progressive cynodont features, most important of which is the articulation of the lower jaw with the squamosal in mammalian fashion.

Collection and preparation of *Probelesodon* and *Probainognathus* were made possible by grants from the National Science Foundation.

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BREVIORA

Museum of Comparative Zoology

Cambridge, Mass. June 1973 Number 402

SPECIATION IN THE GENUS *OCHTHOECA* (AVES: TYRANNIDAE)[1]

John W. Fitzpatrick

Abstract. The nine Chat-Tyrants are small tyrannid flycatchers occurring in the Andes from Colombia and western Venezuela south to Bolivia and extreme northern Chile. Most of the species are divided into numerous isolated races. There are several distinct species-groups, and the species are highly sympatric. The complicated ranges appear to have arisen during the final three Pleistocene glacial periods in the northern Andes. During glacial peaks, the then-existing species dispersed over wide ranges. They were divided during the subsequent interglacials. The three periods of dispersal and subsequent splitting first isolated the species-group precursors, then the species themselves, and finally the races of each species. The many isolated races of each species today are separated by geographic and vegetational barriers which probably affect a number of other montane species as well.

Introduction

Several recent studies (B. Vuilleumier, 1971; F. Vuilleumier, 1969, 1970) have revealed consistencies in the ranges and speciation patterns of the fauna of the South American Andes. The patterns indicate that a large number of Andean species originated and diverged in conjunction with the periodic glaciations of the Quaternary. Alternating glacial advances and retreats resulted in the complex sympatry between related species occurring there today.

The avian genus *Ochthoeca* reflects this type of complex sympatry. Eight of its nine species have widely separated races, and although several species occur throughout the central and northern Andes, others are confined to smaller areas. Sympatry among species in the genus is considerable.

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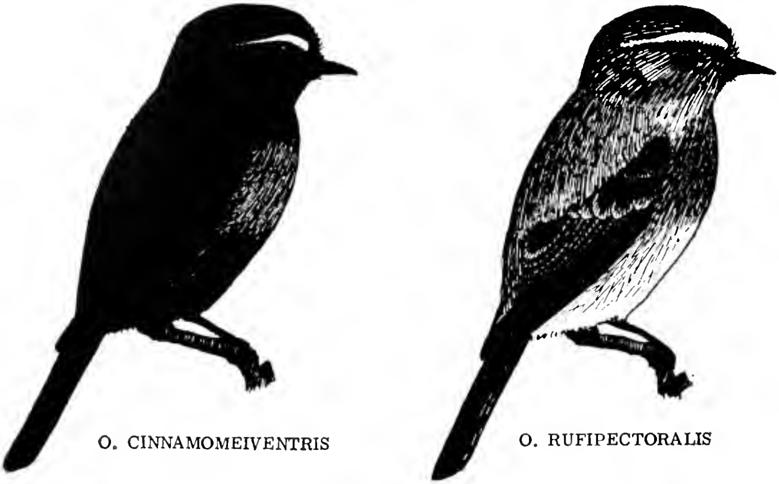
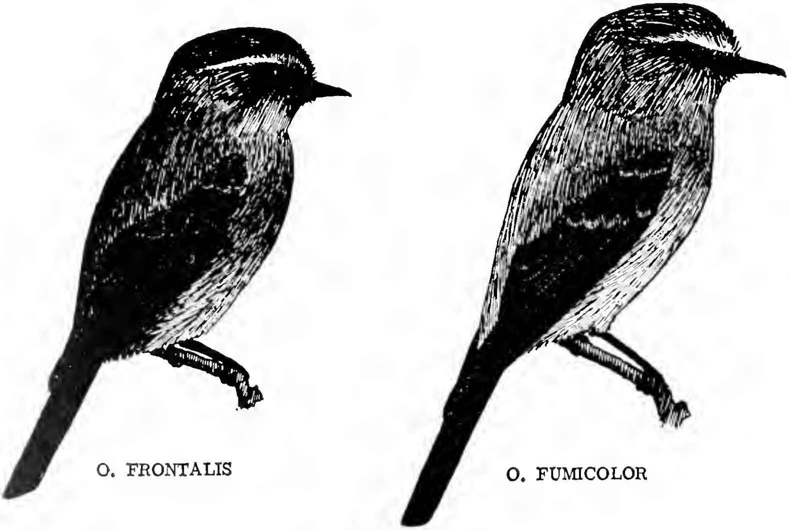


O. CINNAMOMEIVENTRIS

O. RUFIPECTORALIS



O. FRONTALIS

O. FUMICOLOR

Figure 1. Four members of the genus *Ochthoeca*. Species-groups *diadema* and *oenanthoides* are represented by *O. frontalis* and *O. fumicolor*, respectively. About two-thirds life size.

Known collectively as the Chat-Tyrants, all species are tree- or shrub-inhabiting flycatchers of the middle- and high-altitude Andes. They occur in the upper subtropical, temperate, and páramo zones from the mountains of western Venezuela and Colombia south to western Bolivia and extreme northern Chile. Members of the genus have been collected at altitudes from 500 to 4314 meters, and the average for the group is slightly over 2700 meters. They are small, generally chunky and large-headed flycatchers, and all have a conspicuous supraloral stripe, or "eyebrow," varying in length and color (see Fig. 1). Their chief mode of prey-catching is gleaning insects from the vegetation, though several species also sit on conspicuous perches and hawk insects from the air (F. Vuilleumier, 1971). All species are nonmigratory and, with one apparent exception, they are common within their respective ranges.

The ranges of each species, plotted from their collection localities, are shown in Figure 2. Based on these present ranges and on the Andean glacial events during the Quaternary, I shall propose here a sequence of speciation for the group.

THE GENUS

The genus *Ochthoeca*, as recognized by de Schauensee (1966), contains the nine species listed below. Two species are quite distinct from the others and have widespread ranges. The remaining seven have been placed in two species-groups by F. Vuilleumier (1971).

- *O. cinnamomeiventris*
- *O. rufipectoralis*
- *diadema* species-group
  - *O. diadema*
  - *O. frontalis*
  - *O. pulchella*
- *oenanthoides* species-group
  - *O. oenanthoides*
  - *O. fumicolor*
  - *O. leucophrys* superspecies
    1. *leucophrys*
    2. *piurae*

F. Vuilleumier considered *O. pulchella* and *O. frontalis* as members of a superspecies within the *diadema* species-group. Although they are very similar, differing chiefly in the amount of yellow in the eyebrow, both species have been collected at

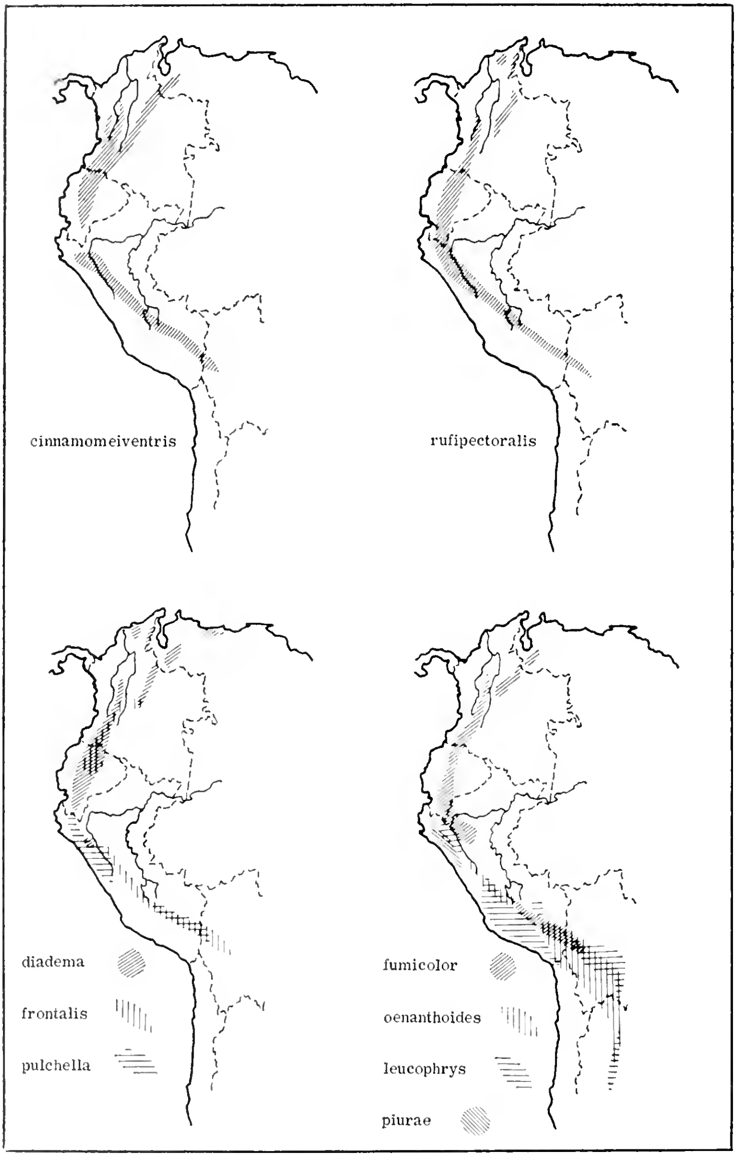


Figure 2. Ranges of species in *Ochthoeca*. The *diadema* and *oenanthoides* species-groups are shown on the lower left and lower right, respectively.

each of four localities, and their ranges show considerable overlap south of the Marañón River. I shall, therefore, treat them as sibling species within the group.

One species, *cinnamomeiventris*, occurs in the moist forests of the upper subtropical and temperate zones. Its dark coloration is adapted to these dense, wooded habitats. Its bill is the broadest and shortest of the genus, reflecting its diet of aerial insects captured by hawking. *O. rufipectoralis* and the *diadema* species-group inhabit open forests of the temperate zones. Their bills are also short, but all are much thinner than that of *cinnamomeiventris*. *O. diadema* is the only species whose plumage is largely green. The *oenanthoides* species-group contains forms frequently found over 4000 meters. *O. fumicolor* lives in moist páramo habitats, while *oenanthoides* and the *leucophrys* superspecies occur in the dry puna scrub and grasslands (F. Vuilleumier, 1971). Members of this group have long, thin bills adapted to their diet of insects gleaned from the vegetation. All have significantly larger bodies than the other *Ochthoeca* species, with relatively longer wings and tails. *O. leucophrys* is predominantly grey, while the other two are buffy brown.

PLEISTOCENE CLIMATIC INFLUENCES

The zoogeographic history of these species seems closely related to the periodic altitudinal lowering of their habitats during the Quaternary glaciations. Glacial climates affected the forest- and grass-life zones in two ways. First, the limits of each were lowered, creating connections or closer proximity between previously isolated habitats. During maximum glaciation, the life zones were lowered sufficiently to become nearly continuous along the entire mountain chains (B. Vuilleumier, 1971). Second, the valleys and lower mountain areas became more humid as the ice and glacial lakes surrounded them. This again resulted in greater proximity between the formerly higher and isolated humid life zones. During the glacial maxima, the lowering of the habitats permitted many avian species to colonize through the northern mountain chains along a north-south axis. During interglacial periods the life zones retreated to higher altitudes, thereby splitting again into isolated "islands." The deep valleys became dry, further decreasing the potential for gene flow between neighboring high-altitude populations. Thus a species whose range had been widespread and nearly continuous during maximum glaciation divided during the subsequent interglacial. New races and species evolved as a result.

Within the central and northern Andes, two particular climatic features affected speciation in high-altitude populations. First, the western slope from southern Ecuador through Peru and northern Chile now receives very little rainfall. Presumably this was the same in the past, and the area remained generally unavailable to the forest-inhabiting *Ochthoeca* species. Only one species, *leucophrys*, occurs in this arid region today. Second, two large areas of low, dry vegetation occur within the range of this genus. The first is the low, semi-arid valley of the upper Magdalena River, which lies between the Eastern and Central Cordilleras of Colombia, creating a significant barrier between a number of montane taxa on either side (F. Vuilleumier, 1969). Five *Ochthoeca* species now occur in northern Colombia and northwest Venezuela. Only that species inhabiting the lowest altitudes does not show a major break and/or subspecific differentiation in this area. A second, equally effective barrier occurs in the region of the upper Marañón River in northern Peru. The low mountains in this area create a wide break between the extensive high-altitude regions of Peru and Ecuador. The ranges of all nine *Ochthoeca* species reach this divide, and six show major breaks at the barrier. Furthermore, evidence exists that warmer Pleistocene interglacial temperatures resulted in even drier conditions still less favorable to alpine life than today's climate (B. Vuilleumier, 1971). Hence these dry barriers isolated populations more effectively in the past than they do today. These two major divides thus created three large, separate areas of montane conditions north of Bolivia which appear to have been the primary centers for speciation in *Ochthoeca*, and certainly for other species as well.

Speciation in Ochthoeca

Geologists recognize four major world-wide glacial advances during the Pleistocene (*e.g.*, Leet and Judson, 1971), but the first had relatively less effect on the northern Andes, since they were the last to attain their present height (B. Vuilleumier, 1971). Data on high-altitude species in the northern Andes indicate that they were derived predominantly from central Andean birds (F. Vuilleumier, 1970). Species originating in these central mountains dispersed northward during the three major glacial periods affecting the northern mountains. The precursor of the genus *Ochthoeca* seems therefore to have originated in the central Andes, and became isolated during the first Pleisto-

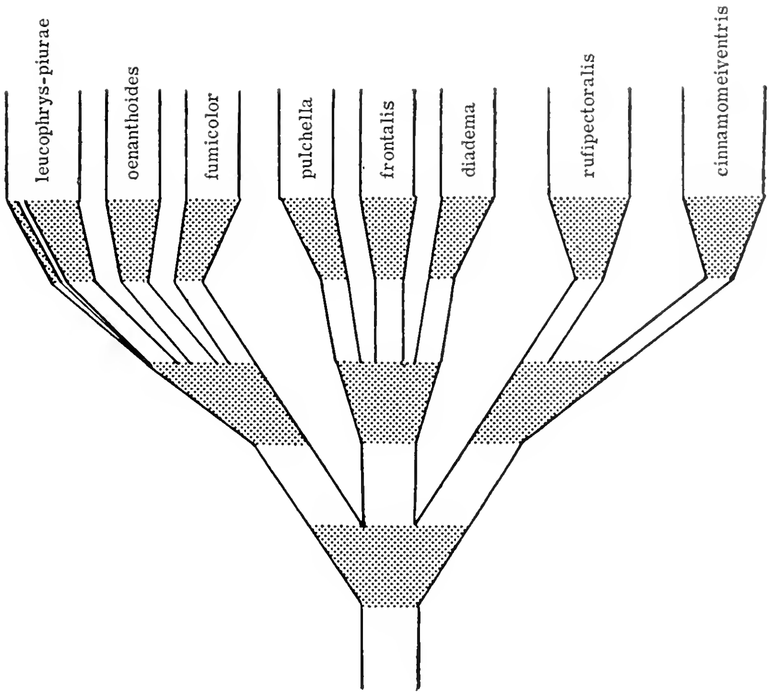


Figure 3. Schematic evolution of the genus through time, from its ancestral stock. Shaded areas show dispersal periods during the final three glaciations; unshaded areas represent interglacial periods, when isolated populations differentiated into new forms.

cene interglacial period. As are most species today, this was probably an open-forest bird. The occurrence of seven of today's nine species in northwestern Bolivia and southern Peru further indicates that the area was probably suitable to the precursor.

The development of the modern genus from this precursor is suggested by the structure of the group as a whole. The existence of clear-cut species-groups, the subdivision of the groups into component species, and the species' divisions into morphologically distinct races indicate three separate occasions of dispersal each followed by isolation. In the first period, the parent species was split into species-group precursors, which in turn split into their component species following the second dispersal period.

Finally, after the third period, each species was broken into the isolated populations found today. These three dispersal periods correspond to the three glaciations following the isolation of the progenitor early in the Pleistocene. This pattern is outlined in Figure 3. A detailed sequence for this speciation will now be presented.

During the first of the three glaciations, the parent species was probably able to colonize northward over the entire Andean chain. Colombia's Eastern Cordillera had by this time gained its present altitude and could support alpine life, particularly during the cold, damp glacial period. At this time there was sufficient gene flow throughout the range to inhibit differentiation and the population remained a single species.

Upon glacial retreat, the two major geographic barriers, the Magdalena and the Marañón valleys, became effective. As illustrated in Figure 4a, the original species was split into three populations that formed the parent stocks of the two species-groups and the precursor to the remaining two species. The southernmost population, in the highest mountain areas, gave rise to the highest-altitude species-group. This precursor shall be referred to as "oenanthoides."[1] This conclusion is further strengthened by the generally southern ranges of these species. While this form was confined to Peru and Bolivia, forest birds

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[1] To avoid confusion between these primitive taxa and the modern species to which they gave rise, the precursors will be called by their species-group name, within quotation marks. Hence "oenanthoides" eventually gave rise to the species now within the *oenanthoides* species-group.

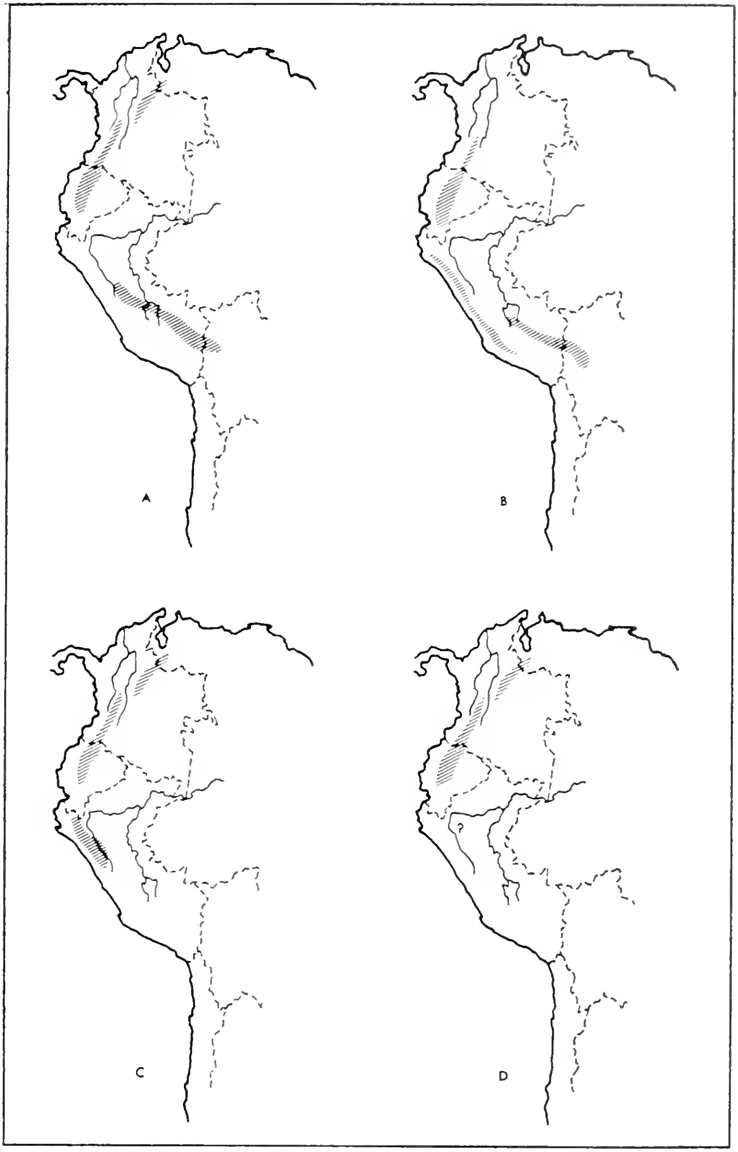
Figure 4. (A) Three populations isolated after the Mindel (second) Pleistocene glaciation; "diadema" (north) and "oenanthoides" (south) gave rise to the respective species groups; "rufipectoralis" (central) differentiated as shown in 4(D).

(B) Status of "oenanthoides" during and following the Riss (third) glaciation; *leucophrys* (west) and *oenanthoides* (east) were separated by glacial ice and lakes. *O. fumicolor* differentiated in the north.

(C) Isolation of *diadema* (north), *frontalis* (central), and *pulchella* (south) from "diadema" following the Riss glaciation.

(D) Isolation of *cinnamomeiventris* east of the Magdalena River following the Riss glaciation. *O. rufipectoralis* (central) may have ranged south of the Marañón River by this time.

Various races have now differentiated following the dispersal of the species during the Würm (final) glaciation.


A
B
C
D
?

in western Ecuador and Colombia differentiated into "rufipectoralis." The population that was isolated in the Eastern Cordillera of Colombia became "diadema." These latter two forms probably remained relatively undifferentiated until the succeeding glaciation brought them into secondary contact, since even today they apparently share similar habitats.

The second glacial episode again resulted in range extensions along the lower valleys. An important occurrence during this period is illustrated in Figure 4b: "oenanthoides," which was evolving into a higher-altitude, páramo-inhabiting species, extended through the central and northern mountains. Its range seems to have been divided during the glacial peak by the extensive ice and glacial lakes that capped the highlands of Peru and Bolivia in complex patterns (B. Vuilleumier, 1971). Thus at least three populations were isolated during this glaciation, as a result of their high-altitude requirements. Restricted by the ice to a portion of the western slope, *leucophrys* developed into a puna-inhabiting species. *O. oenanthoides* differentiated to the east, and the two apparently exclude each other over much of their ranges, for sympatry today remains fairly small; they still reflect somewhat these primitive ranges. *O. piurae* also probably speciated at this time on an isolated puna region in extreme northwestern Peru, never drifting far enough from *leucophrys* to permit extensive sympatry after the glacial retreats.

Figure 4c illustrates the probable spread and differentiation of "diadema" into the species of that group. Again the two barriers created three surviving, isolated populations, which evolved into *diadema* in the north, *frontalis* in the central mountains, and *pulchella* south of the Marañón. Characters shared by these species are nearly identical wing, tail, and bill measurements, wingbars, and bright yellow in the eyebrow, as well as smoky-grey crowns and backs; their close relationship is quite clear. Their current ranges reflect the three primitive ranges, with one exception: the range of *frontalis* now extends southward to overlap that of *pulchella*. To judge from collection data, however, *frontalis* appears less common within this southern range extension. The frequency of *pulchella* south of the Marañón and its total absence farther north indicate that *frontalis* did achieve species rank in the north and move south into *pulchella*'s range.

The second glaciation allowed the expansion of "rufipectoralis" along the forests of the northern Andes, possibly throughout the range of the genus. When the ice retreated, two populations were separated. In the forests east of the Magdalena River, *cinnamomeiventris* differentiated, and in the central Andes, *rufipectoralis* reached species rank. This pattern is suggested by the large gap in the current range of the latter species across the Magdalena. This break is not present in the range of *cinnamomeiventris*, which adapted to the moist forests at a lower altitude in the Eastern Cordillera. Furthermore, the relative frequencies of the two species follow this pattern — *cinnamomeiventris* is common in the north and occurs only at scattered localities south of Colombia. *O. rufipectoralis* is much more common in the south though it has established small populations in the north, where *cinnamomeiventris* originated. Their close relationship is supported by their sharing of the white eyebrow and the conspicuous rufous-chestnut breast band. *O. cinnamomeiventris* appears to be a darkened form of *rufipectoralis* adapted to forest habits (see Figure 1). Their morphological and ecological differences certainly increased upon secondary contact, and both species eventually dispersed throughout the range of the genus. Their phylogenetic relationship appears to be analogous to that of the two species-groups. Their status as taxonomically distinct species arose from their more significant divergence following the second glaciation.

Thus all current species were present at the onset of the final glaciation. Their ranges had already overlapped in several regions, and they probably had become well differentiated. During this glaciation the species colonized new areas as far as suitable habitat and competition with congeners permitted. The northeastern species, *diadema* and *cinnamomeiventris*, moved south, *diadema* stopping where *pulchella* was established. Many populations seem to have crossed the Marañón to invade the moist eastern slopes of Peru, resulting in the seven species occurring there today. *O. leucophrys*, a strictly high-altitude species, crossed to the east and spread south into Argentina. Upon glacial retreat this resulted in a series of isolated populations stretching southward along the mountains at progressively lower altitudes that coincided with the preferred habitat. In short, each species spread to its ecological limits and was subsequently split by the final warming and drying of the valleys. Hence the morphological isolates recognized today give evidence for the geographic barriers that split these last major glacial range expansions.

CURRENT SPECIATION

Isolated races of each species now exist in regions which, following the last glaciation, became sufficiently separated to limit gene flow between them. Several interesting exceptions are worthy of note.

The relative scarcity of *O. frontalis* (I found only twenty localities recorded in the literature) makes meaningful discussion of its subspecific ranges difficult. The apparent large break in its distribution in northern Peru seems insufficient to isolate the populations on either side, as both are apparently the same race (Carriker, 1933; Zimmer, 1937). It appears, therefore, that the gap is a product of the rarity of the species, rather than a genuine absence throughout the region.

The subspecific continuity of *O. fumicolor* across this same low divide is also confusing, for the species normally occurs at altitudes well over 3000 meters. In contrast to *O. frontalis, O. fumicolor* is extremely common in the north-central Andes; apparently the few small isolated páramos within the divide permit the maintenance of gene flow across it. Collection localities from north to south through the divide are: Bestión (3100 m), Taraguarcocha (3200 m), El Tambo (2900 m), Cutervo (3000 m). Hence certain sufficiently common species apparently have the potential for gene flow across this divide.

Among other species, in areas lacking any major geographic barriers, several subspecific discontinuities are found which would seem to be the result of habitat breaks not marked on vegetation maps. In one such area, *O. frontalis, O. cinnamomeiventris,* and *O. rufipectoralis* each split into different races on either side of the extreme upper Marañón, while higher altitude species do not. Excessive taxonomic splitting of clinical differentiation may cause these anomalies.

In general, the modern ranges of the species, with their many isolated races, provide accurate evidence of currently isolated vegetation zones. Such regions, as indicated also by B. Vuilleumier (1971), are presumably equally important in many other upper montane species. These regions, some of which may be areas of current or future speciation, are separated by the geographic barriers listed below. The *Ochthoeca* species split apart by the barriers are listed under each.

1. Huallaga Valley, southern Peru
   fumicolor, leucophrys, pulchella

2. Marañón Valley and low Peruvian mountains
   cinnamomeiventris, diadema
3. Upper Magdalena Valley, northern Colombia
   fumicolor, diadema, frontalis, rufipectoralis
4. Cristóbal Valley, separating mountains of Mérida, Venezuela, from the Eastern Cordillera
   fumicolor, cinnamomeiventris, diadema
5. Yaracuy River valley, isolating the northern coastal mountain ranges of Venezuela
   diadema
6. César Depression, isolating Nevada de Santa Marta
   diadema, rufipectoralis
7. Upper Rio Catumbo depression, separating the Perija Ridge from the Eastern Cordillera
   diadema, rufipectoralis

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B R E V I O R A

Museum of Comparative Zoology

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A NEW LATE PALEOCENE PHENACODONT (MAMMALIA: CONDYLARTHRA) FROM WESTERN COLORADO

Bryan Patterson and Robert M. West[1]

Abstract. A new genus and species of phenacodont condylarth, *Prosthecion major*, is described from late Paleocene beds of the De-Beque Formation of western Colorado. *Prosthecion* is most closely related to the well-known small Paleocene-Eocene phenacodont *Ectocion*, although it also shows some similarities to the larger *Phenacodus*. The new genus contributes additional emphasis to the rather unique nature of the mammalian assemblage of the Plateau Valley local fauna.

Introduction

Among the fossil materials collected by Field Museum of Natural History field expeditions to the early Tertiary of Mesa County, Colorado, in 1932, 1933, 1937 and 1939, are several specimens of a new genus of phenacodont condylarth. These specimens were recognized as novel by one of us, Patterson, who assigned to them a manuscript name, but this was not formalized by publication. The genus has been mentioned, however, without use of the generic name in West (1971: 5). The present paper establishes the new taxon in conjunction with West's review of the family Phenacodontidae.

We thank Dr. William D. Turnbull of the Field Museum of Natural History for the loan of the specimens described herein. The illustrations were prepared by the late John Conrad Hansen.

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ORDER CONDYLARTHRA

FAMILY PHENACODONTIDAE

Prosthecion[1] **gen. nov.**

Type species. *Prosthecion major* sp. nov.

Included species. Type only.

Distribution. Late Paleocene, western Colorado.

Diagnosis. Moderate-sized phenacodont; approximately the same size as *Phenacodus bisonensis* and *P. vortmani*, larger than *Ectocion wyomingensis* and *E. osbornianum*. Upper premolars with complete cingulum and smaller conules and parastyle than in *Ectocion*. P^3 shorter and wider than in *Ectocion*, with separate metacone and paracone. Upper molars similar to those of *Ectocion*. P_3 with strong paraconid, distinct metaconid, rudimentary protostylid, and hypoconid surrounded posteriorly by a cingulum; heel broader than in *Ectocion*. P_4 with hypoconid more central in position than in *Ectocion*, entoconid not differentiated, rudiments of protostylid and metastylid present. Lower molars intermediate between those of *Ectocion* and *Phenacodus*, moderately robust and lacking well-developed paraconid, especially in posterior molars.

Prosthecion major[2] **sp. nov.**

Text-figures 1–4

Type. FMNH P26131, LP^3–M^2 (P^3, $M^{1\text{-}2}$ incomplete), incomplete RP^3, M^3; two lower I's, R and LP_3–M_1 (incomplete). Found by William M. Harris.

Hypodigm. Type plus FMNH P15586, part of left ramus with M_1–M_3; P15570, part of left ramus with P_4–M_2; P26129, LM_1; P15581, RM_1; P14940, RM_2; P14947, RM_3; P15011, incomplete RM_1; P26066, trigonid of M_2; P26128, lower molar fragments.

Horizon and locality. Middle late Paleocene, lower part of Atwell Gulch Member of De Beque Formation[3]; Plateau Valley local fauna. Holotype from "Hell's Half Acre," 6 miles SSE of De Beque on the De Beque-Mesa road, W 1/2 sec. 14, E 1/2 sec. 15, and NW 1/4 sec. 23, T.9S., R.97 W., Mesa County, Colorado. Remainder from scattered nearby localities.

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[1] *πρόςθετος* additional, plus *κιων*, pillar; in allusion to the large paraconid of P_3 and to the relationship with *Ectocion*.

[2] Largest species of *Ectocion* group.

[3] Wasatch Formation *in* Donnell, 1969.

Distribution. Late Paleocene of western Colorado.

Diagnosis. As for the genus.

Discussion. *Prosthecion* is a genus that combines certain characteristics of *Ectocion* and *Phenacodus* with others peculiar to itself. The cingula on the upper premolars readily differentiate *Prosthecion* from the other known phenacodonts. The degree of metacone development is similar to that in *Ectocion*, whereas *Phenacodus* has only slightly developed parastyles and conules. *Ectocion* premolars are less robust than are those of *Prosthecion*. The upper molars, so far as they are known, are *Ectocion*-like, and also show some resemblance to the earlier (and probably ancestral) *Tetraclaenodon* in the position of the metaconule and the small size of M^3.

P_3 of *Prosthecion* is more advanced than that of *Ectocion* in its possession of a metaconid, a strong paraconid, and a rudimentary protostylid. Talonid complexity here differentiates *Prosthecion* from *Phenacodus*. P_4 is peculiar in the possession of stylids and in the central position of the hypoconid. The relatively small paraconid is a departure from the basic *Phenacodus* plan, but the paraconid is larger than in P_4 of *Ectocion*. The molar paraconids form anterior ridges that are decidedly crenulated in P26129, less so in P14940, and smooth in the rest. *Prosthecion* is not so extreme as *Ectocion*, where the paraconid is absent and is replaced by a steeply sloping ridge. The trigonid basin is open antero-internally in all specimens except P15011 and P15581, in which the paraconid ridge unites with the metaconid. Entostylids are present in P15586 (except on M_3) and P26129, rudimentary in P14940, and absent in P15581. External cingula are lacking on most lower teeth, vaguely suggested on a few, and definite only on P26129.

Prosthecion is clearly a close relative of *Ectocion*, which here is considered congeneric with *Gidleyina*; work in progress by West will provide evidence in support of this synonymy. This, then, leaves two genera in an "*Ectocion* group" of phenacodonts. Simpson (1937: 251, note 12) mentioned, and disapproved of, a manuscript proposal by Gidley to separate the *Ectocion* group subfamilially from the *Tetraclaenodon-Phenacodus* lineage. While it is apparent that two rather distinct evolutionary trends were being followed by the phenacodonts, specialists should be able to discuss such minor groups as these without giving them formal hierarchic rank.

Thus, with the addition of *Prosthecion* to the roster of late

Paleocene phenacodonts, there were at least three genera descended from the common middle *Paleocene Tetraclaenodon*: *Phenacodus*, *Ectocion* and *Prosthecion*. The first two of these are abundantly represented in later faunas, and *Phenacodus* underwent a moderate radiation, producing several size-differentiated species. *Prosthecion*, as yet unknown later than late Paleocene and outside of western Colorado, was either a member of an unsuccessful, short-lived lineage, or one that occupied environments as yet poorly sampled. The latter possibility is supported by the rather distinctive nature of the Plateau Valley local fauna.

TABLE 1

Measurements, in mm, of teeth of *Prosthecion major*

		P 26131	P 15570	P 15586
P_3	L	7.7		
	W tri	4.3		
	W tal	4.5		
P_4	L	8.6	8.7	
	W tri	5.5	5.8	
	W tal	5.8	5.9	
M_1	L		9.0	9.4
	W tri		7.5	6.6
	W tal		7.4	7.1
M_2	L		9.0	9.8
	W tri		7.8	7.4
	W tal		7.5	7.2
M_3	L	9.9		9.7(e)
	W tri	6.8		6.6(e)
	W tal	5.9		5.9
P^3	L	7.4		
	W	7.6(e)		
P^4	L	8.1		
	W	9.4		

e — estimated

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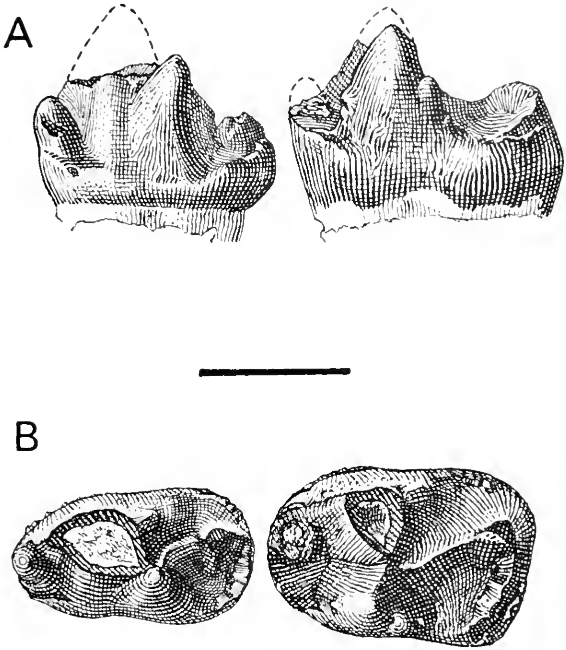

Figure 1. Lower premolars of *Prosthecion major*, P26131, type specimen. Line indicates 5 mm.
A. Occlusal view, P$_3$ and P$_4$.
B. Lingual view, P$_3$ and P$_4$.

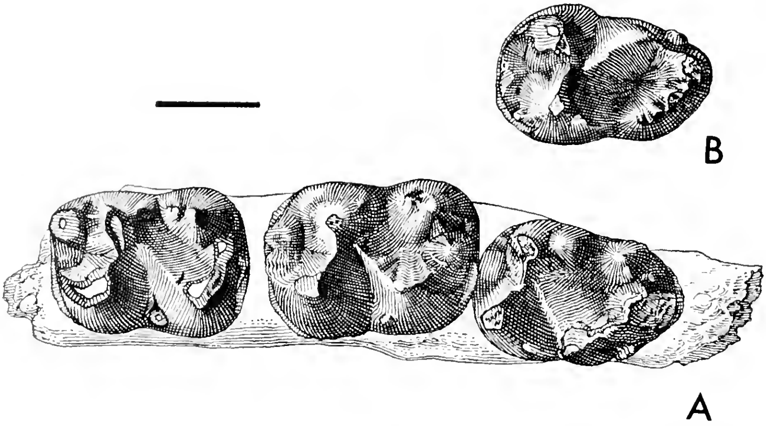

Figure 2. Occlusal view of lower molar dentition of *Prosthecion major*. Line indicates 5 mm.
A. P15586, M_1–M_3.
B. P26121, type specimen, M_2.

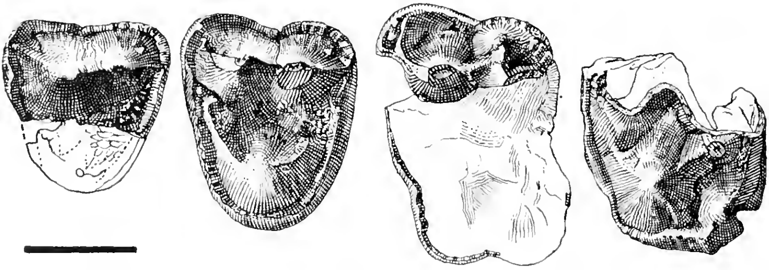

Figure 3. Upper dentition of *Prosthecion major*, P26131, type specimen, P^3–M^2. Line indicates 5 mm.

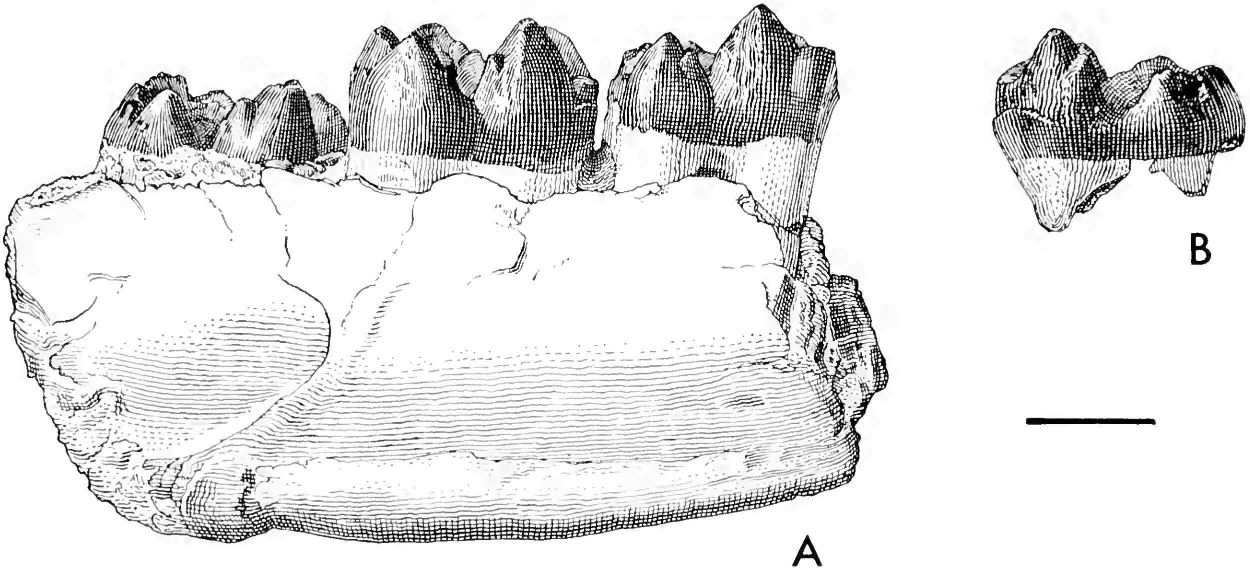

Figure 4. Lingual view of lower molar dentition of *Prosthecion major*. Line indicates 5 mm.
A. P15586, M_1–M_3 (anterior to right).
B. P26131, type specimen, M_3 (anterior to left).

BREVIORA

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NEW STUDIES ON A MONTANE LIZARD OF JAMAICA, *ANOLIS RECONDITUS*

Robert Hicks[1]

Abstract. Data on the natural history of *Anolis reconditus*, an arboreal iguanid lizard, living in the montane mist forest of east central Jamaica, is presented. The animal uses the crown of trees both for sleeping and as a refuge when frightened. It perches facing down on open tree trunks, generally about 12 feet off the ground. Its displays appear to vary a great deal from individual to individual. This animal seems to use a combination of two typically anoline foraging methods: 1) active searching and 2) motionless perching. In addition, *reconditus* displays a characteristic reported in no other Jamaican anole: it does not interrupt its daily activities because of rain. The lizard appears to be less specialized than its Jamaican congeners. This may be related to its apparent isolation from congeneric competition.

INTRODUCTION

Of the seven species of anoline lizards in Jamaica, *Anolis reconditus* is apparently the rarest and certainly the least studied. This relatively large (*ca.* 90 mm snout–vent length), montane reptile was first described in 1959 by Underwood and Williams from a single male specimen. The animal is usually green, brown, and beige. It is mottled and striped laterally and dorsally, often with a prominent small green patch just behind each eye.

The type specimen was collected in 1953 in St. Thomas parish, on the edge of the Blue Mountain rain forest region in east central Jamaica. In 1961 and 1962 A. Stanley Rand collected five lizards at Hardwar Gap, nine miles west of the type locality. In 1965, J. D. Lazell captured five additional *reconditus*, including the first females, in the Hardwar Gap area; he published a paper (Lazell, 1966) that added substantially to the

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scanty data on coloration, squamation, and behavior of this lizard. Robert Trivers in 1969 collected, marked, and released several specimens at the Green Hills field station of the Institute of Jamaica, one mile northeast of Hardwar Gap.

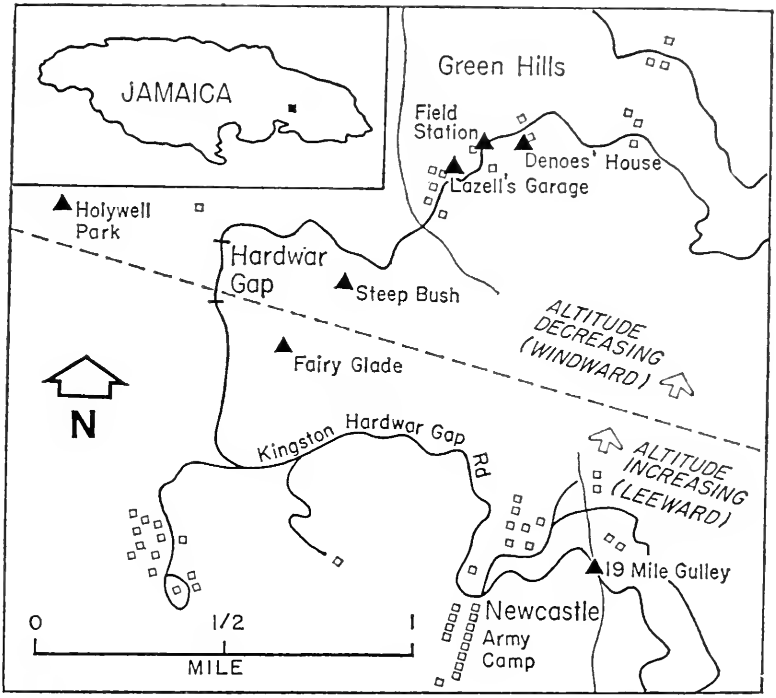
In 1970, I spent the months of April and May in Jamaica observing all seven species of *Anolis* on the island for varying periods of time. I spent two weeks with Robert Trivers, who was working on *A. garmani,* and two weeks with Thomas Jenssen, who was studying *A. opalinus, A. lineatopus neckeri,* and *A. sagrei.* Between April 26 and May 28, I lived three weeks at the Green Hills field station, near Hardwar Gap. During this time I caught, marked, and observed 32 *reconditus.* I saw at least another two dozen. The data that follow are the results of my study.

HABITAT AND RANGE

During my stay at Green Hills, I discovered some specific new localities in the Hardwar Gap region which have substantial populations of this species. The population that Lazell (1966) describes as living in the garage near the field station, I found in the garage and on a stand of trees just adjacent to and east of the garage. I also saw one animal living under the eaves of the Denoes' house, which is just east of the field station and across the road.

One of my main study areas, referred to hereafter as "Steep Bush," was located about one-quarter mile southwest of the field station along the road to Hardwar Gap. The road is cut into the mountainside, which slopes 50° or more. The viney, densely wooded "montane mist forest" (Asprey and Robbins, 1953) is called "bush" by the local people. The area where I worked on seven different days is on the top side of the road. I concentrated on a roughly square area that runs along the road for about 300 yards and extends up the mountainside an equal distance.

The trees there are generally 30 to 50 feet tall, with no branches below 20 feet. Several feet of their root systems are exposed as they cling to the steep mountainside. Moss covers the rocks, much of the tree trunks, and the fallen trees and limbs. There are also 15-foot tree ferns, vines, and saplings. The canopy is quite dense and everything, including the deep leaf litters, is very damp. The trees are generally plane trees. Wild yacca *(Podocarpus urbanii)*, milkwood *(Sapium jamai-*



Map 1. Hardwar Gap-Green Hills vicinity. Note collecting sites for *reconditus* marked by triangles. Open squares are buildings.

cense), and trees known to the local people as "fleura" are most abundant.

In Steep Bush, I caught ten lizards and made many observations. However, movement for an observer is extremely difficult in this "montane thicket" (Asprey and Robbins, 1953), and, owing to the mazelike quality, resightings are nearly impossible.

My best study area was a place, known locally as "Fairy Glade," one-quarter mile east of Hardwar Gap. It is on top of the ridge that lies to the east of the Gap and is the largest area of flat "bush" land that I could find within several miles of Hardwar Gap. The glade is about 10 acres in extent, and has a path 10 to 30 feet wide running through it which leads northeast to St. Catherine's Peak.

Lazell (1966) quotes Rand as saying he found *reconditus* in "mossy, stunted forest — nearly 'elfin woodland' — at Hardwar

Gap." This is an excellent description of the Fairy Glade. Although generally found over 5000 feet, elfin woodland occurs as low as 2500 feet in the John Crow Mountains, which are east of the gap. Asprey and Robbins (1953) regard elfin woodland as a faciation of montane mist forest. Fairy Glade represents an intermediate stage between the montane mist forest of the steeper, lower slopes and the dwarfed, stunted, typically elfin woodland of the higher altitudes. The omnipresent moss is often six to eight inches deep on the ground and on the rotting fallen trees and limbs which litter the ground.

The trees in the glade are generally of large diameter with full foliage but are occasionally twisted, unlike the tall, straight, branchless trees of Steep Bush. The growth of the glade could certainly be described as lush. An early botanical observer, in describing similar Jamaican vegetation, spoke of "the confusing abundance of species and the rich plant life in a muggy, glasshouse atmosphere." (Asprey and Robbins, 1953).

I caught and marked 15 lizards along a 200-yard stretch of the path which runs through the glade. Most of my data are for these lizards.

I also observed lizards at two other localities in the Hardwar Gap region: (1) in the northwestern part of Holywell Park, just west of the gap, and (2) in the "19 Mile Gulley," a steep, dark, damp, rocky ravine about four miles southeast of the gap and along the road to Kingston, just below the 19-miles-from-Kingston roadside marker. This latter area is several hundred feet lower than Steep Bush but has about the same physical character and vegetation. In half an hour on my final day in the Hardwar Gap area, I located four large males and one female in this gulley. In Holywell Park, I saw only one animal, a male.

With the exception of Lazell's garage (see above), I was directed to all the places where I found *reconditus* by local Jamaicans. Consultation with those local people who frequent the "bush" could in the future lead to a better understanding of the extent of the lizard's range.

It seems likely that *reconditus* extends over a narrow, perhaps discontinuous band of montane mist forest running east and west of Hardwar Gap. The band is at least two or three miles wide in places. The Green Hills area is half to three-quarters of a mile north of the gap and the Newcastle area one to one and a half miles south of the gap.

SIZE AND SEXUAL DIMORPHISM

During my month of study, I observed at various times more than 50 different individuals. Thirty-two of these were captured; 29 were measured.

Of the 17 measured males, the largest had a snout–vent length of 100 mm, the smallest 61 mm. The largest lower jaw (tip of snout to back of lower jaw), 33 mm, was that of a 98-mm male, the shortest, 20 mm, that of the smallest male (61 mm). The longest tail, 220 mm, was recorded on a 96-mm male; the shortest unbroken tail was 115 mm, on the smallest individual (61 mm) captured.

Of the twelve females that I measured, the longest snout–vent length was 84 mm. This lizard had the longest lower jaw, 26 mm, of any female. The longest tail, 164 mm, was on a 77-mm lizard. The smallest female, smallest in each of the three measurements taken, was 62 mm snout–vent with a 19-mm lower jaw and an 121-mm tail.

The body length of *reconditus* males is 1.17 times longer than females and the lower jaw of males is 1.19 times longer than females. Robert Trivers (personal communication) has found that for *A. garmani* in southwestern Jamaica, the adult males are 1.31 times longer than the adult females.

COLOR

When describing *A. reconditus,* Lazell (1966) emphasizes a grey component in the coloration of the animal. According to my observations, a more accurate description of the lizard is that a tan or brown component predominates. I never observed any part of a lizard to be black or grey. Often parts of the lizard would be very dark brown. These appeared tan when the lizard changed to a lighter color phase. In my field notes I once described a cryptic male perched on a grey tree trunk as "brown, greyish mottled." However, I still maintain that close observation reveals only shades of brown, never grey.

Interestingly, the populations in my main study areas, three-quarters to one mile apart and physically isolated from each other only by heavy undergrowth and overgrown gulleys, seem to differ in color. The males of the Steep Bush area appear generally light brown with quite dark brown markings and stripes. They are green or slightly bluish green just behind the forelegs. They can change to a mossy dark green or to a dark chocolate. With both these color changes, the markings fade out.

The females of Steep Bush are lighter tan than the males, with prominent green patches on the head, just behind each eye. There is also a green streak just above each foreleg. The females can appear quite beige with the dark markings almost completely suppressed. Larger patches of light green on the upper body can appear with this lightening. The females can also display dark speckled markings over the tan, with green remaining only on the head and above the foreleg. The dewlap of the female, which is about half the size of that of the male, is yellowish green.

The animals of Fairy Glade are generally darker in coloration than those of Steep Bush. The glade receives more sunlight than the bush forest and this may account for part of the color difference. Both males and females have the prominent green patches behind their eyes that characterize the females of the bush described above. In addition, the lower body of the males from just in front of the hind legs to the tip of the tail is fairly green, while the mid-body is mostly brown.

One Fairy Glade female I described in my notes as being "a dull, mousey brown" with a bit of muted green on the shoulder and behind the eyes. I observed a 74-mm Fairy Glade female in a completely chocolate brown phase, with no markings evident. She was delicately rosy red behind each leg, just where the leg joined the body. Females, as well as males, in Fairy Glade seemed also to have the power of males in Steep Bush to turn to a cryptic dark chocolate. In this phase the animals have no markings evident. All color except the brown is suppressed.

In Holywell Park, about a mile west of each of the two other areas, the one male I saw was very green over much of his body. As is typical of *reconditus*, his head and legs were basically brown, but his trunk reminded me of the bright green of *A. garmani*. Markings were evident as patches of darker green on his back and sides. The striking shade of most of his body marked him as a member of possibly a third distinct population.

These data are too scant for speculation about whether *reconditus* occurs in distinct demes each with a specific color pattern. In view of the broken terrain, I may have been sampling separated segments of a continuum. More work is needed before a positive statement can be made about the local distribution and differentiation of *reconditus*.

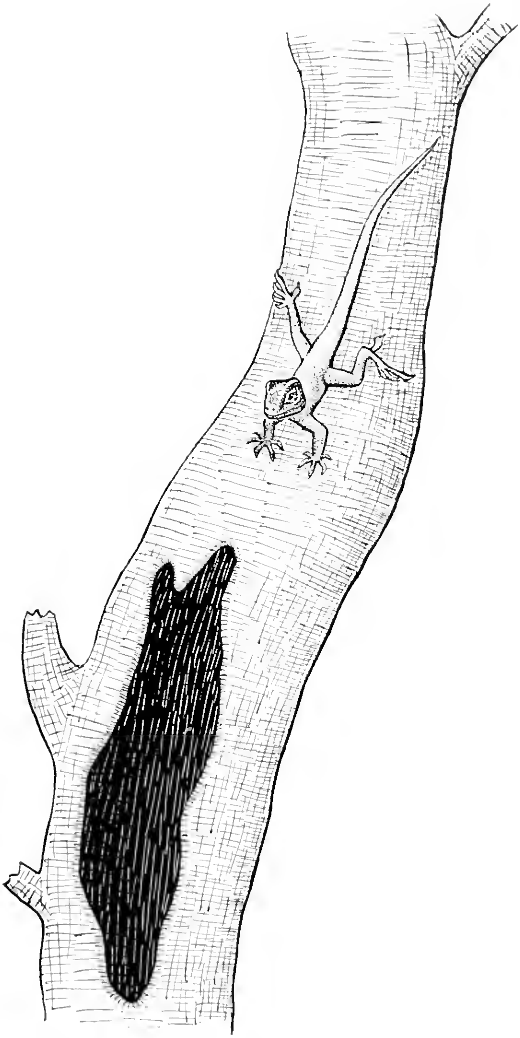


Figure 1. Male perching (Holywell Park). Note proximity of his perch to the hole in the trunk. See ESCAPE BEHAVIOR.

PERCHES

Although I observed *reconditus* on a variety of perches in a variety of positions on the perches, there was one tableau which I observed most frequently. The lizard would be about 12 feet up on a tree trunk or large-diameter branch (more than 4 inches) "in a head-down position, with the neck bent so that the head was nearly parallel to the ground" (Lazell, 1966). A. S. Rand first reported this stance to J. D. Lazell, but reported the perch height as from three to seven feet.

I have two dozen observations of height and diameter of specific perches, 11 for females and 13 for males. According to these I saw only four females and two males perched under seven feet. On the other hand, 16 of the perches were ten feet or over. The highest was about 16 feet. I have four additional entries with only perch diameter. I made many additional observations for which I failed to record perch height or diameter. In such cases the lizard was perched, facing down, between 10 and 14 feet on a four-inch or larger diameter perch. I had come to expect them to be at this height and diameter and only if they were not there did I make note of it.

As stated above, the standard perch was of fairly large diameter. I recorded at least 14 different perches of eight inches or larger. The largest was about 18 inches.

There were a few exceptions to the standard downward-facing posture. I saw one male and one female who were perched for a long period of time facing up. I saw several perched crosswise, coming out of rotten furrows or at a crook in a tree branch. In some cases, crosswise or upward-facing perches would be assumed for a minute or two as transitional positions between two different downward perches or between periods of movement.

One striking and possibly unique element in the site that *reconditus* chooses as a perch is that in a great number of cases it is near a hole in a tree trunk or branch (See Fig. 1). In the Hardwar Gap area with its frequent rainfall and lush vegetation, it is common for a tree to have a partially exposed root system and many dead moss- and vine-covered limbs. Holes into the heartwood of a tree where a branch used to be are quite frequent. I counted no less than eight separate perch sites each within a few inches of prominent trunk or branch holes. One of these had three marked lizards, two females and a male, perched by it at different times. Another hole had two marked animals, one male, one female, who regularly used a perch next to it. Only one lizard at a time was ever seen at any of the holes.

Several times I saw lizards perched half in and half out of these furrows or holes. Rand (1967) reports that *A. valencienni* lays eggs communally in tree-trunk holes but apparently no other anoline lizard uses them in just the same way as *reconditus*. It is possible that the holes are related to the foraging activity of *reconditus* (see FORAGING). They are certainly hiding places (see ESCAPE BEHAVIOR).

The fact that more than one individual uses the perch near a particular hole raises questions concerning the nature of the territoriality of this species. Perhaps there is only one male per hole and the females who use the perch are part of a group that resides within his territory. Robert Trivers (personal communication) has observed for *A. garmani* that individual males, especially large ones, seem to police territories containing several females. Each male appears to maintain exclusive copulatory rights with the females in his territory. Perhaps there is a similar situation with *reconditus* (also see HOME RANGE AND TERRITORIAL STRUCTURE).

The holes raise another question. If a lizard is going to escape into a hole, instead of up a tree, he has to be sure that the hole is not already occupied. Indeed, the intimacy of a hole is a great deal more than that of the crown of a tree, and a lizard cannot see from a distance if he will have company in a hole, the way he can at the top of a tree. Therefore it seems likely that at any time the lizards on a particular tree must have a good idea of where the other lizards on that tree are perched and where to go in case of danger.

HOME RANGE AND TERRITORIAL STRUCTURE

In an attempt to learn something about the habits of *A. reconditus*, especially about its territoriality, I noosed and marked individual animals. After its capture, the sex of each lizard was determined, it was measured, given a number, and marked in two ways. For a permanent mark, part of one or two toes was clipped (see MARKING SYSTEM at end for details). This allowed me to give each individual a unique identification number. Also stripes of paint of various colors were painted on the lizard's back so that different individuals could be distinguished at a distance. The location of the perch where the lizard was caught was recorded and then the animal was returned to this site. The lizards were rarely held captive for more than fifteen minutes.

During my study I resighted nine marked lizards. One, a 62-mm female, I saw seven separate times. All the resightings were in Fairy Glade. Although my data is scanty, it points toward a large male having a home range shared by two or more females, three large trees (30–40 feet × 12–18 inches) and a few saplings. In the heavy growth of Fairy Glade, the ground area of a range might be only 500 to 750 square feet.

I have no data on whether *reconditus* defends these areas or any parts of them. Robert Trivers (personal communication) has found that males of *A. garmani* do defend territories, slightly larger in extent than the *reconditus* home range described here. Further study may reaveal whether *reconditus* also defends a territory.

On two very large adjacent wild yacca trees, each of which had two 12–18-inch trunks, I regularly saw a 74-mm female, a 77-mm female, and an 88-mm male. The larger female I saw on six different occasions, five times on the same tree, four times on the same perch. Once I saw her on the adjacent tree, occupying the perch on which I had often seen the male. The male I also saw half a dozen times, four times on "his" tree and twice on the perch where I usually saw the female. The small female I saw only twice. The second time she was on the perch on the "male's" tree which had been used by both other lizards.

The smallest female (62 mm) that I caught I saw six times at exactly the same perch. This was a small tree (four-inch diameter), five feet away from the tree on which I first caught her. She was always perched four feet off the ground next to the same furrow in the tree trunk.

I saw an 81-mm male three times, always within ten feet of where I first caught him. He was caught on a straight, branchless tree (*ca.* 30 feet × 6 inches) and resighted on two adjacent trees, one a sapling (one- to two-inch diameter) and one a small tree (three-inch diameter).

I repeatedly saw a 95-mm male and a 75-mm female on or in the vicinity of two medium-sized (8 inches × 35 feet each), well-foliaged, adjacent trees. They spent most of their time at one perch, nine to ten feet up, next to a hole in the tree in which I first caught the male. One day I would see one on the perch, another day I would see the other.

One large male (95 mm s–v; 30 mm jaw) I saw on three successive days reveal either an enormous home range or rather atypical behavior. I caught him one day about 8 a.m. along the path, close to the entrance of Fairy Glade. Three hours later, I saw him again 12 feet further up the path. He must have crossed several large trees on his way to this new perch. The next day I saw him on the other side of the path, about halfway between the two trees on which I had seen him the day before. Four hours later he was nowhere to be found.

On the third day I spotted him at noon on the side of the path on which I originally caught him but ten feet further up the path than I had ever seen him. I proceeded to follow him and photograph him for two hours as he covered an 80-foot stretch which contained many large trees. My field notes that describe this remarkable journey follow.

May 17, 1970
Fairy Glade

12:00 noon — #5 (95 mm s–v; 30 mm jaw)
Spotted 10 feet further up path (on side he was originally caught on) than seen previously.
12:10 — Following #5. Moved up beyond tree where #11 (62-mm female) was caught.
12:35 — Much head bobbing after assuming new perch. Many ½ inch diameter sapling perches.
12:45 — Ate some ants.
12:50 — Dewlapped 3½ times.
1:10 — 5 dewlaps preceded by head bobbing.
1:15 — Moved further up path and dewlapped 4 times with head bobs. Sitting out on tree fern fronds, 10 feet up.
1:25 — Taken up downward facing perch 12 feet up on 3 inch diameter tree. Brown, greyish mottled shading very much color of the bark.
1:50 — Still perched. Light rain. I left. #5's run started about 30 feet further up path than tree he was caught on. Run documented above roughly followed path up farther into glade. Lizard covered 80 feet in an approximately linear fashion. In that 80 feet were about 30 trees greater than 1½ inches in diameter and many, many smaller trees. On other side of path where #5 was observed perching on May 16, this same 80-foot stretch contained six large trees. The dis-

tance between the two rows of trees, *i.e.*, distance across the path, was about 40 feet.

Clearly much more work has to be done to establish a reasonable knowledge of *reconditus*' home range size or territorial structure. I caught no other lizards, except the 62-mm female, in the vicinity of the trip of the large male described above. It is not impossible that all the ground he covered was "his." It is also true that my best resighting data is on females who seem to occupy one or two adjacent perches quite regularly. You might expect a female to spend more time in a specific spot in a male's home range while the male himself roams around more within the area. Perhaps I did not see a male regularly because he was much of the time out of my view, in some other part of his quite large home range.

It is difficult to get an idea of the size of the *reconditus* population of Fairy Glade. If I had a good estimate, I would understand the dispersal of the species better. I only caught fifteen lizards, eight males and seven females, along the 200 yards of the path which I used for my study area. If that represents half or even possibly a third of the resident males, then it is possible that *reconditus* males have a large home range, some even as big as that of the particular large male I have described. I am quite certain that there were many more females in my area than I was able to catch because they are smaller, more cryptic, and have a less obvious display. Owing to the cryptic nature of this species, the general lush growth of the habitat, and the apparently quite timid character of the animals once they have been exposed to man (see ESCAPE BEHAVIOR), I think it is very likely that I missed many more lizards than I caught. This would indicate that my conservative estimate of home range size, at the beginning of this section, is a reasonable one.

INTRASPECIFIC INTERACTION

I rarely had more than one *reconditus* under observation at a time. On only two occasions did I observe interaction between two lizards, in both cases between a male and a female.

The first interaction was one morning in Steep Bush. Initially the male (*ca.* 90–95 mm) was ten feet up on a tree trunk (eight inches in diameter), facing down; the female (84 mm) was about seven and a half feet up on the same tree, also facing down, about 120° to the right of the male. After I had been watching them for half an hour, the male dewlapped once. Fifteen minutes later he ran up the tree two feet, dewlapped three times and assumed an upward-facing perch. After another five minutes, the male ran down about a foot and toward the female slightly. He gave three head bobs, paused and gave three more. His downward-facing perch was now about three and a half feet above and 60° to the left of the female.

Ten minutes later, the female finally moved, running down and around the back of the tree. A bit of vine fell behind the tree and then she returned. Probably she was eating. For the next forty minutes the two lizards remained motionless. Then the male moved down a few inches toward the female, but also to the left, putting more lateral distance between himself and her. He dewlapped three times, the second and third being from a half open position of the dewlap. Five minutes later the female opened her mouth. After another five minutes, the male dewlapped again three times in a manner similar to his earlier series.

Although the female appeared to display no direct response to the male, it looked to me as if the male was courting her. Neither before this occasion nor after did I see two lizards so close together. Because of the extreme peripheral vision of these lizards, it seems likely that the female could have been watching the male's displays despite his position above and behind her. Although I was quite close at the time, nothing about the male's behavior suggested that he was reacting to me. He may of course have been making territorial displays either in general or to specific other lizards that I could not see.

On the second occasion the object of the male's display was even more ambiguous. I caught a 74-mm female about ten feet from where an 88-mm male, previously caught and marked, was perched. Both lizards were on different trunks of the same large tree.

A minute or so after I returned the newly marked female to the perch from which I had captured her, the male began one of the most elaborate displays I have ever seen. He dewlapped five times, head-bobbed quickly twice, dewlapped once again, head-bobbed several more times, and then dewlapped once more while bobbing. Finally he head-bobbed and then dewlapped an eighth time.

Five minutes after this display the female assumed the exact perch and position she had occupied before I captured her. In the next fifteen minutes both the male and the female rotated their perches through 90°. Then twenty-five minutes after his grand display, the male resumed his original position and dewlapped two and a half times.

The male's elaborate display was certainly in response to either myself or the female. If it was an aggressive display toward me, it was a minute or two after I had put the female back on the trunk and returned to my close-by observation post. Normally, if a lizard saw me he would sit and wait motionless, and then rapidly move away if I got too close. This makes me tend to think that the male was reacting to the female to whom I had specifically drawn his attention. The movements of the male and female described above after the male's display may also have been part of the courtship interaction.

DISPLAY

I observed no pattern to the displays of *reconditus.* In general the displays are, in regard to specific body movements, much like those of other Jamaican anoles. There is head-bobbing; four-leg pushups; a front-legged, half pushup and pulled back, slightly cocked head preceding dewlapping; dewlapping combined with head bobbing; and sometimes, at the end of a series of dewlaps, a half dewlap pulse. On characteristic of the species is that the displays are slower and seemingly more "methodical," as I called them in my field notes, than those of other Jamaican lizards.

I saw females display only three times; each time the lizard I was observing head-bobbed on assuming a new perch. One of these females I watched for nearly four and a half hours and saw only the single head-bob display.

Males displayed much more frequently, generally dewlapping intermittently while they maintained a specific perch. One individual that I watched for three hours dewlapped five or six times at various intervals, sometimes every ten to twenty minutes, sometimes every 30 to 40 minutes. Two different displays of possible courting males are discussed in INTRASPECIFIC INTERACTION. Although I recorded that a 95-mm male head-bobbed and dewlapped each time he assumed a new perch (see HOME RANGE AND TERRITORIAL STRUCTURE), I also observed males take new perches without display. Occasionally males directed what were probably aggressive displays toward me. These consisted of dewlapping once or twice.

The elaborate display of one male just before he "went to bed" is worth describing. I had been watching this lizard continuously for three hours. He had not moved for the last hour while darkness fell. Suddenly he shifted his downward-facing position on a three-inch trunk 30° to the right and began a rapid display: three head bobs, a dewlap, two more bobs, a dewlap, one bob, and finally two dewlaps. Seven minutes later he ran up two feet on the trunk, assumed a downward position, and again displayed: four pronounced head bobs followed by three dewlaps. Three minutes later he ran up two feet more, stopped and looked around. After a brief pause, he ran up six feet more, stopped, paused, and then continued up the trunk, disappearing in the dark foliage.

It seems likely that males, and females to a lesser degree, display to announce their position in their home range or territory to other members of the species in typically anoline fashion. But I could ascertain no pattern to this type of display, and my data is not extensive enough to identify consistent features of aggressive or mating displays.

INTERSPECIFIC INTERACTION

On only one occasion did I see *reconditus* in close proximity with a lizard of another species. In the stand of imported yaccas, next to the garage where Lazell worked, I saw a large male *A. garmani* perched 20 feet up on a tree. A foot away on an adjacent tree, perched slightly lower, was a male *reconditus* that I was trying to catch. Contrary to Lazell's speculation (1966), it seems that the niches of *garmani* and *reconditus* do overlap at least occasionally.

On the steep path up to Fairy Glade from the Hardwar Gap road I also once saw a male *garmani* perched 30 feet up on a tree. I never saw any *reconditus* on the trail to the glade, but this *garmani* was less than 100 feet below the glade. It is possible that the two species share the same habitat at the outer edge of Fairy Glade. I saw neither *A. opalinus* nor *garmani* in Steep Bush, inside Fairy Glade, or in the Nineteen-Mile Gulley, the three areas that I located with substantial *reconditus* populations. It may be significant that of all the anoles in Jamaica, only *reconditus* lives for the most part without congeners (see DISCUSSION).

ESCAPE BEHAVIOR

Lazell (1966) describes the "wary and timid behavior" of *reconditus.* I too found this to be true, but usually only after the lizards had become "wild," as the local people refer to the lizards after they have become frightened of man. Generally, "naive" lizards, individuals who have had no contact with man, are quite easily approached, and with a little care easily caught. Owing to their cryptic nature and restricted range, they are often hard to find, but once you find them, you usually can catch them.

However, after you have caught, measured, and marked them once, even if you can find them again, which is difficult, you will have an incredibly hard time recapturing them. One day in Fairy Glade I saw a 75-mm female which three days previouly had been caught and marked. She edged her way into the trunk hole next to her perch. I was 20 or 30 feet away when this happened, and it suddenly occurred to me that the reason I was resighting few marked lizards was because they would see me coming and hide.

I only made one recapture, that of a 78-mm female whom I had originally caught and measured, but who had escaped before she was marked. I attempted to recapture her half a dozen times before I succeeded. She grew more and more wary. It is not surprising at all that Lazell (1966) had trouble catching the lizards in the garage and under the house. Most Jamaicans fear lizards and try to kill them or drive them away whenever they encounter them. Lizards are especially disliked around human dwellings. Lazell's lizards were probably quite afraid of humans.

I often saw *reconditus* next to the garage he describes in his paper, in a stand of imported yacca trees. Although I tried more than a dozen times to catch some of them, they would invariably escape up the straight 40-foot trees. I finally caught one 77-mm female on the roof of Lazell's garage. I was very lucky indeed to do so. I heard reports that the sons of the caretaker of this garage threw stones at the lizards on the trees next to the building. The boys were afraid of the harmless animals, and I could not persuade them of the folly of their actions. The lizards around the garage were definitely "wild."

Although Lazell in his paper agrees with Underwood and Williams (1959) that *reconditus* usually escapes "under objects and into holes," I found this to be only partially true. In the great majority of cases, I observed *reconditus*, when attempting to evade my noose, to go up the tree in typical *Anolis* fashion. On four specific occasions, three times with males and once with a female, I watched lizards go into trunk holes, conveniently next to and at least as high off the ground as their perches, to hide from me. I never chased a lizard down to the ground or under the exposed roots of a tree, seemingly an adequate hiding place. They invariably went up.

REACTION TO WEATHER

The "moisture-laden easterly trade winds," which blow all year long bring the Hardwar Gap area of the Blue Mountains over 200 inches of rain annually. During much of the fall and spring, there is daily rain. Although there are occasional dry days, it usually rains for several hours during the day and sometimes for several days continuously. The area is described as "montane mist forest" because of the mist or fog which envelops it every day. The mist remains even during the rain and lasts for 30 to 70 percent of the daylight hours, often forming shortly after dawn and remaining until an hour before sunset (Asprey and Robbins, 1953).

Because of the weather conditions and also because of the full canopy of the forest in which the lizards live, it is very difficult to get any idea of how *reconditus* reacts to heat or sunlight. In all my observation time, I very rarely saw a lizard perched in direct sunlight. This was not because the lizards chose to avoid it by picking shady perches, but because the sun was rarely shining; if it was sunny, the canopy usually prevented direct sun from striking the lizards. On the few occasions when I did see sunlight on the lizards, they seemed to have no apparent reaction to it. Basking would have been futile since the sun rarely shone more than a few minutes, if that, in one place and, as I said, seldom shone at all. Further study should be carried out during the summer months, which according to the local people are drier, often 80° or more, and sunny. It would be interesting to see if the sun ever gets hot enough in the bush to drive the lizards to seek shade and damp.

The local name for *reconditus* is "water lizard." The animals seem to prefer the damp, often living in mountain-side gulleys where water flows during heavy rains. But to truly grasp the significance of the local name, you have to watch one in a drenching downpour: water streams off the body of the lizard, while, with no apparent concern, it remains passively perched. On three separate days of heavy rain I watched a total of seven individuals display no apparent reaction to the precipitation. Four of these were females; three were males. One of the females was active during an entire hour of downpour, but her movements seemed to have nothing to do with seeking shelter. She was also quite active before the rain and during its tapering-off stages.

On numerous other occasions I saw lizards in light rain show no concern for the weather. Only once did I see a female run down a tree and under the exposed roots during a heavy rain. She stopped every few feet during her descent to head-bob. A few minutes before, I had unsuccessfully tried to capture a large male and chased him up into the crown of the same tree. It is not clear whether the female's actions were related to the heavy rain or to the frightened male I chased up the tree.

In any case the tolerance for rain which *reconditus* seems to have is unusual in anoles. Robert Trivers, in his extensive studies of *A. garmani* and *A. valencienni* in Jamaica, reports (personal communication) that it is nearly impossible on rainy days to find even one individual in an area with a large, well-studied population. However, Thomas Schoener (personal communication) has seen *A. sagrei* perched in the rain. Still, every observer of anoles that I have talked to has corroborated the usual pattern as avoidance of the rain.

Since *A. opalinus* is smaller and *A. garmani* is larger than the "water lizard," apparently size cannot be the determining factor in tolerance for rain. The habitat involved is undoubtedly important. The tolerance that *reconditus* has seems to me a reasonable adaptation in an environment where wet weather is so frequent. A great deal of energy would be wasted if the lizard had to move to shelter every time it rained.

FORAGING

In my many hours of observation, I saw only three instances of feeding by *reconditus*.

An 84-mm female was perched seven and a half feet off the ground, facing down, on a 45-foot × 8-inch tree. I had been watching for half an hour when suddenly she turned 180° around and seemed to take something off the bark with her mouth. Then she "chewed" (opened and closed her mouth) four times and then turned back around to resume the standard downward-facing perch. Half an hour later she ran around the back of the tree and down. A bit of vine fell from the back of the tree. Then she returned. All of this took place in about a minute. Presumably she had gone after a bit of food.

On another occasion I watched a 74-mm female traverse six feet of a rotten furrow in a horizontal tree trunk. The trunk was about eight inches in diameter and four feet above the ground. The lizard licked the rotten wood inside the furrow, perhaps "tonguing" ants. Then, after assuming a horizontal perch facing out of the furrow at one end of the trunk, the female snapped out of the air a mosquito which was buzzing around her mouth. Ten minutes later, she caught another, larger, flying insect, presumably a fly. Half an hour later she withdrew from this perch back into the furrow and proceeded to traverse the length of the trunk again, inside the furrow. She made the trip quite slowly, moving from side to side as if searching for something.

The final instance of feeding I observed was by a 95-mm male. I saw him eat some ants while he was making a long, relatively fast-moving journey of 80 feet through densely forested Fairy Glade (see field notes in HOME RANGE AND TERRITORIAL STRUCTURE). The eating of ants appeared at the time to be a digression from the business at hand, that is, his long, steady trip up the path. He ate only once in two hours. However, it is not impossible that the whole trip was a food search.

Robert Trivers has shown (personal communication) that *A. valencienni* feeds by actively searching for prey. Generally Jamaican anoles maintain a perch until they see a food item, and then go after it. Perhaps the feeding habits of *reconditus* include both searching and waiting. More study is necessary to determine whether this is true.

SLEEPING

It seems likely that *reconditus*, just as *A. garmani* and several other *Anolis* species, sleeps in the foliage of the crown of trees. The first lizard that I caught at Hardwar Gap was seen at 7:50 a.m. walking down the trunk of a 45-foot tree. The sun was up, of course, but had not yet reached the incredibly steep, densely forested northwest mountainside of Steep Bush. It is possible that this 96-mm male was coming down from his sleeping perch to a lower daytime perch. On two later occasions, both at sunset, I put individual lizards "to bed" to see where they went.

The first time, I watched a large male (*ca.* 90 mm) for more than three hours. He maintained until sundown his perch place 12 feet above ground with only occasional sideways movements from the downward-facing perching position. Then, in a period of 12 minutes, as darkness was rapidly falling, he went through a flurry of activity and elaborate displays (see DISPLAY). This culminated in his disappearance into the higher foliage.

Two weeks later, I watched a 62-mm female at sundown. She suddenly changed to a crosswise perch from the uncharacteristic upward-facing perch she had maintained all day. The perch was four feet above the ground on a small tree. Ten minutes later, she jumped to a nearby straight sapling and looked around. Four minutes later she ran up a few inches and looked around. Then she disappeared up the small tree. It seems reasonable that a female of this size, indeed the smallest I caught, would sleep in a sapling such as this, a great deal smaller than the large tree, where, as noted above, it is likely that a big male sleeps.

DISCUSSION

Anolis reconditus is unique and at the same time unspecialized. The lizard is apparently isolated from congeneric competition. This may be one of the keys to understanding the morphology, ecology, and behavior of the animal. E. E. Williams (Williams *et al,* 1970) makes such a point in his discussion of the solitary Venezuelan lizard *Anolis jacare.*

Reconditus does not occupy any of the typically anoline structural habitats defined by Rand and Williams (1969). Of the six categories they set up, it seems most like a "trunk anole." But it is unlike that category in that it often goes farther up the tree and occasionally down to the ground. Of course, being isolated as it is, there is no reason for it to be restricted to any one structural habitat, as is necessarily the case when several species live syntopically. In addition, the perch that *reconditus* most frequently takes seems a very reasonable adaptation for a solitary species. From 10 or 12 feet up on a trunk, the animal gets about as good a view of the surrounding forest as is possible and can reach either the ground or crown with equal facility.

In the Lesser Antilles, islands with only one *Anolis* species are common. However, on the larger islands of the Greater Antilles, each of which supports several to many species, there is much overlap of congeneric range. *Reconditus* in Jamaica is in a situation similar to that of *A. jacare* on the continent of South America. It is on a "mainland island, just like *jacare,*" at its Blue Mountain retreat. A detailed comparative study of *A. reconditus* in its montane mist forest and *A. jacare* in its "Premontane Humid Forest" (Williams *et al*, 1970) might yield some interesting insights into the adaptations of isolated species.

Thomas Schoener (1969 and unpublished data) shows that the male snout–vent length (mean of the largest third of his sample) for lizards inhabiting islands of the Lesser Antilles which have only one species of *Anolis* ranges between 60 and 94 mm. *Reconditus*, at 97 mm, would fall only a bit beyond the high end of this range. From the few individuals of *jacare* that have been measured, male size seems to be about 75 mm.

Reconditus is possibly the only Jamaican anole which actively searches as well as motionlessly perches in attempts to obtain food. Other than *A. sagrei*, it is unique among anoles in its ability to function normally in the rain. It does not fit into a Rand and Williams' perch category, but instead ranges over several of the structural habitats that they define. No other anole, except *A. valencienni* (Rand, 1967), is known to crawl into large holes in the tree trunks on which it perches.

These features of the behavior of *reconditus* suggest perhaps that the animal is adapted to its habitat in a more general way than some of its aparently more specialized congeners. *Reconditus* appears less restricted in foraging methods, in ability to cope with the weather, and in perch and refuge space than almost all other anoles. Further study of these and additional aspects of the lizard's behavior and ecology might reveal whether it is indeed less specialized than its congeners.

Possibly because *reconditus* is isolated from congeneric competition it is free to fully exploit its habitat. If this is the case, it may be that within its restricted montane mist forest habitat, it can, living alone, use more of the resources of the environment through generalized rather than specialized adaptations.

AN EXPLANATION OF THE MARKING SYSTEM

I marked lizards at the two main study areas, Steep Bush and Fairy Glade (see HABITAT AND RANGE and map for location of these places). In each area I used a numerical marking system for permanently identifying individual lizards. A single toe or, in the case of the large toes, just the terminal joint, was clipped off the lizard's foot.

The toes were numbered as described below:

Starting with the lizard on its ventral side with its dorsal side facing you, the toes on the front left leg (your left) were numbered consecutively 1 to 5 from smallest to largest. The toes on the right front leg (your right) were labelled 6 to 10 from smallest to largest. The toes on the left hind leg were labelled 11 to 15 from smallest to largest. Finally the toes on the right hind leg were labelled 16 to 20 in a similar manner.

Should anyone catch any of these marked animals at Hardwar Gap, I would greatly appreciate his sending me size data (lower jaw, snout–vent, and tail lengths) and any other interesting features about the lizards. I can be reached care of Professor E. E. Williams, Museum of Comparative Zoology, Cambridge, Massachusetts.

ACKNOWLEDGEMENTS

I want to thank especially Ernest E. Williams for introducing me to the study of anoline ecology and behavior. This project would not have been possible without his constant advice and support throughout all stages of the work.

Robert Trivers' contributions were invaluable. Not only did he help with details such as initial identification of *reconditus* in the field but also he generously contributed his ideas and his field techniques. Thomas Jenssen gave me much help and advice while I was in the field. Preston Webster and A. Stanley Rand both provided extensive and valuable criticism on earlier drafts of this paper.

I want to thank C. B. Lewis, Director of the Institute of Jamaica, for allowing me to use the Institute's field station at Green Hills for the duration of my study.

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A FOSSIL TRIONYCHID TURTLE FROM SOUTH AMERICA

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and
Bryan Patterson

Abstract. A hyoplastron of a large trionychid turtle from the middle Pliocene (Huayquerian) Urumaco Formation of northern Venezuela constitutes the first indisputable record of a member of this family from South America. The reported occurrence of a trionychid from the late Cretaceous or Paleocene of Patagonia (*Trionyx argentina* Ameghino 1899, *nomen dubium*) cannot be substantiated. The species represented by the Venezuelan fragment was presumably a waif immigrant from Central America that was unsuccessful, very possibly owing to competitive exclusion, in establishing an enduring foothold in South America.

Living trionychid turtles are known from Africa, Asia, the Indo-Australian archipelago and North America. Paleontological evidence indicates that this group formerly had an even more extensive distribution. Fossil forms are known from parts of Africa, Asia, and North America where they no longer occur, and remains are found in European Tertiary deposits as well. Until now, with one dubious exception (discussed below), no members of the family, living or fossil, have ever been encountered in South America. Discovery of an unquestionable trionychid fragment from late Tertiary sediments in Venezuela during the summer of 1972 is therefore of considerable interest.

The specimen (Museo de Ciencias Naturales, Caracas, no. 238) was recovered from the upper part of the lower member of the Urumaco Formation about twelve kilometers WSW of Urumaco and .75 kilometer north of Kilometer 153 on the oil pipe line running from Punta Gorda to the Paraguaná Penin-

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sula. It was found on the surface, together with parts of a pelomedusid that was in the process of weathering out. The Urumaco Formation (Gonzales de Juana *et al.*, 1970: 612–613) is now believed to be of Huayquerian age (Pascual and de Gamero, 1969; Wood and de Gamero, 1971). Outcrops are restricted to a relatively small area in the northern part of the state of Falcón. The vertebrate fauna, for the most part not yet described (see, in addition to the publications cited above, Royo y Gomez, 1960, and Sill, 1970), consists of numerous aquatic reptiles (some half dozen species of both crocodilians and turtles), a testudinine, fish, and various kinds of mammals. The depositional environment was in the main a near-shore marine one, with fluctuations involving a variety of paralic and near-shore continental conditions.

The find consists of a large, well-preserved hyoplastron (Figure 1). Its sculptured external surface, covered with anastomosing ridges, is characteristic of trionychids. These rugosities, coupled with the distinctive outline of the bone, leave no doubt regarding the familial reference. Dimensions are as follows: width along the hyo-hypoplastral suture = 22.2 centimeters; length at narrowest part = 7.3 centimeters; greatest dorsoventral thickness along hyo-hypoplastral suture = 2.8 centimeters. From the condition of the sutural surface, it is clear that the hyo- and hypoplastra were distinct bones rather than fused as is the case in various genera of the family. The hyoplastron appears to be unusually thick for its size, the thickness/width ratio being 0.126. Measurements of shell thickness are scarcely ever given in the literature. A few T/W ratios can roughly be estimated from the figures and sporadic measurements given by Hay (1906) for North American fossil trionychids; these range from 0.083 to 0.019. The hyoplastra of those living forms available to us are as follows regarding this ratio: *Lissemys punctata*, 0.087; *Chitra indica*, 0.081; *Trionyx hurum*, 0.067; *T. sinensis*, 0.079; *T. cartilagineus*, 0.090; *T. spinifer* (6), 0.107–0.064; *T. ferox* (4), 0.081–0.070; *T. muticus* (2), 0.077–0.049. This, of course, is a wholly inadequate sample, but as far as it goes it confirms our impression that the Urumaco hyoplastron is unusually thick. Further, the sample suggests that thickness decreases, relatively, with age; in all species of which we have more than one specimen the smallest individual has the highest ratio and the largest the lowest. The thickness of the Urumaco specimen is not, we accordingly suspect, due to size.

This hyoplastron is sufficiently distinctive for reasonable as-

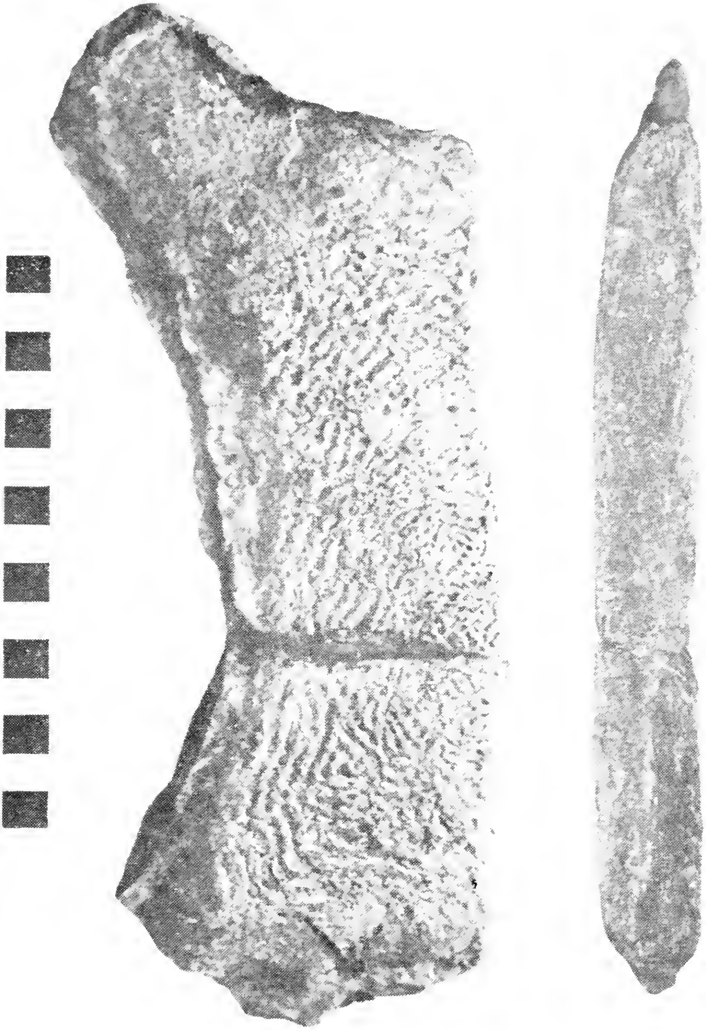

Figure 1. Trionychidae, gen. et sp. indet. Ventral and posterior views of hyoplastron. Scale in centimeters.

surance that we are dealing with a representative of the group sometimes recognized as the subfamily Trionychinae (group I of Loveridge and Williams, 1957: 414), but quite inadequate for further taxonomic refinement. Assessment of precise relationships within the family must await discovery of more complete material. The geographically nearest living species of the family are *Trionyx spinifer*, whose range extends from the United States down into northeastern Mexico, and *T. ater*, which is confined to the Cuatro Cienegas Basin of central Coahuila, Mexico (Webb, 1962). Neither attains great size; in fact, the Urumaco form was clearly larger than any of the living American species. Some fossil trionychids (*e.g.*, the late Paleocene *Paleotrionyx quinni* Schmidt, 1945) are known from North America, however, whose size is comparable to that of the Venezuelan specimen.

The earlier record of a South American trionychid must now be considered. Ameghino (1899: 10) published a very summary "diagnosis" of *Trionyx argentina* from the "Cretaceous of Patagonia (Guaranitic Formation)." In his only subsequent mention of it, he stated that *Tryonix* [sic] *argentina* had come from the "Sehuenian" (1900: 216). No locality was ever given. His "Guaranitic Formation" included marine and continental strata ranging from Cretaceous to early Oligocene (Deseadan), and his "Sehuenian" formed part of it. On the basis of his last statement concerning the age it could be assumed that *T. argentina* came from the type area of the "Sehuenian" (now the Mata Amarilla Formation, Coniacian; Leanza, 1972: 695, 701) on the Río Shehuen (or Sehuen or Chalía) in the west-central part of the province of Santa Cruz, and Feruglio (1949a: 257) believed that it had. This is not certain, however.

In 1898 (p. 121) Ameghino included in his "Sehuenian," or "Piso Sehuense," deposits occurring in regions other than the type area, among them the Río Chico del Chubut. It would seem possible that *T. argentina* could have come from this general region, and there is some indication that it may have. In the introduction to his paper of 1899 Ameghino stated that all species proposed in it had been collected by his brother Carlos since the manuscript of his paper of 1898 (to which 1899 was a supplement) had been delivered to the printer, which was done at the end of July, 1897 (letter from F. Ameghino to D. de la Fuente, August 7, 1897; *in* Torcelli, 1935: 688). By that time Carlos Ameghino's collecting activities had centered on northern Santa Cruz and Chubut. Reporting on the results of his expedition of 1898–99 to the Golfo de San Jorge, he wrote (letter to Florentino, February 15, 1899; *in* Torcelli, 1935: 106) that he had found "more or less in the center of the gulf . . . characteristic fossils (sharks, chelonians, crocodiles, etc., the same as those of Sehuen and Lake Argentino)." These chelonian remains could have included the material on which *T. argentina* was based. Florentino's statement (1899) that a trionychid had just been found ("acaba de encontrarse") could be so interpreted. At any rate, years later, Staesche (1929) described turtle fragments collected, together with crocodilian remains, by von Huene near the center of the gulf, "mainly at Cabo Peligro," and several of these answer to Ameghino's "diagnosis" of *T. argentina* in one respect, vermicular sculpturing. Staesche believed the age of these specimens to be Late Cretaceous, but the bed from which they came was the *banco negro inferior* at the base of the Río Chico Formation or perhaps at the top of the Salamanca Formation (Feruglio, 1949b: 27, fig. 87), both of which are now considered to be Paleocene in age. Turtle remains, according to Feruglio, commonly occur in this bed or beds in the region of the gulf. Against the possibility that *T. argentina* may have been recovered from this area, however, is the fact that by 1900 (p. 119) Ameghino had begun to make a distinction between the "Sehuenian" and the beds in Chubut containing *Ostrea pyrotheriorum* (now the Salamanca Formation). As in the case of *Niolamia argentina* (Simpson, 1938), also described in 1899, no conclusion can now be reached as to the precise age and locality of *T. argentina*, although we regard Paleocene and the gulf as being the more likely alternative.

The affinities are even more uncertain. Ameghino's "diagnosis" reads, in free translation, "*Trionyx argentina* n. sp., size small, surface of shell with vermicular sculpturing, ossification incomplete, without scute sulci."[1] No information was given as to the type material. This is wholly inadequate to define a species of *Trionyx* or even to demonstrate the familial assignment. Other turtles have what could be termed vermicular sculpturing; what is meant by "incomplete ossification" is not clear; and the absence of sulci is not a certain indication that scutes were lacking. The specimen or specimens on which the taxon was based

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[1] ". . . de talla pequeña y superficie de la coraza con esculptura vermicular pero de osificación incompleta y sin surcos externos que indiquen la presencia de escudos corneos."

would appear to have been lost; Wood failed to encounter them in the course of an examination of the turtle remains in the Ameghino collection. Consequently, we regard *"Trionyx argentina"* as a *nomen dubium* and we feel that the existence of a late Cretaceous or Paleocene South American trionychid has not been demonstrated.

The specimen described here is thus the only definite record of a trionychid for the continent. Representatives of the family did obtain a foothold there, but for how long and in what manner? During 1970 Wood spent four months in South America examining collections of fossil turtles ranging in age from Cretaceous to Pleistocene and nowhere saw so much as a fragment that could be identified as a trionychid. The extensive collections made in the late Oligocene and later Miocene of Colombia by University of California parties include turtle remains but no representative of this family. Among the hundreds of turtle specimens in all stages of completeness seen by us in the Urumaco Formation only this one trionychid fragment was found.[1] On the face of it, therefore, it would seem possible that the invasion was a Huayquerian event and only briefly successful in the geological sense of the word. Why this should have been so is puzzling, for the great river systems of South America encompass habitats surely suitable for members of the family. Simpson (1943: 423) has suggested that trionychids and chelids may be ecologically incompatible. Chelids are clearly an old South American group in the sense of Dunn (1931). Wood has in hand undescribed material from the early Eocene Casamayor of Argentina.[2] Undescribed chelids have recently been discovered at Tremembé, in Brazil, now known to be a deposit of early Oligocene, Deseadan, age (Paula Couto and Mezzalira, 1971). Specimens occur in the Oligocene and in the Miocene of Colombia (Stirton, 1953: 614) and have long been known from Paraná. We have good material of *Chelus* from the Urumaco Formation, and additional undescribed material of this same genus has been found in Pliocene deposits along the upper reaches of the Juruá River in the territory of Acre, Brazil. The Chelidae was not the only family that could have provided

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[1] It was collected midway in the season and a very close watch for others was maintained thereafter.

[2] Ameghino "diagnosed" three species of *Platemys* from his "Guaranítico" in 1899, but these records are *nomina dubia* and the specimens evidently lost.

competition to invading aquatic turtles.[1] Pelomedusids, also Old South American forms, are known in the continent from the late Cretaceous on and are very numerous in the Urumaco deposits. The demonstrated failure of trionychids to maintain themselves in South America could be interpreted in terms of competitive exclusion. Chelids and pelomedusids have evolved together in South America throughout the Cenozoic, and in the course of this time no doubt parceled out between them a wide variety of habitats. That they would have completely saturated the continent is unlikely, but such diversification would have lengthened the odds against an invader. The species represented by our Urumaco trionychid may well have had the misfortune to encounter upon arrival a comparably adapted resident and have failed to compete successfully with it. It was, indeed, similar in size to the commonest Urumaco pelomedusid, *Podocnemis venezuelensis* Wood and de Gamero.

Such mammalian remains as occur in the Urumaco Formation are all of South American type, a finding in accord with Argentinian evidence suggesting a Montehermosan date for the joining of the American continents. On this basis, then, the Venezuelan trionychid would appear to have been a waif immigrant carried by ocean currents. Members of the family may well be rather prone to such accidents. There is some evidence that several of them enter brackish or even salt water (summary and references in Neill, 1958: 26–27). These would be particularly liable to hazards of this kind, but tolerance for saline waters need not necessarily be prerequisite. The African *Trionyx triunguis* also occurs in rivers and swamps along the eastern Mediterranean littoral. Flower (1933: 754) has suggested that this extension results from individuals being swept to sea by Nile floods and carried eastward by the prevailing current. The ancestor or ancestors of the Venezuelan trionychid presumably came from Central America, the nearest land area, and arrived in South America at approximately the same time as did the extinct *Cyonasua* group of the Procyonidae. No trionychid now

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[1] At the present time there is one area in which chelids and trionychids come together. This is southern New Guinea where the wide-ranging trionychid *Pelochelys bibroni* has established itself — rather recently in Darlington's opinion (1957: 210). There it is in contact with several chelids. So far as we are aware no information is available on possible interactions, but direct competition would seem unlikely. *P. bibroni* is a large species, much larger than any New Guinean chelid.

lives in Central America — it is a decidedly odd fact of distribution that all living North American species of *Trionyx*, in contrast to a number of their Old World congeners, are extratropical. None has been recorded fossil there, but in view of our abysmal ignorance of the Tertiary vertebrates of the region no weight can at present be given to their absence.[1]

This note records a momentary success in range extension resulting from waif dispersal. Such transitory events must surely have been commoner than those more enduringly successful, but in the nature of things the chances are against their entry into the fossil record. They could have played a part in furthering distribution. In the case of organisms such as freshwater turtles each new toehold gained, for however brief a time, in a suitable environment would have provided a potential base for further waif dispersal. The distribution of pleurodirans, for example, may have been to some degree forwarded in this way.

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[1] Webb (1962: 584) has credited Mullerreid (1943) with recording a fossil trionychid of unknown provenance from Mexico. Actually, that author mentioned seeing the internal mold of an unidentified turtle. The owner of the specimen, which has probably been lost, stated that he had found it on the Mesa de Capolla, a short distance SSW of Tuxtla Gutierrez, Chiapas. Cretaceous and early Tertiary sediments are present there, and Mullerreid believed that the mold had come from the latter. With the exception of the Oligocene or Miocene testudinine *Geochelone costarricensis* (Segura) (Auffenberg, 1971), this is the only published record of a Tertiary turtle from Central America. (In addition, we know of undescribed material from two Tertiary localities in Panama; no trionychids are included among the specimens.) Aguilera (1907: 241) listed *Tryonix* [sic] sp. as occurring with marine invertebrates in Turonian deposits at Peyotes, Coahuila. This is the only North American fossil record of the family south of the United States. It requires confirmation, and is in any event within the present range of *T. spinifer emoryi.*

Arnold D. Lewis (the finder of the specimen here discussed), Daniel C. Fisher, Robert W. Repenning, and Michael F. Stanford. The participation of Messrs. Fisher, Repenning, and Stanford was due, respectively, to the generous provision of a summer scholarship from the Department of Geological Sciences, Harvard University, and of grants from the Shell Oil Company and the Creole Petroleum Corporation. Wood's work in South America during 1970 was supported by the National Geographic Society.

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TWO NEW LYGOSOMINE SKINKS FROM NEW GUINEA WITH COMMENTS ON THE LOSS OF THE EXTERNAL EAR IN LYGOSOMINES AND OBSERVATIONS ON PREVIOUSLY DESCRIBED SPECIES

Allen E. Greer, Jr.

Abstract. Two new species of the *fasciatus* species group of *Sphenomorphus* are described from New Guinea: *S. anotus* is unique among its relatives in lacking an external ear opening and *S. microtympanus* can be distinguished by the greatly reduced size of its tympanum.

The earless lygosomines are reviewed and it is noted that, while the loss of the external ear opening is apparently a prerequisite for a burrowing way of life, it is uncertain whether the loss of the external ear in burrowers is a primary adaptation to burrowing or whether it is a preadaptation inherited from a nonburrowing ancestor.

Certain aspects of the morphology of the previously described but poorly known species *Sphenomorphus forbesi*, *S. oligolepis* and *S. schultzei* are discussed and photographs of type specimens are provided.

In 1964 members of the Seventh Archbold Expedition collected two small scincid lizards on the Huon Peninsula which differed from all other known skinks in New Guinea in having a scaly auricular depression instead of the more external ear opening. These were thus the first "earless" skinks to come out of New Guinea. The specimens were sent to Dr. Richard Zweifel at the American Museum of Natural History, but he was unable to identify them and he put them aside in the hope that more specimens would be forthcoming.

Five years later two more very similar skinks were collected by Angus F. Hutton at Garaina and given to Dr. Zweifel during his 1969 trip to New Guinea. Dr. Zweifel recognized the great similarity between these two specimens and the Huon Peninsula specimens but, still being unable to identify them, he kindly turned them over to me for further study.

On close examination the two specimens from the Huon Peninsula prove to be members of the *fasciatus* species group of *Sphenomorphus* (Greer and Parker, 1967), but they differ strikingly from all known members of this species group in being "earless." The two Garaina specimens are also clearly members of the *fasciatus* species group and are indeed similar to the Huon Peninsula specimens. They differ from the Huon Peninsula specimens, however, in having a relatively small, but nonetheless distinct, tympanum instead of a scaly auricular depression, and they differ from all previously described members of the *fasciatus* species group in the extreme reduction in the size of the tympanum. The Huon Peninsula and Garaina specimens are thus distinct enough from each other and from their closest relatives in the *fasciatus* species group to be described as new.

DESCRIPTION OF TWO NEW SPECIES

Sphenomorphus anotus new species

Figure 1

Holotype. American Museum of Natural History 95880; an adult collected on 5 May 1964 by Hobart M. Van Deusen and Stanley O. Grierson in the Morobe District of the Territory of New Guinea at MASBA CREEK (Figure 4) at an elevation of approximately 2000 feet. For an account of this locality see Van Deusen (1966).

Paratype. AMNH 95881; a badly mangled young juvenile collected by Van Deusen and Grierson on 7 May 1964 at the same locality as the holotype.

Diagnosis. This species is a typical representative of the *fasciatus* species group of *Sphenomorphus*[1] (Greer and Parker, 1967) except that it has a scaly auricular depression instead of the more usual external ear opening. In other words, it is the only "earless" member of the *fasciatus* species group known to date.

Etymology. The species name *anotus* calls attention to the absence of an external ear (*an* — without and *otus* — ear).

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[1] The diagnostic features of the *fasciatus* species group of *Sphenomorphus* are as follows: digits and limbs usually well developed but the limbs generally not overlapping when adpressed to the body; frontal in contact with the two anteriormost supraoculars; generally four supraoculars; a single anterior loreal; no supranasals; usually a series of two or more paired nuchal scales; generally 36 or fewer scales around midbody, the scales of the paravetebral rows being larger than the scales of the more lateral rows; generally a postorbital bone that is usually long and thin.

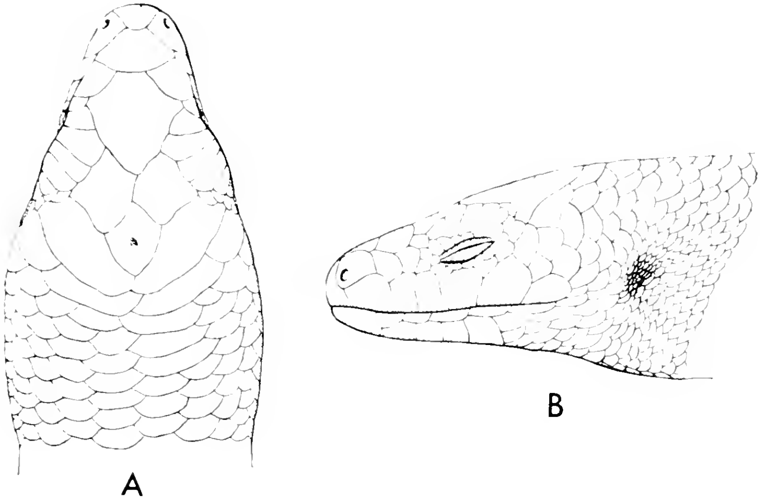


Figure 1. Dorsal (A) and lateral (B) view of the head of the holotype of *Sphenomorphus anotus* (AMNH 95880) from Masba Creek, Huon Peninsula, New Guinea.

Description of the holotype. A small attenuate skink measuring 48 mm in snout–vent length with a complete tail measuring 68 mm in length; head bluntly conical; limbs short, pentadactyl, widely separated when pressed against the body; uniformly brown above and light yellowish brown below (in preservative).

Rostral about as deep as wide and projecting well onto dorsal surface of snout; nasal large with external naris situated well forward and ventral in nasal scale; no supranasals; frontonasal wider than long and forming a short suture with rostral and a slightly wider suture with frontal; prefrontals separated; single anterior and posterior loreals; frontal slightly longer than wide and in contact with two anteriormost of four supraoculars; lower eyelid movable and scaly; frontoparietals and interparietal distinct, approximately subequal in size, and measured together along midline, about equal in length to frontal measured along midline; parietals meet behind interparietal; two nuchal scales on left side and four on right; six supralabials, fourth situated most directly below eye (Fig. 1).

External ear opening lacking and in its place an auricular depression completely lined with small scales; body scales smooth and in 26 longitudinal rows at midbody; scales of paravertebral scale rows slightly wider than other dorsal scales at midbody and numbering 71–72 in distance from parietals to midpoint of insertion of hind legs; medial pair of preanal scales enlarged; medial row of scales on underside of tail only slightly larger than adjacent lateral rows; 8–9 obtusely keeled lamellae beneath fourth toe; fourth toe covered dorsally by a single row of scales on distal third of length, by two rows of scales over medial third, and by three rows over proximal third (Group III of Brongersma, 1942).

Color of the holotype. No color notes were made on the specimen in life. In preservative, however, the dorsum is a uniform light chocolate brown while the venter is a light yellowish brown anterior to the vent and a slightly darker brown posterior to the vent. There is no sharp transition line between the dark dorsal color and the light ventral color. There is only the slightest trace of scattered dark spotting on the throat.

Variation in the paratype. The single paratype of *Sphenomorphus anotus* is a small (snout–vent length = 24 mm), badly mangled specimen obviously of very young age. In the characters that can be evaluated it differs but little from the holotype: there are 26 midbody scale rows, the fourth supraocular lies most directly beneath the eye, there are 3–4 nuchals, and most importantly, there is a scale-lined auricular depression instead of an external ear opening. In color the paratype is similar to the holotype but it lacks the yellowish wash to the venter.

Distribution. Sphenomorphus anotus is known only from the type locality on the Huon Peninsula of New Guinea (Fig. 4).

Habitat. The Masba Creek locality where the two types were caught is in a "stretch of unbroken rain forest" (Van Deusen, 1966) and both animals were taken as the litter was being scraped level for the tents and work flys. Thus it would seem that, like other members of its species group, *S. anotus* is a cryptic burrower in the litter.

Relationships. S. anotus appears to be very closly related to the following species, but a discussion of the relationships of both forms is deferred to the end of that species' description.

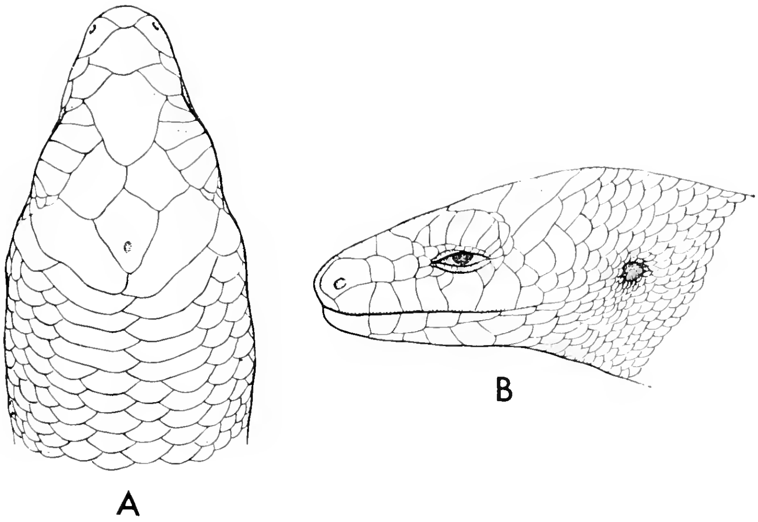


Figure 2. Dorsal (A) and lateral (B) view of the head of the paratype of *Sphenomorphus microtympanus* (MCZ 132767) from Garaina, New Guinea.

Sphenomorphus microtympanus new species
Figures 2, 3, and 5 (top)

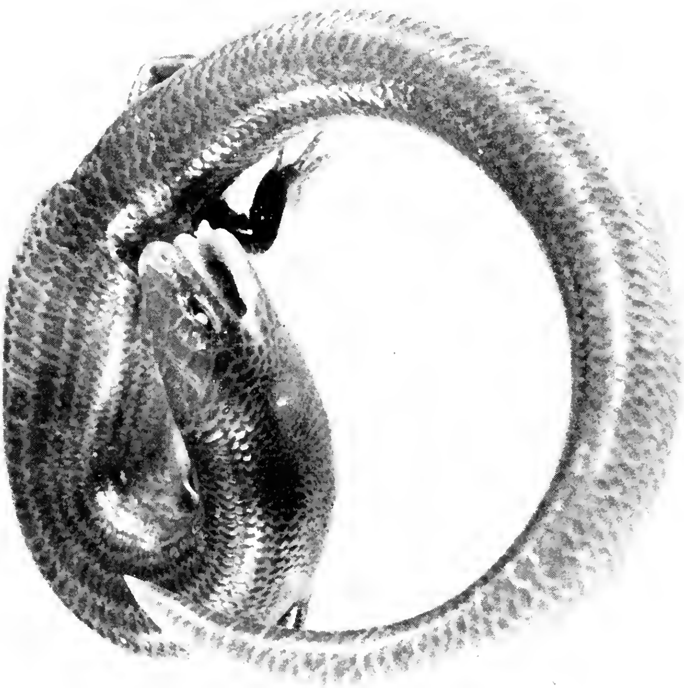
Holotype. AMNH 104076; an adult collected on 7 July 1969 by Angus F. Hutton in the Morobe District of the Territory of New Guinea at GARAINA (Fig. 4) at an elevation of approximately 2300 feet.

Paratype. MCZ 132767; same data as the holotype.

Diagnosis. S. microtympanus is a member of the *fasciatus* species group of *Sphenomorphus* and in that it lacks an ectopterygoid process to the palatine running along the outer edge of the palatal ramus of the pterygoid it is most similar to the *fasciatus* subgroup of that species group (Greer and Parker, 1967). It differs from all members of its species group, however, in having the tympanum both much reduced in size and decidedly more opaque (thickened?).

Etymology. The name *microtympanus* calls attention to the relatively small size of the tympanic membrane of the species.

Description. Since *S. microtympanus* is so similar to *S. anotus* just described, I will only give specific counts and mea-



surements for *S. microtympanus* and will describe only those aspects of the species' morphology in which it differs noticeably from *S. anotus*.

Both the holotype and paratype have a snout vent length of 45 mm; in the paratype the tail is broken but in the type it is complete and measures 60 mm. Both specimens of *S. microtympanus* are a richer chocolate brown above than *S. anotus* and in preservative both lack the yellowish wash on the undersides shown by the holotype of *S. anotus*. These color differences may, however, be an artifact of preservation.

There is a scaly auricular depression very similar to the auricular depression of *S. anotus*, but at the bottom of the depression there is a small, opaque tympanum instead of scales as in *S. anotus* (Fig. 2).

Both type specimens of *S. microtympanus* have four pairs of nuchal scales, and, in three out of the four cases, there are six supralabials with the fourth situated most directly below the eye; on the right side of the head in the paratype there are seven supralabials and the fifth is under the eye. There are 26 scale rows at midbody and the scales of the two mid-dorsal rows number 75 in the paratype and 71 in the holotype when counted from the parietals to the midpoint of the insertion of the hind legs. The subdigital lamellae on the fourth toe number 8–10.

Color. In addition to being richer brown above and lacking the yellowish wash below, the type and paratype of *S. microtympanus* differ from *S. anotus* in having a very noticeable brown wash on the throat and chest instead of a very faint brown wash limited to the throat as in the type of *S. anotus*. This wash is much more pronounced in the paratype of *S. microtympanus* than in the holotype.

Distribution. *S. microtympanus* is known at present only from the type locality (Fig. 4).

Habitat. According to Dr. Zweifel (letter, 14 February 1973), the "undisturbed habitat around Garaina is rain forest on river terrace and foothills."

Figure 3. The holotype of *Sphenomorphus microtympanus* (AMNH 104076) from Garaina, New Guinea. The specimen has a snout-vent length of 45 mm and a tail length of 60 mm.

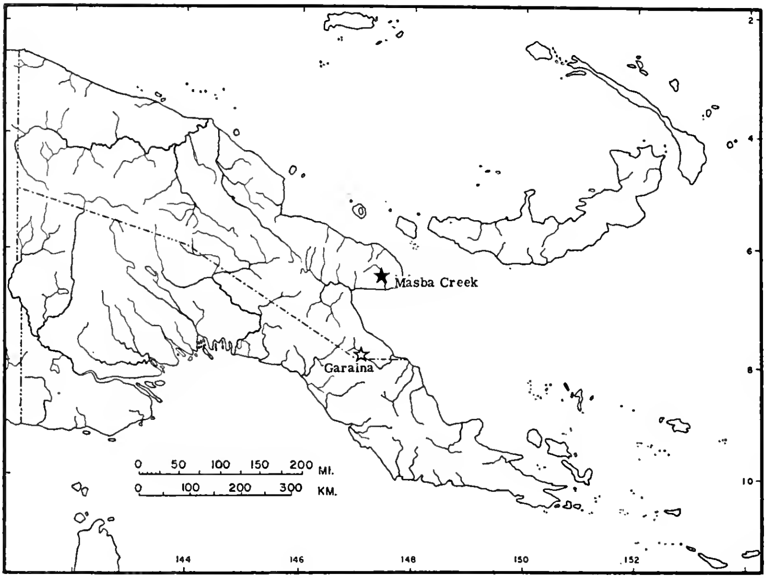


Figure 4. Map of eastern New Guinea showing the type localities of *Sphenomorphus anotus* (Masba Creek = closed star) and of *S. microtympanus* (Garaina = open star). The two species are known only from their type localities.

Relationships between S. microtympanus and S. anotus. These two species are so similar in all aspects of their external morphology, save for the nature of the external ear, that they are almost certainly each other's closest known living relatives. Indeed, it looks as if *S. anotus* could have easily evolved from a *microtympanus*-like ancestor simply by having the scales on the sides of the auricular depression extend down and over the very small tympanum at the bottom of the depression.

The relationship between these two taxa appears to be so close that I originally thought it might be possible to describe them as the same species. To do so would have required only that one believe that the variation shown in the external ears of the specimens exists within a single species. But this kind of variation is unknown in better studied skink species (*e.g.*, the skinks of the earless genus *Hemiergis* or the many species of *Lerista*, which have minute ear openings), and to conclude that it exists within or between the populations represented by these four specimens seems presumptuous.[1]

Relationships with other skinks. Within the *fasciatus* species group of *Sphenomorphus* there are only four other previously described species that are like *microtympanus* and *anotus* in possessing the following suite of characters: relatively small size (maximum snout–vent length 55 mm or less); more or less uniformly dark dorsal color; a moderate number of midbody scales (overall range, 20–28; range of modes, 24–26), and a low number of subdigital lamellae on the fourth toe (upper limit of range not exceeding 16). All four species occur in New Guinea and in the order discussed below they are *forbesi, schultzei, beauforti,* and *oligolepis.* Comparative data for these four species plus *microtympanus* and *anotus* are presented in Table 1.

Forbesi. On the basis of palatal morphology, *forbesi* seems quite distant from *microtympanus* and presumably also *anotus,* although I was not able to examine the palate of this last species. In *forbesi* there is an ectopterygoid process to the palatine which excludes the palatal ramus of the pterygoid from a position on the infraorbital vacuity. In *microtympanus* and presumably also in *anotus* there is no ectopterygoid process and the palatal ramus of the pterygoid enters the infraorbital vacuity. The presence or absence of the ectopterygoid process may reflect a basic evolutionary dichotomy in the *fasciatus* species group (*solomonis* subgroup vs. the *fasciatus* subgroup—*fide* Greer and Parker, 1967) and on this basis alone I would exclude

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[1] There is one poorly analyzed precedent for including skinks both with and without an external opening in the same species. Fuhn (1969) has treated the earless *Ablepharus grayanus* as a subspecies of *A. pannonicus,* a species with a minute external ear opening. His hard-core evidence for this taxonomic move is apparently contained in the following sentence: "Mertens (1964, in litt.) records also specimens of Afghan *A. pannonicus* populations with no ear openings (coll. Dr. K. Lindberg)." But Mertens' (1965) published evidence is nothing more than a brief description and much discussion of one specimen (the only one from that locality) which he said looked like *pannonicus* but which lacked an external ear opening, the key character of *grayanus.* Fuhn himself examined a total of only six specimens of both specimens (three *pannonicus* from one locality and three *grayanus* each from a different locality), none of which he reports as being unusual with regard to the external ear. Perhaps more evidence exists in Mertens' *in litt.* communication, but until that is forthcoming the case for intraspecific variation in the presence or absence of an external ear in skinks is, at best, on shaky ground.

TABLE 1. Morphological data for *Sphenomorphus anotus* and *S. microtympanus* and the four species of the *fasciatus* species group of *Sphenomorphus* most similar to them in size, color and scale counts.

Species	Midbody scale rows (modal number in parenthesis)	Subdigital lamellae on fourth toe	Maximum known snout-vent length (mm)	Subocular supralabial	Prefrontals meet medially
anotus	26	8 - 9	48	4th	No
microtympanus	26	8 - 10	45	4th	No
oligolepis	24 - 28 (26)	9 - 12	55	4th (17%) or 5th (83%)	No, rarely yes
forbesi	24 - 26 (26)	10 - 12	44	4th	No
schultzei	20 - 26 (21)	8 - 13	39	4th	Yes, rarely no
beauforti	26	12	46	4th	Yes

forbesi from close relationship with *microtympanus* and *anotus*.

Schultzei. The palate of *schultzei* is similar to that of *microtympanus* in that it lacks an ectopterygoid process, but other features of its morphology cause me to exclude it from the close relatives of *microtympanus* and *anotus*. The most notable of these features is the unique fusion of the first supralabial and nasal scales (see below), the medially meeting prefrontals (in most specimens), and the proportionately longer legs.

Beauforti. As far as I can tell, *beauforti* is known only from the type specimen (de Jong, 1927) and I have not seen this specimen. I feel, however, that the absence of nuchal scales and the medially meeting prefrontals are enough to make *beauforti* an unlikely near relative of *microtympanus* and *anotus*.

Oligolepis. In contrast to the preceding three species, *oligolepis* is in every way a perfect candidate for the closest living relative of *microtympanus* and *anotus*. The palate of *oligolepis* is very similar to that of *microtympanus* and presumably also to that of *anotus;* all three species are similar in size and body proportions, and there is no significant difference in the general details of squamation. *Oligolepis* differs markedly from *microtympanus* and *anotus* only in having a well-defined external ear opening and ear canal at the bottom of which is a translucent tympanum (Fig. 5), but since this kind of ear was undoubtedly primitive for the *microtympanus*→ *anotus* line, it simply serves to make *oligolepis* the closest living species, morphologically, to the ancestor of that line: *oligolepis*→ *microtympanus*→ *anotus*.

COMMENTS ON THE LOSS OF THE EXTERNAL EAR IN LYGOSOMINES

With the desecription of *Sphenomorphus anotus*, the total number of known "earless" lygosomines comes to 33. This is about 5 percent of the total number of known species in the subfamily.[1]

Taking a very conservative view of the species relationships, I believe that these 33 species represent no fewer than ten different lineages. Or, to put it another way, the external ear has been lost at least ten different times in the evolutionary history

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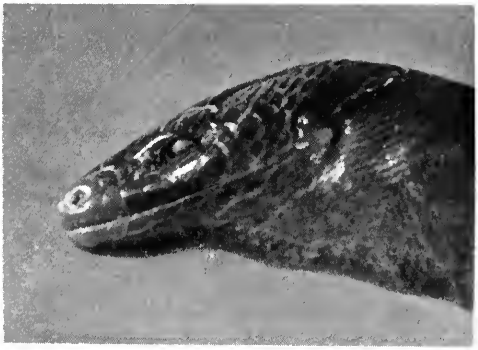
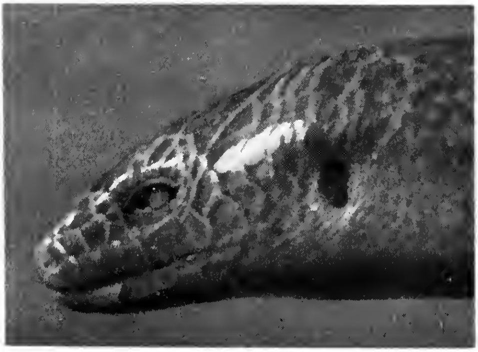
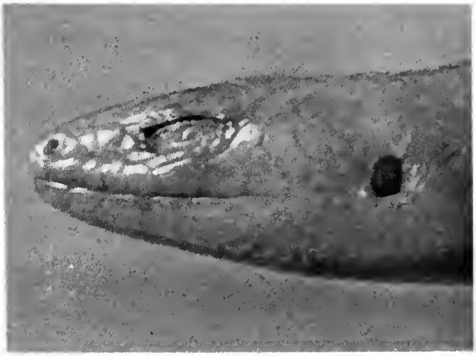
[1] This percentage is very low compared to the other three subfamilies of skinks. All of the feylinines (4 species) and acontines (15 species) lack an external ear opening and just under 25 percent of the scincines, of which there are a total of approximately 182, are also "earless."







of the living lygosomines. The species in these ten groups, along with their distributions and other pertinent data, are listed in Table 2.

Unfortunately, it is difficult to say anything very conclusive about why the skinks in these different groups have lost the external ear, but I can make a few comments and suggestions for further research along these lines.

First, there is probably no one unifying reason for the loss of the external ear in all ten groups since there is nothing in the biology of these skinks beside the absence of an external ear that sets them apart from other lygosomines. It is true that all the earless species are in some sense cryptic in their habits but this is the rule rather than the exception for skinks.

Second, the only outstanding ecological feature of any of the species in the list of earless lygosomines is that certain of the species, *i.e., Isopachys,* most of the *australis* group and perhaps the *sumatrense* group, appear to be the most confirmed burrowers among lygosomines. This fact indicates that the absence of the external ear is probably a prerequisite for an in-depth evolutionary commitment to burrowing life, but there is no way of knowing whether the loss of the external ear in these skinks was achieved as a primary adaptation to burrowing life or whether it was a preadaptation, *i.e.,* originally evolved for other reasons in nonburrowing ancestors. The large number of earless lygosomines that show no exceptional proclivity to a burrowing life, *e.g.,* the *quadrivitattum* group, *Anotis mariae,* and *Ablepharus grayanus,* would argue that the loss of the external ear could be as much a preadaptation to burrowing life as it is a primary adaptation.

Third, Minton (1966) has suggested that, along with the ablepharine eye, the absence of an external ear opening in *Ablepharus grayanus* is a protective adaptation that allows this species to feed unmolested on the ants that are said to form much of its diet. This is an interesting idea, but to be convincing, it will have to be shown more rigorously than it can now be shown that *A. grayanus* is more of an ant specialist

Figure 5. Lateral view of the head of *Sphenomorphus microtympanus* (top; paratype: MCZ 132767), *S. oligolepis* (middle; syntype: BMNH 1946.8.3.47), and *S. solomonis* (bottom; syntype: BMNH 1946.8.34–37). Note the relatively small external ear opening and small tympanum of *S. microtympanus* compared to its close relative *S. oligolepis* and its more distant species group relative *S. solomonis.*

TABLE 2. The 33 species of "earless" lygosomine skinks arranged in the smallest plausible number of monophyletic groups, along with notes on their distribution, relationships, and ecology. Generic names have been omitted for those groups for which the systematics are so poorly known that the use of a generic name is almost pointless. To identify these species I have given the author and date of the original description.

Species	Distribution	Relationships	Ecology Notes
Isopachys (roulei, anguinoides, and *gyldenstolpei)*	Thailand	Unknown	Totally limbless; found underground and known to burrow with ease (Taylor, 1963).
australis Peters 1873	C and SE Queensland	Perhaps derived from the *fasciatus* species group of *Sphenomorphus*	*Australis* and *frontalis* only other limbless lygosomines besides *Isopachys*: *truncatus* — burrowing in damp areas (Arnold, 1966), under logs in rain forest (Copland, 1952); *verreauxi* — burrowing in damp soil, and under logs (Arnold, 1966); *scutirostrum* — partly buried in humus under logs (Longman, 1916); *equalis* — under logs (Bustard, 1961).
frontalis De Vis 1888	NE Queensland		
truncatum Peters 1876	SE Queensland and NE New South Wales		
lentinginosus De Vis 1888	C and SE Queensland and N New South Wales		
verreauxi Duméril 1851	C and SE Queensland and N New South Wales		
reticulatus Günther 1873b	SE Queensland and NE New South Wales		
equalis Gray 1825	SE Queensland and N New South Wales		
scutirostrum Peters 1873	SE Queensland		
sumatrense Günther 1873b	Sumatra	Unknown	Unknown but attenuated body and greatly reduced limbs and digits suggest burrowing habits.
larutense Blgr. 1900a	Malaya		
miodactylum Blgr. 1903	Malaya		
trifasciatum Tweedie 1910	Malaya		
Hemiergis (initiale, peroni, tridactylum, decresiense, and *quadrilineatum)*	Southern parts of Australia	Perhaps derived from the *fasciatus* species group of *Sphenomorphus*	Burrowers in litter and loose soil.

TABLE 2 — continued

Sphenomorphus anotus	New Guinea	Member of the *fasciatus* species group of *Sphenomorphus*	Burrower in forest litter.
quadrivittatum Peters 1867 *infralineolatum* Günther 1873a *subvittatum* Günther 1873a *relictum* Vinciguerra 1892	Philippines; Sula Is., Palawan, Borneo Celebes and adjacent islands Philippines; Celebes Java and islands off W coast of Sumatra	Closely related to the light and dark striped "*Leiolopisma*" of the western Pacific area	Arboreal but cryptic; *quadrivittatum* and *subvittatum* have been found in the root tangles of aerial ferns.
surdum Blgr. 1900b[1] *cophias* Blgr. 1908 *palawanensis* Brown and Alcala 1961 *poilani* Bourret 1937 *tridigitum* Bourret 1939[2] *sanana* Kopstein 1926	Malaya Malaya Palawan I. C Vietnam C Vietnam Sula Is.	Unknown, but perhaps close to the small *Sphenomorphus* of the western Pacific area	Cryptic; *surdum* from roots of epiphytic plant and from beneath dead fiber on ground; *palawanensis* from beneath a rotting log in forest; *sanana* from beneath stones.
Anotis mariae	New Caledonia	Two other *Anotis* also on New Caledonia	Cryptic; found under rocks in forest.
Ablepharus grayanus	Tadzhikistan (USSR), E Iran, Afghanistan and Pakistan	Other *Ablepharus* of eastern Europe and SW Asia	Terrestrial and secretive; found under cover.

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[1] Of all the groups in this table this group is the least likely to be monophyletic. In fact, it is very possible that none of the skinks in this group are very closely related.

[2] Bourret's (1939) figure of this species shows what appears to be a minute external ear opening, but on the basis of his statement "absence de tympan" in the type description, I have included it among the earless lygosomines.

than its close relatives that have external ear openings. I know of only one careful study on the feeding habits of an earless lygosomine (Smyth, 1968, on *Hemiergis peroni*), and this species showed no special fondness for ants or any other small insects that might pose a serious threat to an exposed tympanic membrane.

The most profitable next step in the study of the evolution of earlessness in lygosomines would be to take a group of earless lygosomines that are known to have close relatives with external ears and make detailed ecological comparisons between the two groups. The three best groups for this kind of study now are 1) the *quadrivitattum* group and its close relatives — the sharply light and dark striped skinks in the genus *Leiolopisma* of southeast Asia, the Philippines, the Indo-Australian archipelago, the Palaus and the New Guinea area; 2) *Ablepharus grayanus* and its congeners in eastern Europe and southwestern Asia, and, perhaps somewhat impractically because of the distribution, 3) *Anotis mariae* and its two congeners on New Caledonia.

Observations on *Sphenomorphus forbesi*, *S. oligolepis* and *S. schultzei*

Sphenomorphus forbesi Blgr. 1888 and *S. oligolepis* Blgr. 1914

In spite of the fact that *S. forbesi* and *S. oligolepis* have an osteological difference in the palate (see pages 9, 10) that serves to separate them rather distantly in terms of relationship, the two species are extremely similar in their external morphology. They are so similar, in fact, that Miss A. G. C. Grandison of the British Museum and I both agreed, after an initial examination of the type specimens, that the two forms were conspecific. It was only after a second and more detailed look with more specimens that I was finally convinced that the two forms are good species. It was not, however, until after I had decided that the two forms were good species on the basis of external morphology that I discovered the confirming osteological difference in the palate. Thus the two species can be distinguished without resorting to the sometimes rather destructive process of opening the mouth in preserved specimens and examining the palate. Because the two species are so similar externally they are reviewed here together.

Sphenomorphus forbesi was described by Boulenger (1888) from a single specimen collected at Sogere (= Sogeri) by H. O. Forbes at an elevation of 1750 feet on his expedition into the

Owen Stanley Range behind Port Moresby. The only other specimen to be reported since the original description is a single specimen from Bara Bara, Milne Bay, collected by L. Loria (Boulenger, 1897).

Sphenomorphus oligolepis, also described by Boulenger (1914), was based on two specimens from the Mimika River collected on the British Ornithologists' Union Expedition, and the only new locality information published on this species since its original description has been de Rooij's (1915) listing of a specimen from the Lorentz River.

Both *forbesi* and *oligolepis* are very similar to each other in terms of general squamation and color pattern, but they can be distinguished from each other in terms of size, small details of squamation and subtle differences in color pattern. These differences have been worked out from an examination of the following specimens: the type of *forbesi* (BMNH 1946.8.3.13); ten topotypic or nearly topotypic *forbesi* (MCZ 118845–47, 118851–53: Sogeri, 2000 feet; MCZ 118848–50: Sogeri road, 2 miles east of Rouna Falls, 1500 feet; American Museum of Natural History 103602: Sogeri, 460 meters); and three specimens that appear to be *forbesi* on comparison with the type (MCZ 13357–58; AMNH 105626: Wipim) one syntype of *oligolepis* (BMNH 1946.8.3.47); and 25 specimens which I identify as *oligolepis* after comparing them with the syntype (MCZ 118857: Soliabeda, 1800 feet; MCZ 109330–47; 118854–56: Oroi; 130716: Matkomrae; MCZ 130717: Mendua, and MCZ 130718: Bikim, 500 feet).

The significant differences between the two species are as follows:

Size. *Forbesi* is a smaller species than *oligolepis;* the largest *oligolepis* I examined (including the syntype) measured 55 mm in snout–vent length, whereas the largest *forbesi* I examined measured only 44 mm.

Squamation. In *forbesi* the fourth supralabial is centered beneath the eye (in all 28 cases provided by the 14 specimens) whereas in *oligolepis* it is the fifth supralabial that is more usually centered beneath the eye (the fifth in 43 out of 52 cases and the fourth in 9 out of 52 cases).

In *forbesi* the first infralabial is only about 1/2 to 2/3 the size of the second infralabial, whereas in *oligolepis* the first and second infralabials are about the same size.

Color. In preservative *forbesi* is generally golden brown to light brown above with small dark blotches and vermiculations;

Figure 6. Lateral view of the holotype of *Sphenomorphus forbesi* (top: BMNH 1946.8.3.13; snout-vent length = 40 mm) from Sogeri and *S. oligolepis* (bottom; BMNH 1946.8.3.47; snout-vent length = 55 mm) from the Mimika River. Note that the dark longitudinal lateral lines contrast with the dark color of the dorsum in *forbesi* but not in *oligolepis.*

oligolepis, on the other hand, is a more uniform and darker brown above and lacks the contrasting darker blotches or vermiculations. In both *forbesi* and *oligolepis* pigment tends to concentrate in longitudinal lines running between the lateral scale rows, and in *forbesi* these longitudinal lines stand out because the pigment is generally darker than the general ground color of the back, whereas in *oligolepis* the longitudinal lines do not stand out because the pigment is no darker than the dorsal ground color (Fig. 6).

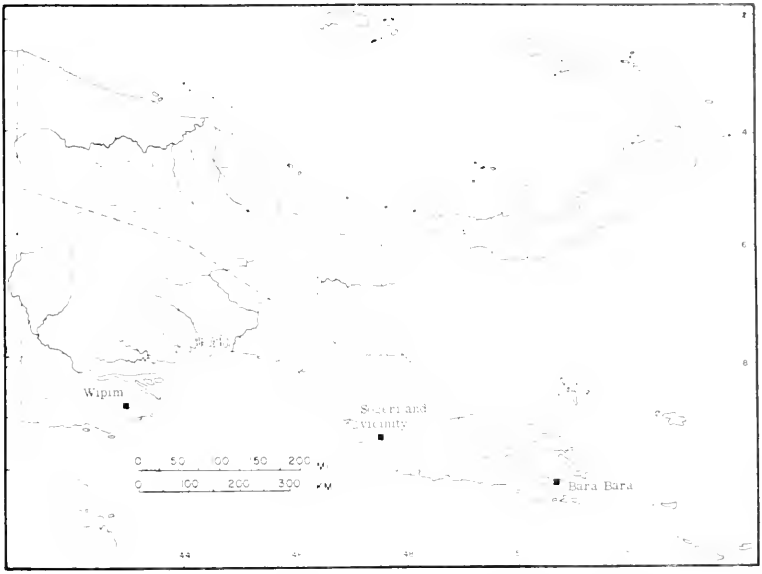

Figure 7. Map of eastern New Guinea showing the known localities for *Sphenomorphus forbesi.*

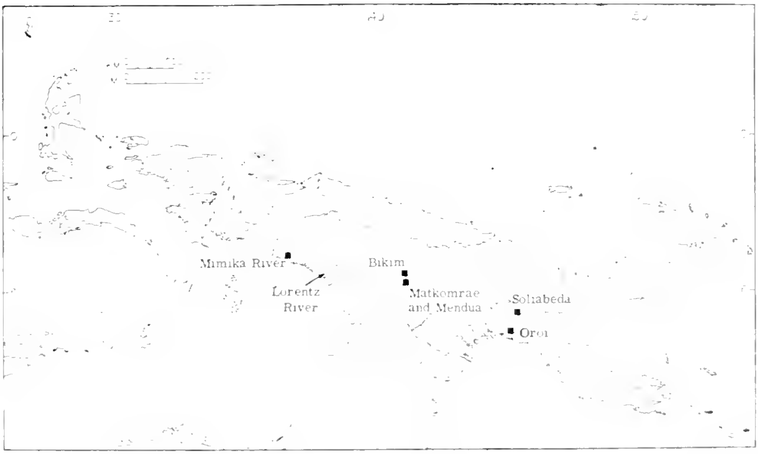

Figure 8. Map of New Guinea showing the known localities for *Sphenomorphus oligolepis.*

Two of the MCZ *forbesi* which I examined were gravid. One specimen with a snout–vent length of 40 mm contained a single thin-shelled egg in the right oviduct and the other specimen, which measured 43 mm in snout–vent length, contained two thin-shelled eggs, one in the right oviduct and one in the left. To judge from the texture of the egg shells in both specimens, it is likely that the species is oviparous.

Five of the MCZ *oligolepis* were gravid: four with a thinly shelled egg in the right and left oviduct and the fifth with a single large ovum in each ovary. It would thus appear that *oligolepis* is oviparous. The smallest of these gravid females had a snout–vent length of 43 mm and the largest had a snout–vent length of 53 mm.

The known distribution of *forbesi* and *oligolepis* is shown in Figures 7 and 8 respectively.

Sphenomorphus schultzei Vogt 1911

The two types of *Sphenomorphus schultzei* (Berlin 22135) were examined because the species seems to be a member of the *fasciatus* species group and within this group it combines a moderate to low midbody scale count with a low fourth toe subdigital lamellae count (Table 1).

Theodore Vogt (1911) described this species on the basis of two specimens captured by Leonard Schultze on an unnamed mountain at an elevation of 1570 meters in the region of the Sepik River below 5° latitude. Four years later de Rooij (1915) listed the Sermowai River as an additional locality for the species, but beyond this no new records have been published for the species.

In examining Vogt's two syntypes (Fig. 9) I immediately discovered that the first supralabial and nasal scale are fused into a single scale. That this fusion is not an anomaly is proved by the fact that it exists in the 11 *schultzei* from four different localities which have recently been added to the MCZ collections through the efforts of Fred Parker (MCZ 89897–99: Bomai, Tive Plateau, 3500 ft.; MCZ 124037–40: Tifalmin, 4300 ft.; MCZ 124041–43: Wangbin, 4800 ft.; MCZ 124044: Imigabin, 4200 ft.). These and other known localities are shown in Figure 10.

Apparently neither Vogt nor de Rooij noticed the scale fusion for neither author mentions it. There is a crease between the two scales that may have been mistaken for a suture with early optical equipment, but with good light and modern optics there is no doubting that the scales are fused.

Figure 9. Lateral view of a syntype of *Sphenomorphus schultzei* (Berlin 22135; snout-vent length = 34 mm) from the region of the upper Sepik River.

To my knowledge no other lygosomine skinks have a fused first supralabial and nasal scale, and thus this character provides a blessedly certain method of identifying at least one species of a notoriously difficult "generic" assemblage of lygosomines.

Variation in the taxonomically important characters of the 13 *schultzei* that I have examined (12 intact and one decapitated) may be summarized as follows: The two types have 20 midbody scale rows, but the 11 MCZ specimens have from 22 to 26 midbody scale rows. The modal number for all 13 specimens is 24. The range in the number of subdigital lamellae on the fourth toe for all specimens is 8–13 (avg. = 10.9). The number of nuchal scales on the left and right side of the midline in the 12 intact specimens ranges from 0–0 to 3–2. In all but two of 12 intact specimens the prefrontals meet medially

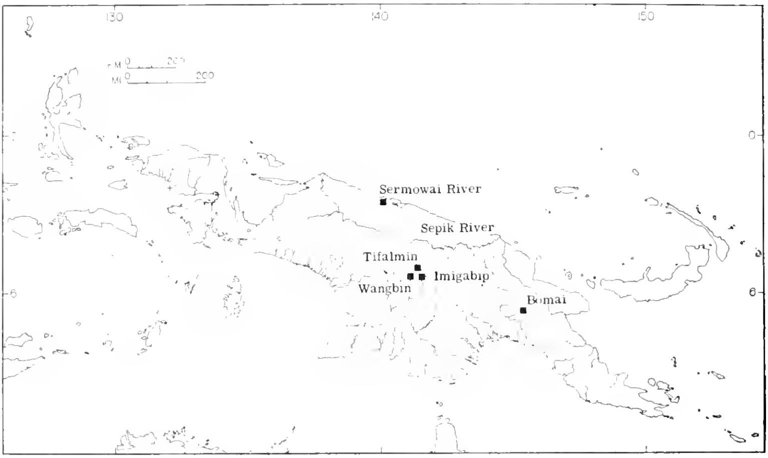

Figure 10. Map of New Guinea showing the known localities for *Sphenomorphus schultzei.*

and form a broad suture; in the remaining two specimens the right prefrontal is lacking in one and the prefrontals are separated in the other. In all 12 intact specimens the fourth supralabial is situated beneath the eye. The largest specimen measures 39 mm in snout–vent length.

In two of the MCZ specimens I found a single large, heavily shelled egg in the right oviduct. And in the only specimen of these two in which I looked for a left oviduct, I could find none, although there was a left ovary. It would appear, therefore, that the species is oviparous with a clutch size of one, and that it may lack a left oviduct.

Fred Parker has very kindly summarized his field notes on *schultzei* for me, and I have extracted the following information nearly *verbatim* from his notes. In the Bomai area (Fig. 10) *schultzei* is found in dense rain forest where it lives under decaying logs and vegetable matter on the forest floor in damp valleys. It is a fairly slow moving species. It is subject to rapid dehydration if not kept damp.

In life the iridescence of the scales almost conceals the color pattern. The dorsal surfaces are mottled pale and dark brown. There are some fine white specks on the lips and face. The flanks are brown with paler spots. The ventral surfaces are pale translucent yellow with some grey spots in the ventrolateral regions.

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Mr. Fred Parker generously gave me his field notes on *schultzei*.

Mr. Laszlo Meszoly did the drawings for Figures 1 and 2, and a grant from the Milton Fund administered through the Harvard Medical School financed the photographs of the type specimens in Figures 3, 5, 6 and 9.

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B R E V I O R A

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THE CHAÑARES (ARGENTINA) TRIASSIC REPTILE FAUNA. XIX. POSTCRANIAL MATERIALS OF THE CYNODONTS *PROBELESODON* AND *PROBAINOGNATHUS*

Alfred Sherwood Romer and Arnold D. Lewis

Abstract. Descriptions are given of postcranial materials of *Probelesodon* and *Probainognathus* and a restoration of *Probelesodon lewisi* is attempted.

Because of the phylogenetic position of the cynodont therapsids as the probable ancestors of mammals, their structure is of great importance in the story of vertebrate evolution. A number of excellent studies have been made of cranial structures of cynodonts. As regards the postcranial skeleton, there have been numerous descriptive papers, but few which have attempted a broad study of cynodont skeletal materials from an evolutionary or functional viewpoint. Early essays of this sort were those of Watson (1917), Gregory and Camp (1918), and Romer (1922); a recent comprehensive work is that of Jenkins (1971; cf. also Jenkins, 1970).

Postcranial remains of African cynodonts have been comprehensively studied and summarized by Jenkins (1971); some data on *Permocynodon* of Russia have been given by Konjukova (1946). Of the South American cynodonts, descriptions of gomphodont skeletons have been given by Bonaparte (1963) for *Exaeretodon*, and by Jenkins (1970) for *Massetognathus*, and Huene (1944) has described a limited amount of postcranial material of *Traversodon*. For the carnivorous cynodonts of South America, all so far published has been the description of a partial skeleon of *Belesodon* by Huene (1944), and of a limited amount of material of *Chiniquodon* by Romer (1969).

The purpose of the present paper is to place on record such data as are available on the postcranial skeleton of the carnivorous cynodonts of the Chañares Formation — *Probainognathus* and *Probelesodon.* Together with their relatives, *Chiniquodon* and *Belesodon,* from the Santa Maria Formation of Brazil, they include the latest in time and most advanced of therapsids leading in a mammalian direction. As Jenkins has noted (1971), the postcranial skeleton of cynodonts shows in general a remarkable consistency of pattern, and hence little novelty is to be expected from the description of the Chañares genera. Collection and preparation of *Probelesodon* and *Probainognathus* were made possible by grants from the National Science Foundation.

Postcranial Material of *Probelesodon lewisi*

A major source of information is MCZ 3781 (field no. 79), the remains of a nodule that contained a nearly complete and mostly articulated specimen of this form, with a skull approximately the size of the type. This is preserved as a slab, prepared on both surfaces. Photographs of the two sides (which we will call the obverse and reverse sides) are shown in Figures 1 and 2. Outlines of the materials seen on the two surfaces are shown in Figures 3 and 4. Figures 3 and 4 were derived from the photographs and, owing to perspective, the two are not completely superposable. Unfortunately, some parts of the specimen were lost before collection; further, the specimen had undergone considerable weathering and penetration by grass roots, with the result of obscuring much detail and rendering interpretation difficult.

MCZ 4002 (field no. 98), in addition to a good skull, included a fair amount of mostly disarticulated postcranial material; this material is, in general, in better shape than that of MCZ 3781. Several other concretions include postcranial materials that may be of *Probelesodon,* but for the most part such materials either add little to the data available in MCZ 3781 or MCZ 4002 or are of doubtful assignment. We may note, however, that MCZ 3801 includes a mélange of bones, certain of which rather surely pertain to *Probelesodon,* notably a pair of excellent femora.

Axial skeleton. At burial the specimen constituting MCZ 3781 appears to have had a complete vertebral column, articulated for the most part. However, before collection, a considerable portion of the dorsal vertebrae had been lost, leaving

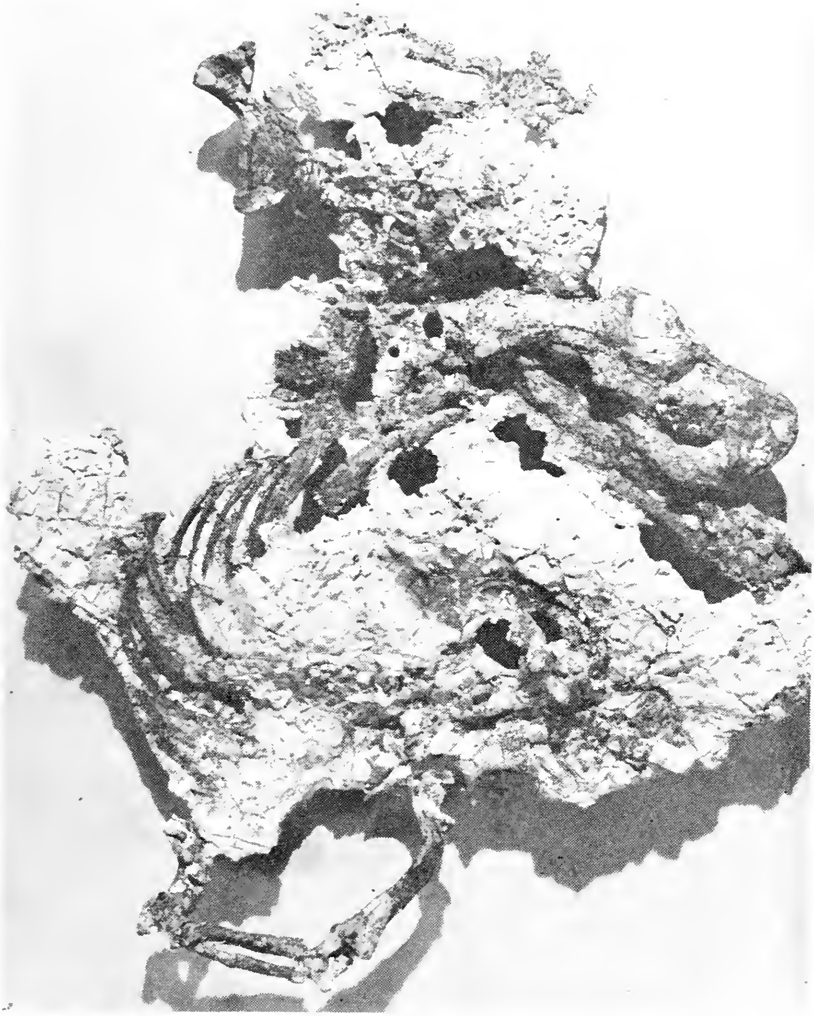

Figure 1. Obverse side of the slab, MCZ 3781, containing a skeleton of *Probelesodon lewisii.* Slightly less than 1/3 natural size.

Figure 2. Reverse of the slab shown in Fig. 1.

Figure 3. Diagram of the structures on the obverse side of the slab shown in Figs. 1 and 2. Slightly less than 1/3 natural size. Abbreviations for Figs. 3 and 4: *l*, left; *r*, right; *cl*, clavicle; *f*, femur; *fib*, fibula; *h*, humerus; *ic*, *interclavicle; i*, ilium; *is*, ischium; *r*, radius; *sc*, scapula; *S1*, first sacral; *S5*, fifth sacral; *t*, tibia; *u*, ulna.

Figure 4. Diagram of the reverse side of the same slab. Slightly less than 1/3 natural size. Abbreviations as in Fig. 3.

a small number of cervical vertebrae present anteriorly, then, following a gap, posterior dorsals, "lumbars," sacrals and part of the tail. Although the articulated condition of the posterior part of the column and the forward continuation of a rib series in seemingly natural position indicates that much of the column was articulated at the time of burial, it is obvious that the column had been broken at about the posterior end of the cervical series. Several isolated vertebrae, obviously from the region of the break, are present above and behind the skull.

It is impossible to be certain of the exact presacral vertebral count. As noted below, there is some question as to the position of the first sacral, but the articulated series anterior to this appears to include 14 posterior dorsals and "lumbars." For the most part the ribs associated with these vertebrae are preserved, and anterior to the vertebrae present, this rib series is continued for eight segments further to the 22nd segment anterior to the sacrum. The most anterior rib is not complete at its head, but has a moderately long shaft, and hence can be no farther forward than the posterior end of the cervical series. If 27 presacrals — a typical cynodont number — were present, this rib would pertain to vertebra 6. Since presumably the anterior cervical ribs were short, no more anterior position for this rib seems probable and we have hence assumed for purposes of restoration the typical count of 27 presacral vertebrae.

In general the preservation of the vertebrae present is not good, but as far as can be seen the structure is of the general cynodont type. Remains of three vertebrae are present close to the back end of the skull. The most anterior vertebra preserved has a neural spine (broken above) of considerable length anteroposteriorly, suggesting that we are dealing with the axis. Little more can be made out as to details of structure on the three further cervicals present in MCZ 3781 except for the presence of normal zygapophysial regions, well developed transverse processes slanting outward, backward and downward, and in two of the three, neural spines that are relatively narrow anterposteriorly (the other — apparently the fourth in this series — appears to have a widened spine). Isolated vertebrae that appear to be cervicals are present in MCZ 4002. As preserved, the centra are subcircular in end view, with a diameter of 11–12 mm, and a central length of perhaps 10 mm. Transverse processes are well developed and extend strongly out from the arch bases.

Posterior cervicals and much of the dorsal region is missing in MCZ 3781, although represented by a few scattered vertebrae. A number of dorsal vertebrae are present in MCZ 4002. Those best preserved have central lengths of about 12 mm, and height of centrum of 12–13 mm. They are deeply biconcave; the centrum, as seen in end view, is oval in outline, with a width somewhat less than the height. Both anterior and posterior margins of the centra are somewhat thickened; presumably the capitulum was carried on the anterior rim, but there is little indication of a discrete articular facet. The transverse processes are stout but short, extending but little outward beyond the level of the arch base, and face strongly downward. The posterior zygapophyses are almost directly above the base of the transverse processes; anteriorly the arch bases extend far forward, so that the spine extends upward about opposite the front margin of the centrum.

Of the series of 14 presacrals preserved in MCZ 3781, and mainly visible on the reverse surface of the slab, the second to fourth are seen in side view and are fairly well preserved. The neural spines are relatively short, rising to about 15 mm above the level of the zygapophyses, and broad anteroposteriorly. Centrum lengths are 12–13 mm. Beyond this point the vertebrae are seen from above, and the neural arches and spines are for the most part absent, revealing the neural canal on the surface of the slab. The series is continuous, except for the last two presacrals, which are disarticulated and damaged.

Beyond this point the sacrals and anterior caudals are articulated. Here the vertebrae are seen from above and somewhat to the left side. Eleven caudals and part of a twelfth are present. The neural arches, still well developed on the posterior sacrals, decrease in height and become more slender as we continue along the caudal series; the transverse processes, as preserved and seen on the left, likewise decrease in length posteriorly. Length of centra, about 12 mm in the sacrals, decreases to about 8 mm on the last caudal preserved. On the obverse side are seen the rounded ventral surfaces of some of the vertebrae in the series. Beneath the articulated caudal series are obscure remains of additional caudal vertebrae. On MCZ 4002 is found a series of seven articulated caudals, five of which are well preserved. The centra have lengths of 8 mm each; they are apparently somewhat compressed vertically. The height of the centra is about 5 mm; the neural spines are very short, and as preserved there is little trace of any transverse process. It seems certain that we are dealing with elements distal to the

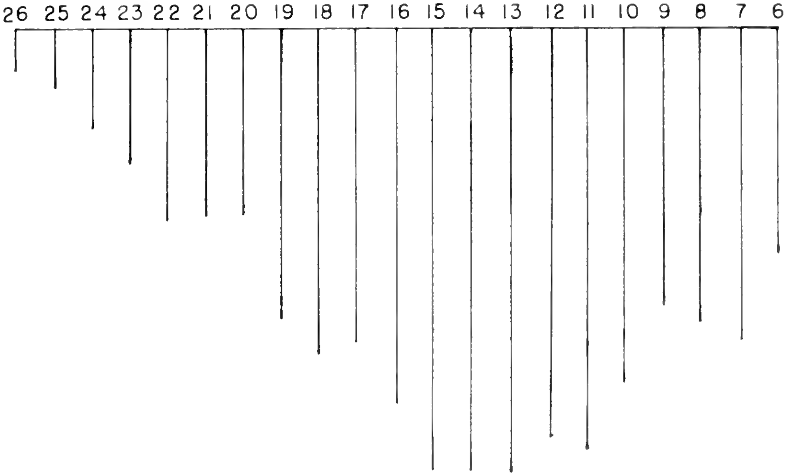

Figure 5. Lengths of right ribs of *Probelesodon lewisi,* MCZ 3781, from presumed vertebra 6 to 26. Measurements are direct between the two ends of the parts preserved; rib heads are complete only on ribs 14 and 15. × 2/3 natural size.

tail "stump" seen on the slab, which strongly suggest the presence of a fairly long tail.

No interpretable remains of anterior cervical ribs are preserved. Of ribs of the left side, a few dorsals are present in isolated fashion on the reverse surface of the slab. Posteriorly, a few stumps of left rib are present in the posterior dorsal-lumbar series; these have a broad head but rapidly decrease to the base of a slender shaft. There is no indication of the interlocking expansions seen in various other cynodonts.

The ribs of the right side are better preserved. Only on two ribs, which we interpret as presacrals 14 and 15, are the heads preserved; these are expanded proximally for capitular and tubercular attachments to the vertebrae, but taper rapidly distally, with no trace of proximal overlapping expansions. A proximal series of right ribs, commencing with that which we assume pertained to vertebra 6, are seen on both obverse and reverse surfaces posteriorly. The ribs attributable to vertebrae in the posterior presacral series are seen on the reverse surface, their heads concealed beneath the vertebrae. In Figure 5 we have plotted the lengths of ribs as preserved (measured directly between the two ends). Although we cannot be sure how much has been lost proximally or distally in most cases, we see a reasonable distribution in lengths, with an increase to a maximum in the anterior dorsal region followed by a gradual decrease as we enter the lumbar region and approach the sacrum.

On MCZ 4002 a number of dorsal ribs are preserved in their entirety, including the heads; they are similar in nature to numbers 14 and 15 on the slab and appear to be mid-dorsals of both sides with average lengths of about 10 cm. Although the usually imperfect nature of transverse processes makes difficult the interpretation of the orientation of ribs to the backbone, the rib structure strongly suggests a broad, barrel-shaped abdomen.

The lumbar ribs as preserved are slender (except for the presumed first presacral) and although the heads are concealed beneath the centra, there obviously was none of the interlocking found in the lumbar series of certain other cynodonts.

In the sacral region some seven ribs on the left side show distal expansion (the first broken off from its vertebra). As the length of the associated right ilium indicates, five members of this series are sacrals; but which five? Possibly incorrectly, we assume that the first (whose vertebra is disarticulated from the sacral-postsacral series) is the last presacral (and we have used this assumption in making a count of presacral vertebrae). The first four, particularly, of the assumed sacral series are expanded at their distal surfaces for iliac articulation; two sacrals are visible in ventral view, which better shows this prominent distal expansion. A slender rod of bone, extending forward, is attached without evidence of sutural separation to the outer end of the presumed fourth left sacral; this appearance, however, is probably due to the peculiar type of preservation in this specimen, and this rod is perhaps a fragment of the left ilium.

Limbs and girdles. Remains of the shoulder girdle are present in MCZ 3781. The interclavicle is present, and on the obverse are the lower ends of the two clavicles. The interclavicle as preserved (slightly incomplete anteriorly) measures 57 mm in length. A better preserved interclavicle (slightly incomplete distally) is present in MCZ 4002 (Fig. 6b). This is of similar size, with a length of 59 mm, a width of 33 mm across the head, and, following a constriction, to a width of 11 mm back of the head, a modest increase in width distally. The structure is that typical of cynodonts in general. The anterior "quadrants" for clavicular reception are deeply incised; a median keel is present between these quadrants but there is little de-

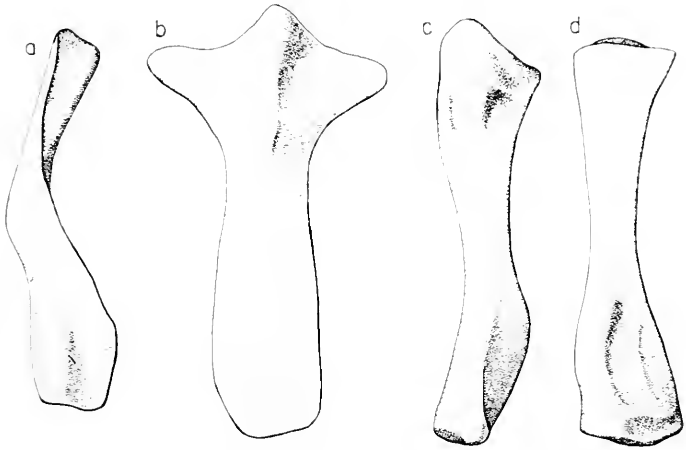

Figure 6. *Probelesodon lewisi*, *a*, left clavicle in lateral view; *b*, interclavicle in ventral view; *c*, ulna; *d*, radius of right side seen from extensor surface. All from MCZ 4002. × 1.

velopment of a median ridge more posteriorly. The left clavicle is well preserved in MCZ 4002 (Fig. 6a). It is of typical cynodont build. Its length, measured directly between the ends, is 51 mm. The relatively thin shaft curves about 45° between proximal and distal ends. The dorsal end is somewhat expanded and excavated medially for acromial apposition. A well-defined ridge descends the posterior margin of the shaft and continues on to the posterior margin of the ventral expansion for articulation with the interclavicle.

Of the primary girdle in MCZ 3781, an obscure fragment of the left scapula is present; the girdle of the right side is present, but is poorly preserved and incompletely seen (Fig. 7). On the reverse side is visible the glenoid region and incomplete coracoids, in poor condition; on the obverse is the medial surface of the scapular blade. This is, as in other chiniquodonts, unusually tall and narrow, with a length (probably incomplete) from the glenoid articulation with the coracoid of 55 mm, and a width at mid-height of 11 mm. The exposed medial surface of the blade is strongly convex in the transverse plane and obviously the external surface was strongly ridged longitudinally on both front and back margins. In MCZ 4002 a scapular blade was present, but is represented by little but an impression

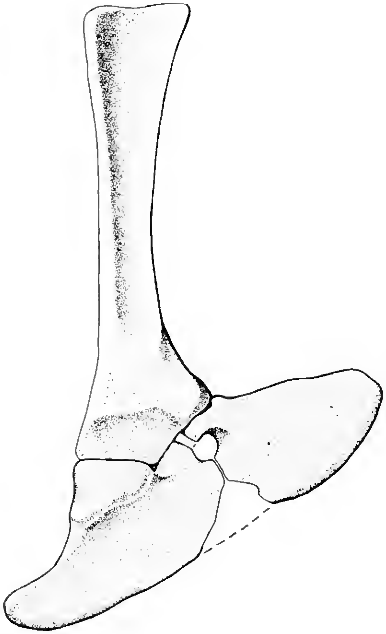

Figure 7. *Probelesodon lewisi,* right scapula and coracoids; the anterior coracoid poorly preserved, the acromial region of the scapula incomplete. From MCZ 3781. × 1.

indicating that it was elongate and slender. Both coracoids are present, the posterior element complete and well preserved; the anterior coracoid is incomplete. In MCZ 3801 there is a scapular blade of *Probelesodon* type, narrow and deeply concave, externally with strong ridges posteriorly and (especially) anteriorly. As preserved, the blade is 48 mm tall, 12 mm wide at the summit, with the width decreasing to 6 mm below. Unfortunately, the scapula is incomplete ventrally, but there was obviously little acromial development and no indication of any beginning of a supraspinous surface.

Both humeri are present in MCZ 3781, and are essentially complete although somewhat crushed, and a good left humerus is present in MCZ 4002 (Fig. 8). The bone in general corresponds well with that of typical cynodonts, as described in detail by Jenkins (1971). Lengths of the humeri of MCZ 3781 as preserved are 72 and 66 mm, that of MCZ 4002 68 mm. The

Figure 8. *Probelesodon lewisi*. Right humerus in distal ventral, lateral, and distal dorsal views. From MCZ 4002. × 1.

head of the bone is unusually expanded anterodorsally, so that the articular area extends into a "lip" overhanging the anteroproximal corner of the dorsal surface. The deltopectoral crest is somewhat more expanded than in typical cynodonts. The distal end of the bone is unusually broad; its width in MCZ 4002 is 43 mm, thus being about 63 percent of the length, in contrast with lower figures in most cynodonts. This increased width appears to be associated with a greater expansion than usual of the entepicondyle. On the ventral distal surface the areas for radial and ulnar articulations are well ossified in MCZ 4002.

In MCZ 3781 the right radius and ulna and left ulna and partial radius are present, but poorly preserved. In MCZ 4002 the right radius and ulna are well preserved (Fig. 6, c, d). In this specimen the radius has a length of 53 mm, the ulna 56 mm. Both bones conform well to typical cynodont structure. The radius is essentially columnar in shape, but as preserved somewhat flattened between extensor and flexor surfaces. Proximally the bone is expanded and deeply cupped for humeral articulation. Distally the width of the bone is increased toward the medial margin and thickened on the flexor surface to make

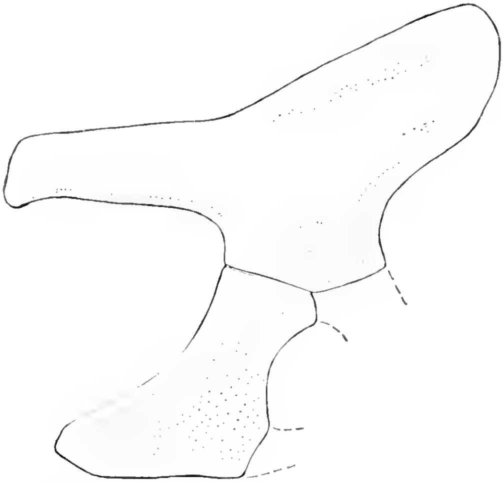

Figure 9. *Probelesodon lewisi*, right ilium and ischium, composite, MCZ 4002 and MCZ 3781. × 1.

possible a broadly oval distal surface for carpal articulation. As in *Thrinaxodon,* a ridge, perhaps for biceps attachment, is present proximally on the flexor surface; a flattened area at its summit was presumably for apposition with the ulna. A ridge with a rounded summit descends the distal third of the medial margin, presumably marking the boundary between extensor and flexor muscle areas.

The ulna has the typical cynodont pattern. As usual, the olecranon is unossified except for its base, the sigmoid notch, represented only by its basal portion. At the expanded dorsal end of the bone the medial area is somewhat concave for radial apposition; lateral to this area a pronounced ridge is present proximally, fading out rapidly below. The proximal part of the flexor surface is markedly concave, bounded externally by a distinct ridge. Below, the shaft of the bone narrows, to be only moderately expanded distally for carpal articulation. Deep to the transverse plane of the shaft, however, a very strong ulnar crest is present, as in other cynodonts; this is conspicuously developed along the distal half of the bone.

Remains of the manus of both limbs are present in MCZ 3781, but in poor condition. Little certain data can be made out concerning the carpus, except for the presence of three prominent distal carpals. All metacarpals are present on the left side, four on the right. Exact measurements are meaningless, owing to the imperfect nature of the material, but the average length of metacarpals II–V is about 18 mm. A limited number of poorly preserved phalanges are present but in no case is there a complete digit. The digits are, however, sufficiently preserved proximally to show that the vestigial "extra" phalanges present in primitive cynodonts were absent.

In MCZ 3781 the incomplete upper margin of the left ilium is seen on the reverse side of the slab; the vertically oriented complete right ilium is seen on the margin of the slab, and a nearly complete left ilium is present in MCZ 4002 (Fig. 9). The iliac length is about 70 mm. For the most part the structure is typical of that of cynodonts generally, but the posterior part of the blade is much more slender than in most cynodonts, suggesting that *Probelesodon* is advancing toward the mammalian condition of forward migration of the gluteal musculature. The right ischium is present in MCZ 3781, and has a normal cynodont form. Except for the area of iliac articulation of the right pubis, there are no identifiable remains of the pubis in available material.

Hind limb material is poorly preserved in MCZ 3781. Only the proximal part of the left femur is present and the right femur (with a probable length of about 80 mm) is badly crushed and broken. Only fragments are present of the left tibia and fibula. The right tibia and fibula are present but in such poor condition that little can be said except that they appear to conform generally to the usual cynodont pattern. As preserved their lengths are 74 mm and 63 mm (the fibula is incomplete proximally).

In the mélange of material in field number 188 (MCZ 3801) are two well-preserved cynodont femora which seem quite surely to belong to *Probelesodon lewisi* (Fig. 10). With a length of 63 mm each, they represent an animal smaller than MCZ 3781, but they are too large to pertain to *Probelesodon minor* or *Probainognathus*, and they differ in structure from the gomphodonts in the fauna. In nearly all respects these femora are closely comparable to the *"?Cynognathus"* femur illustrated by Jenkins (1971, fig. 48) — even to the presence, part-way down the shaft, of a groove of unknown nature. These femora, however, differ markedly from all hitherto described cynodont femora in the position of the greater trochanter. In all cynodonts hitherto described the greater trochanter lies some

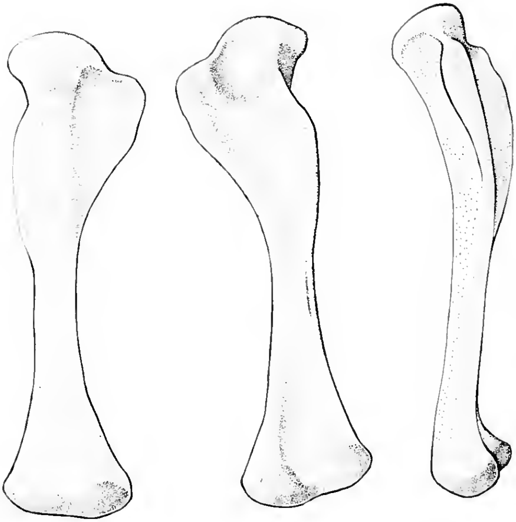

Figure 10. *Probelesodon lewisi,* left femur in dorsal, ventral and medial views. From MCZ 3801. × 1.

distance down the posterior margin of the femur and faces as much laterally as proximally. In this specimen it is placed definitely farther toward the proximal end of the bone and its somewhat expanded tip faces nearly directly proximally. We have here a position splitting the difference between typical cynodonts and the mammalian condition. A femur of the chiniquodontid *Chiniquodon* described by Romer (1969, fig. 9C) shows a somewhat comparable proximal movement of the greater trochanter, but the specimen is not too well preserved.

The feet are poorly preserved. Of the left foot, a few disarticulated metatarsals, phalanges, and tarsal remains are seen on the reverse side. The right foot is nearly complete but difficult to interpret. Astragalus and calcaneum can be made out on the obverse side. Two complete and two incomplete metatarsals are present; the two complete — perhaps the third and fourth — are 17 mm in length as preserved. Although too much reliance should not be placed on measurements of such poor material, it would appear that here, in contrast to certain other cynodonts, front and hind feet were of approximately equal size. A number of phalanges are present, but except for

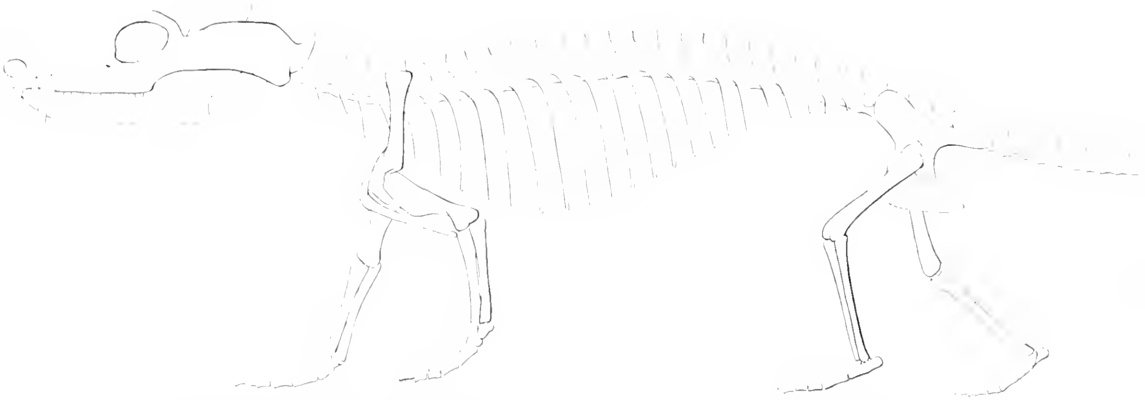

Figure 11. Restoration of *Probelesodon lewisi*, × ¼. As noted in the text, various elements are absent or poorly preserved, including pubis, distal phalanges, cervical ribs and vertebrae, etc.

the certain presence of two phalanges on supposed digit IV (and the obvious absence of "vestigial" phalanges), we cannot be sure of their arrangement.

Restoration. On Figure 11 we have attempted a restoration of the skeleton of *Probelesodon.* We believe that this restoration gives correctly the general appearance of the animal, although, as noted in the description above, knowledge is lacking in a number of regards, such as cervical ribs, the distal portion of the tail, the pubis, and the distal phalanges; even the probable presacral count of 27 vertebrae is uncertain. The body was surely stockily built, and although we have included in the tail only those vertebrae in MCZ 3781, the evidence indicates that *Probelesodon* (and not unlikely other cynodonts as well) had a tail of rather good length. A notable departure from the situation in many cynodonts is the almost complete absence of the overlapping of the ribs, seen at its height in *Thrinaxodon.* This type of structure has been discussed by Jenkins (1971: 76ff); unless we assume that such a late cynodont as *Probelesodon* has evolved independently from the very base of the cynodont stock, the situation, as Jenkins believes, is one in which there has been a return to "normal" rib structure.

Presumably such cynodonts actively pursued their prey, but their limbs would seem to have been relatively inefficient for speedy locomotion as compared with later mammals or contemporary archosaurs (although an improvement over the pelycosaur condition). As in early tetrapods generally, the hind legs were longer than the fore, the combined length of femur plus tibia being about 30 percent greater than that of humerus plus radius. Again, as in primitive forms generally, the podials are longer than the epipodials; the humerus is about 30 percent longer than the radius, the femur about 15 percent longer than the tibia.

Probelesodon may be compared with a canid, *Vulpes*, of similar size, and with presumably somewhat comparable habits. We may use as a crude base for comparison the length of dorsal vertebrae (approximately the same length in *Vulpes* and *Probelesodon*). To give a rough estimate of comparative limb length we may use the length of humerus and radius for the front leg, of femur and tibia for the hind leg. In *Vulpes* this front leg measurement is 19 times the length of a dorsal vertebra, in *Probelesodon*, little longer than the length of nine vertebrae. The hind leg of *Vulpes* is 21 vertebrae long, of *Probelesodon* 12 vertebrae. It is immediately obvious that for speedy loco-

Figure 12. One surface of a block containing material of the shoulder region and front leg presumably belonging to *Probelesodon minor*. On this surface are seen the clavicle and interclavicle, most of the primary girdles, and part of the left humerus and ulna. The left scapulocoracoid is seen in external view, extending dorsally as far as the acromion. The right scapulocoracoid is seen in posterior view. MCZ 4164. × 1.

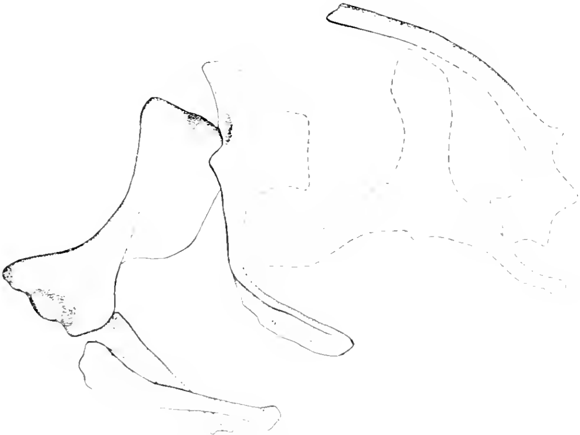

Figure 13. The opposite side of the block seen in Fig. 12, showing the left humerus, ulna, incomplete radius and part of the primary girdle. × 1.

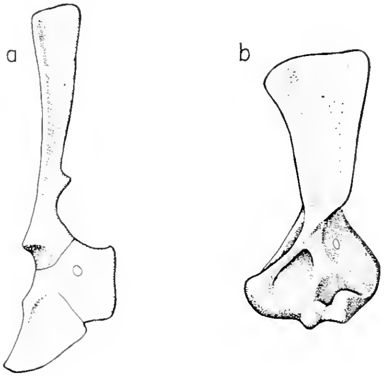

Figure 14. *Probelesodon minor*. *a,* external view of the right scapulocoracoid; *b,* ventral view of the left humerus. MCZ 4164. × 1.

motion, the limbs of *Vulpes* are far superior to those of *Probelesodon*. The contrast is still stronger if it is noted that *Probelesodon* had not completed the shift from the sprawled pelycosaurian limb position to the fore-and-aft mammalian pattern. Carnivorous cynodonts are still moderately abundant in the early Middle Triassic Chañares beds, but become rarer in the formations succeeding this horizon; meanwhile there are appearing various thecodonts of a seemingly more sprightly nature, and it is not to be wondered at that carnivorous cynodonts were reduced in competition with these rivals.

Postcranial Material of *Probelesodon minor*

There is no positive association of postcranial materials with skulls of *Probelesodon minor*. However, in field number 40, a nodule containing a "mixed grill" of material, there is present the pectoral region of a small cynodont (MCZ 4164) which is of a size appropriate for this form and in which the scapula is of the unusually tall slender type seen in *Probelesodon lewisi*. It is highly probable that MCZ 4164 pertains to *P. minor* (Figs. 12, 13, 14).

On one surface of the block there is preserved an articulated pair of clavicles and the interclavicle. The clavicles, about 28 mm in length, are gently curved ventromedially from the presumed acromial articulation. The shaft is slender; there is a slight expansion proximally at the acromial articulation, and a greater distal expansion, so that the two clavicles cover the anterior quadrants of the head of the interclavicle. The shaft exhibits a marked posterior "twist" below the acromial region. The interclavicle, slightly imperfect posteriorly, has a length of 31 mm. It has a typical cynodont shape — relatively broad and flat, with an anterior expansion for reception of the clavicles, a modest narrowing behind the head, and a distal expansion. The longitudinal ridge is little developed.

Both primary shoulder girdles are present. As in *Probelesodon lewisi*, the scapula is tall and very slender, with a height from the glenoid fossa of 38 mm, and a width at half-height of but 4.5 mm. The upper end widens to about 8 mm; below, it widens again to a distinctly developed acromial process (present on one scapula, broken off on the other). The scapula is curved longitudinally to about 45° from summit to glenoid fossa. It is strongly concave externally in cross section, with both anterior and posterior borders outturned — the former more strongly so. There is no development of a supraspinous fossa. At its base the posterior margin thickens to present a well-developed upper portion of the glenoid cavity, which appears to have faced nearly directly ventrally in life. The anteroposterior breadth of the scapula increases ventrally to give a broad area of articulation with the two coracoids. Sutures between the scapula and the coracoids are not clear. The posterior coracoid is incomplete on the left girdle; as preserved on the right side, it is of normal cynodont type. The posterior coracoid bears the lower half of the glenoid; it appears to extend to a relatively greater distance posterolaterally than in typical cynodonts, with a V-shaped surface, somewhat convex in cross section. The anterior coracoid is of unusual shape, in apparent contrast to that of *P. lewisi*. It attaches to the anterior edge of the scapula, and its upper margin curves strongly forward from this point, reinforced by a thick strut of bone internally. The anterior margin of the bone is broad and essentially a straight dorsoventral line, sharply set off from the upper and lower margins. The procoracoid foramen is large. A notch on the ventral margin indicates the point of division between anterior and posterior elements.

Both humeri are present, and radius and ulna are preserved on the right side. These elements conform to the general cynodont pattern, and differ from those in *P. lewisi* mainly in a more slender build correlated with smaller size. Humeral lengths are 37 and 35 mm; proximal widths 17 mm and 16 mm; distal widths 19 mm. As in *P. lewisi* the deltopectoral crest is highly developed. The slender radius is incomplete distally; its length as preserved is 25 mm, the width of the head 6 mm. The ulna is 30 mm in length, its width proximally 8 mm, distally 5 mm. As usual in cynodonts, the olecranon is unossified.

The block of material in which this shoulder region is imbedded includes considerable further bony material; it is, however, quite uncertain that any of it belongs to this same form, and some of it certainly does not.

POSTCRANIAL MATERIALS OF *Probainognathus jenseni*

Because of the advanced nature of *Probainognathus* (at least in the type of jaw articulation) a description of the postcranial skeleton of this genus would be of considerable value. Regrettably, little can be done. In no case is postcranial material articulated with a *Probainognathus* skull. In a number of concretions containing skull materials of this genus there is present cynodont postcranial remains that may pertain to this genus. But since such concretions usually include a mélange of materials of different forms, attribution of specific elements to *Probainognathus* is in general highly questionable.

In one instance, however, pectoral and pelvic assemblages can be reasonably assigned to *Probainognathus* (Figs. 15, 16, 17). As mentioned earlier, Chañares field number 40 is a concretion including some remains of *Massetognathus*, some thecodont elements and a shoulder region described above as probably belonging to *Probelesodon minor*. Still further, however, it includes (MCZ 4021) a shoulder region of a small cynodont definitely differing from that of *Probelesodon minor* and appropriate in size for *Probainognathus*, and, nearby, a pelvic region also of appropriate dimensions.

The scapula of this specimen is quite different from that of *Probelesodon*, being relatively short and broad. Its height is 28 mm, the distal width 10 mm. The external surface is concave in cross section but anterior and posterior borders are not as sharply outturned as in *Probelesodon*. There is a well-developed acromion. The ventral anterior portion of the bone is not completely preserved, but there is a well-developed area extending forward just below the acromion, suggesting the

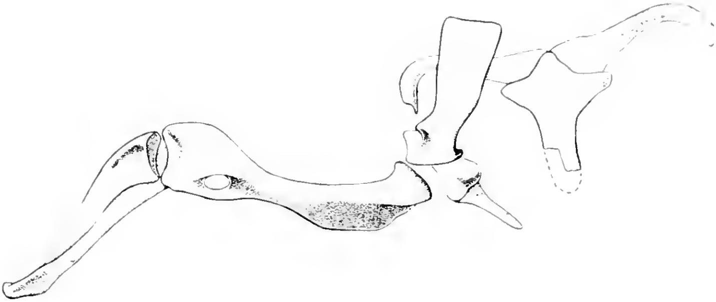

Figure 15. Shoulder girdle and front limb material of a specimen probably pertaining to *Probainognathus jenseni*. MCZ 4021. × 1.

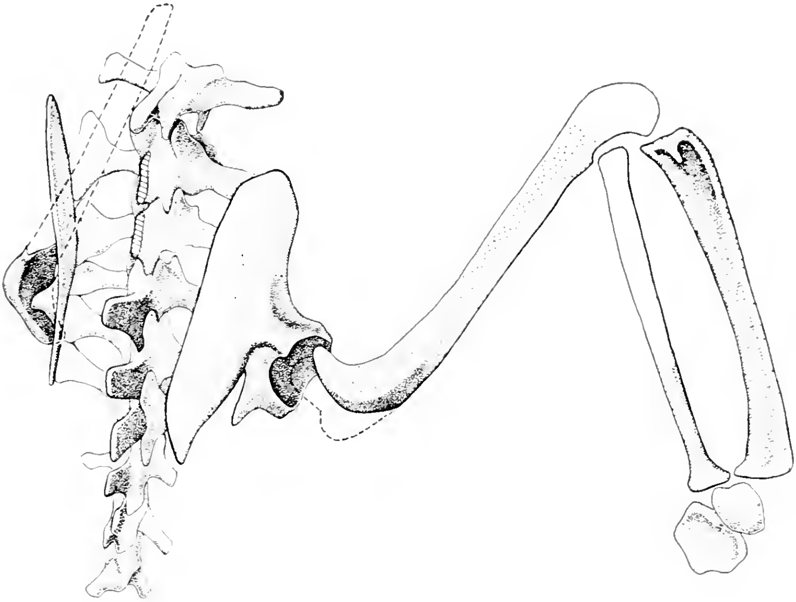

Figure 16. Pelvic region and hind leg material as seen on a block perhaps pertaining to *Probainognathus jenseni*. MCZ 4201. × 1.

Figure 17. Left femur and acetabular region of the pelvis as seen on the opposite surface of the block illustrated in Fig. 16. × 1.

initiation of a supraspinous fossa. The posterior coracoid (seen from the upper surface) is present, extending 19 mm back from its articulation with the anterior coracoid. This latter element, partially concealed within the block, extends well forward, with an anteroposterior length of about 13 mm. The coracoid foramen is unusually large, but this may be due to accidents of preservation or over-preparation. Well-preserved clavicles and a nearly complete interclavicle are also present, the three articulated. These dermal elements are of normal cynodont structure. The interclavicle, as preserved, is 26 mm long and is relativelv shorter than in *Probelesodon minor.*

The left humerus is complete with a length of 49 mm. It is unusually long and slender, the length being nearly half again that of *Probelesodon minor,* an animal of roughly similar size. The entepicondylar foramen, as prepared, is of unusually large size. Both radius and ulna of the left side are complete, with lengths of 35 mm and 34 mm, respectively. As usual, there is little ossification of the olecranon.

Various other limbs and axial skeletal elements are present in the block close to this girdle and limb assemblage, but there is no guarantee that any of them pertain to the same animal.

Not far removed from this shoulder assemblage are articulated remains of the pelvic region and hind legs of a small cynodont. There is here even less guarantee that this material is assignable to *Probainognathus* than in the case of the shoulder region, but the elements present definitely differ from those of the Chañares gomphodonts, and to some degree differ from those of *Probelesodon;* hence they quite probably pertain to the present genus.

An articulated series of vertebrae includes the last presacral, five sacrals and four proximal caudals. The transverse processes and ribs of the last presacral are developed in much the same fashion as the sacrals, and are somewhat expanded distally, but show no evidence of connection with adjacent elements. The first sacral is obviously the strongest of the series and most expanded distally, the further sacrals decreasing in strength posteriorly.

The left and right ilia have lengths as preserved of 37 mm and 42 mm respectively. Unfortunately, their upper margins are imperfect, so that the possible contrast between the expanded anterior portions and narrower posterior portions of the ilia cannot be clearly made out. The acetabulum is deeply excavated and the supra-acetabular buttress is strongly developed. There are no remains of pubis and ischium other than the areas immediately adjacent to the acetabulum.

The right femur is nearly completely preserved; the left (seen mainly on the under surface of the block) is incomplete distally. The length of the right femur (slightly imperfect at its head) is 58 mm; the bone is quite slender, the shaft width at mid-length being only about 4 mm. The head is well seen on the left femur on the under surface of the block. As in the femur attributed to *Probelesodon* the greater trochanter is somewhat more proximally placed than in most cynodonts, but is not as thickened nor as laterally divergent as in that form, nor is there any distinct separation of trochanter from the articular surface of the head. There is no line of division of the intertrochanteric fossa from the more distal portion of the ventral surface. The lesser trochanter is highly developed and extends far down the shaft.

The right fibula, with an apparent length of 47 mm, is represented for much of its length by an impression only. The slender tibia has a length of 51 mm, with a width at mid-length of but 4 mm. As preserved the shaft is strongly concave in transverse section. Astragalus and calcaneum are imperfectly preserved.

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A TAXONOMIC COMPARISON OF THE AMERICAN *UPOGEBIA* (DECAPODA, THALASSINIDEA), INCLUDING TWO NEW SPECIES FROM THE CARIBBEAN[1]

David Thistle[2]

Abstract. This study examines morphological variability as a means of establishing taxonomically useful characters of American *Upogebia*. The variability of measured characters was analyzed by regression; the variability of meristic characters was considered in a nonstatistical manner for *U. affinis* and *U. omissa*. The analyses make it possible to further differentiate these two species. Relatively invariant and therefore useful characters were combined with characters from the literature to delineate the known species. Three Eastern Pacific-Western Atlantic species-pairs are indicated and interpreted as being the result of speciation by geographic isolation caused by the closing of the Central American seaway. Two new species, *U. jamaicensis* and *U. annae*, are described. *Upogebia rostrospinosa* Bott is redescribed and figured.

Introduction

Twelve species of the burrowing mud shrimp genus *Upogebia* are known from North and South America. Two species, *U. operculata* and *U. rugosa*, are morphologically distinct; the remaining ten species are very similar. A study of the variability of characters in two sympatric species, *U. omissa* and *U. affinis*, was made to find characters of low variability which might be suitable for distinguishing among the ten species.

Upogebia have been found from mean low water to 229 m depth. They occur most often in mud flats but are known from

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coarser substrates. Their burrow openings are marked by mounds of material removed during excavation. The animal digs by using the third maxillipeds and carries the particles to the burrow opening with pereopods 1 and 2 (Stevens, 1928: 346). Burrows are Y-shaped or may be more complex warrens. The animal feeds by creating currents in the burrow by fanning its pleopods. Food particles are removed by a basket of setae on the inner surfaces of the anterior pairs of pereopods. Burrows contain several individuals. In North Carolina, Pearse (1945: 305) repeatedly found egg-bearing females and juveniles in the same burrow.

Twelve species of this genus are known from the Americas: *Upogebia affinis* from Massachusetts to southern Brazil; *U. annae* n. sp., *U. jamaicensis* n. sp. and *U. operculata* from the Caribbean; *U. omissa* from Panama and Brazil; *U. noronhensis* and *U. brasiliensis* from Brazil; *U. pugettensis* from Alaska to Lower California; *U. rugosa*, *U. rostrospinosa* and *U. longipollex* from the west coast of Central America; and *U. spinigera* from the west coast of Nicaragua to Columbia.

To provide a quantitative estimate of the variability expectable in this group of similar species, I examined in detail two species, *Upogebia affinis* and *U. omissa*, using characters selected from the literature and from my own preliminary survey. On the basis of this examination, it was possible to clarify the distinctness of these two species, whose morphological similarity could have been a source of confusion. Also, by assuming that characters useful in separating *U. affinis* and *U. omissa* were likely to be useful in separating other related species, I constructed a diagnostic matrix comparing the members of the species-group. This matrix of characters made apparent the close morphological similarity of two Pacific-Atlantic species-pairs, *U. rostrospinosa* and *U. omissa*, *U. spinigera* and *U. noronhensis*. *Upogebia rugosa* and *U. operculata* are distinct from the other American species of *Upogebia* and were not analyzed in detail but they apparently form a third species-pair. The occurrence of these pairs of species appears to be the result of the separation of populations by the closing of the Central American seaway and subsequent differentiation of the isolated segments of each original population.

In the course of this study, two new species were recognized (*Upogebia annae* and *U. jamaicensis*) and were analyzed with those previously known. Their descriptions as well as a redescription of *U. rostrospinosa* Bott are given as an appendix along with a dichotomous key to the American members of the genus. The synonymy of *U. sturgisae* Boone with *U. spinigera* and of *U. californica* (Stimson) with *U. pugettensis* after Holthuis (1952: 3) and Stevens (1928: 318) respectively is followed.

MATERIALS AND METHODS

This study is based on alcohol-preserved museum collections of *Upogebia affinis* (Say, 1818) and *U. omissa* Corrēa, 1968 (see Table 1). Material was obtained from the following sources: Dr. H. W. Levi, Museum of Comparative Zoology, Harvard University; Mr. H. B. Roberts, United States National Museum; Dr. L. B. Holthuis, Rijksmuseum van Natuurlijke Historie, Leiden; Dr. Thomas Biffar, Old Dominion University, Norfolk, Virginia; and Dr. A. L. Castro, Museu Nacional, Rio de Janeiro. Dr. Richard Bott, Senckenberg Museum, loaned to me four paratypes of *Upogebia rostrospinosa*. I would like to express my thanks to these gentlemen for their kind cooperation.

Specimens were examined with the use of a dissecting microscope. Drawings were made with a camera lucida. Overall length was measured from the tip of the rostrum to the posterior edge of the telson by rotation of the specimen in a clear dish along a rule. This method is accurate to ± 2 mm. Other measurements were made with the use of an ocular grid calibrated with a stage micrometer. Table 2 summarizes the characters used and gives the manner in which they will be referred to in the text. Figure 1 shows the meaning of these characters on diagrams of the animal. The abbreviations used in the text and tables, P1, P2, etc., refer to the first pereopod, second pereopod, etc.

The measured characters were analyzed by regression. This procedure eliminated the effect of variability introduced by differences in the sizes of individuals and allowed the setting of confidence limits, which permitted statistical comparisons. The method used was a nonparametric, graphic procedure which is efficient on small, non-normal samples (Tate and Clelland, 1957, 78–82). In all cases the dependent variable was regressed on overall length. Comparisons between species were made by the use of 90 percent confidence limits, but since the procedure decreases in efficiency with distance from the median, all comparisons were made at the point midway between the x-axis medians of the two lines to be compared. In all cases one is

Table 1. Summary of locality, number of individuals in total sample, number of adults of each sex used. and the range in overall length of the subsample. An asterisk after a locality indicates the presence of at least one ovigerous female. Specimens of *U. omissa* from Fortaleza-Ceará are paratypes.

	Sample size	Subsampled males	Subsampled females	Range of overall length in subsample (mm)
	Upogebia affinis (Say)			
Wellfleet, Massachusetts	67	5	4	34 – 52
Beaufort, North Carolina*	11	3	6	45 – 60
Miami, Florida*	18	3	6	27 – 43
Mississippi Gulf Coast*	2	0	2	32 – 33
Chandeleur Is., Louisiana	2	0	2	32
Rockport, Texas	2	1	1	32 – 33
Cumana, Venezuela*	18	6	4	32 – 60
Total	120	18	25	
	Upogebia omissa Corrêa			
Limon Bay, Canal Zone, Panama*	2	1	1	34 – 44
Fortaleza-Ceará, Brazil	2	1	1	27 – 32
Mamanguape Stone Reef, Brazil*	6	2	4	25 – 40
Parahyba River, Brazil	2	0	1	29
Rio de Janeiro, Brazil	7	0	0	0
São Paulo, Brazil	7	3	2	26 – 30
Total	26	7	9	

Table 2. Characters used in the analysis of *Upogebia affinis* and *U. omissa,* and indicated by number in Fig. 1. Each character is referred to in the text and tables by the words in italics.

Number	Character
1	Number of *ocular spines*
2	*Rostral* ventral *spines*
3	Number of *spines* on *epistome*
4	Number of *spines* behind the *cervical* groove
5	Ventral *abdominal spines*
6	*Serration of uropod* distal *edges*
7	Number of *uropodal spines*
8	Style of *dactylar teeth* (P1)
9	Style of *teeth* on *fixed finger* (P1)
10	*Carpal* exterior lateral *spines* (P1)
11	Number of dorsal *palm ridges* (P1)
12	Proximal *meral spine* (P2)
13	Width of the rostral base
14	Rostral length
15	Length of eye stalk
16	Length of rostral lateral teeth
17	Length of sixth abdominal segment
18	Length of telson
19	Width of telson distal margin
20	Width of telson proximal margin
21	Length of fixed finger (P1)
22	Length of dactylus (P1)
23	Length of palm (P1)
24	Width of palm (P1)
25	Length of merus (P1)
26	Width of merus (P1)

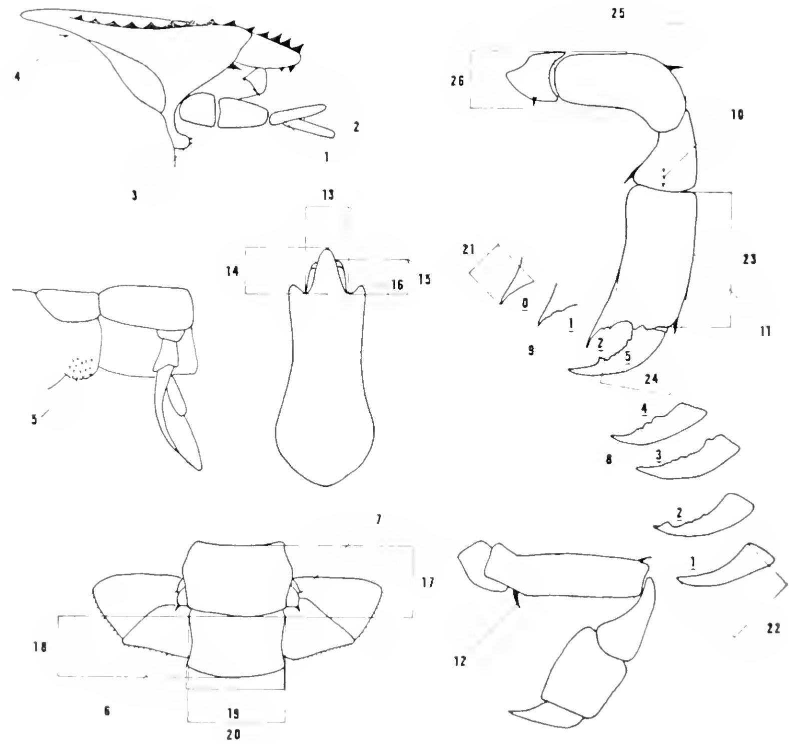

Figure 1. Diagrammatic presentation of characters analyzed, numbered as in Table 2. Underlined numbers are scores for the dentition patterns of fixed finger and dactylus.

testing the position of the lines at this grand median rather than differences in slope (E. W. Fager, personal communication).

When tested for sexual bias in terms of numbers of individuals, none of the collections departed significantly from the null hypothesis of a binomial distribution ($p = q = \frac{1}{2}$) at the 90 percent level. Assuming that the sex ratio is 1:1 in both species, these lots are not significantly biased in terms of sex.

In order to minimize the effect of ontogenetic changes in morphology on interspecific comparisons, this study used the overall length of the smallest ovigerous female in each sample as a criterion for restricting the analysis to adults. This procedure assumed that overall length, age, and maturity were highly correlated so that the probability of females longer than this minimum being adult was large. The overall lengths of males versus females in each sample were such that a Mann-Whitney "U" test (Tate and Clelland, 1957: 89–91) revealed no significant difference at the 90 percent level. Because the samples were not biased in terms of sex (see above) nor were the sexes different in overall size, it seemed reasonable to extend the adult overall length minimum to males. Thus, an adult upogebiid was defined as an individual that was larger, and by inference older, than the smallest sexually mature female present in the sample. In two cases this criterion was set aside for practical reasons. The available specimens of *Upogebia omissa* contained only two ovigerous females (36, 44 mm), while the lengths of all specimens ranged from 19 to 44 mm (Table 1). Corrēa (1968) reports adults ranging from 27 to 47 mm. Those individuals smaller than Corrēa's minimum were considered juveniles, as Corrēa's range of adult overall lengths was based on 106 ovigerous females. The Wellfleet, Massachusetts, collection contained no ovigerous females. The closest population of *U. affinis* in overall length is that from Miami and its minimum (28 mm) was used. After the removal of subadults in this manner, subsamples for analysis were taken at random from samples of more than ten individuals.

RESULTS

Measured characters. To provide a quantitative estimate of the variability within a species, *Upogebia affinis* and *U. omissa* were analyzed by the regression of 14 measured characters on overall length. Each character was tested for sexual dimorphism by the comparison of 90 percent confidence limits erected about regression lines formed for each sex. For *U. omissa* none of the 14 characters differed significantly between sexes. In *U. affinis* fixed finger length (21) and palm width (24) were significantly sexually dimorphic (Figs. 2, 3); the remaining characters were not. Interspecific comparisons using the regression lines for each sex separately revealed no significant difference for either sex on any character. Regression lines formed from both sexes still showed no significant difference between species on any character, excluding characters 21 and 24.

The characters measured contain information about the shape of much of the animal. The results show the two species to be largely indistinguishable in gross morphology, making speculation about the origin and niche separation of these two partially

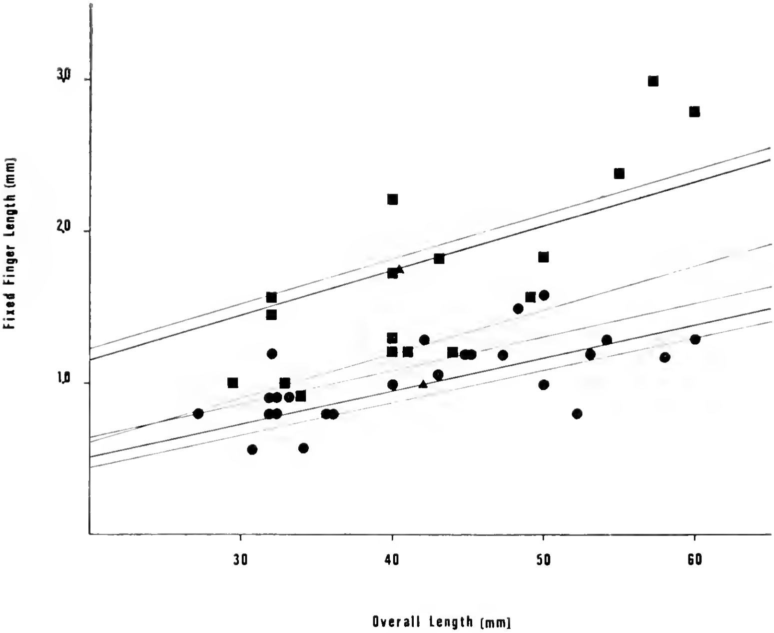

Figure 2. Regression of the fixed finger length onto overall length for males (squares) versus females (circles) of *Upogebia affinis*. The upper triangle is the x-axis median for males; through it passes the best-fit median, regression line. The envelope of lighter lines are 90% confidence limits. The lower triangle marks the female x-axis median point with a similar set of lines.

sympatric species interesting, but to little purpose until their natural history is better known. The analysis does point to problems latent in the use of measured characters in this genus. One must quantify the variability and examine it comparatively before any but the most obvious differences in proportion are given taxonomic weight.

The regression analysis confirmed one feature of taxonomic interest. *Upobegia affinis* has conspicuous sexually dimorphic chelipeds. In the males the cheliped is consistently more robust, larger, and better calcified than in the female. In *U. omissa*, while the males tended to be more variable about the regression line reflecting the occasional dimorphic individual as reported by Corrêa (1968), there was no significant difference between

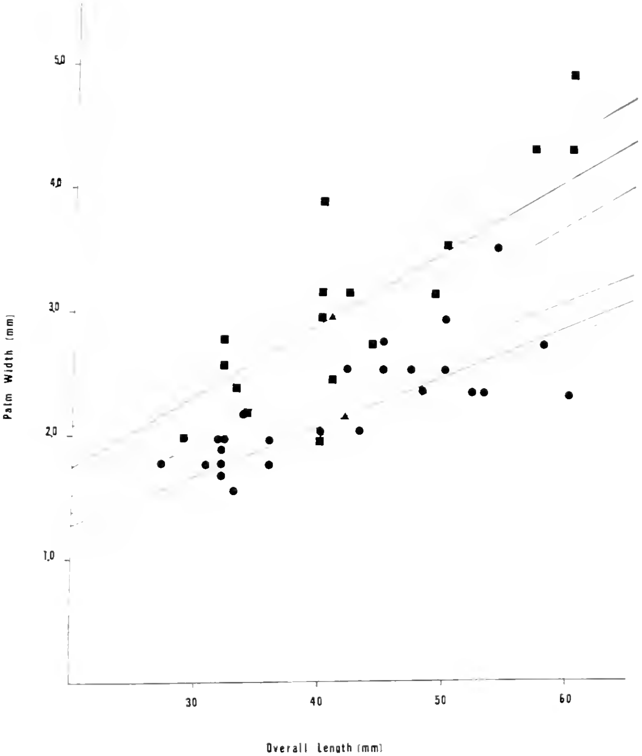

Figure 3. Regression of the width of palm (P1) onto overall length for male (squares) versus female (circles) *Upogebia affinis*. The upper triangle is the x-axis median for males; through it passes the best-fit median, regression line. The envelope of lighter lines are 90% confidence limits. The lower triangle marks the female x-axis median point with a similar set of lines.

sexes. *Upogebia affinis* is sexually dimorphic in palm width and fixed finger length; *U. omissa* is not. This dichotomy helps to distinguish the species.

Meristic characters. Despite this similarity of shape, there are differences between *Upogebia affinis* and *U. omissa.* The diagnostic characters of these two species are differences in ornamentation, as are those which distinguish the other species. Table 3 summarizes the results of an examination of 12 of these characters. In it one can see the type of individual and geographic variability present in *U. affinis* and *U. omissa,* the features which separate them, and some of those they share.

In delineating *Upogebia affinis* from *U. omissa,* clear disjunctions are most useful. *Upogebia omissa* has ventral abdominal spines and P4 is armed; *U. affinis* does not have these spines. The other characters that show differences between species are less distinct. For a given character, each species has a different dominant state, though some individuals of each species exhibit the character state of the other species. The greater the frequency of the inappropriate character state, the less useful the character, but because of the obvious effect of the interaction between those populations contributing the most specimens to the relative frequency of a character state within a species, these frequencies were not tested statistically.

De Man (1927) redescribed *Upogebia affinis* from a few Carolina specimens. His detailed description agrees with my material. He did not comment on variability beyond two localities. Table 3 can be considered to supplement his description. In addition, the rostrum is not always longer than wide; the telson is rectangular to wider posteriorly; and the upper surface of the telson is not always punctate. De Man refers to reports of *U. affinis* from the "coast of Brazil, Mamanguape stone reef, Parahyba river . . ." On reexamination these specimens were found to be *U. omissa* (Table 1).

Corrêa (1968) described *Upogebia omissa* in detail, including its variability. Beyond those features already discussed, I found the following differences. The eyes are slightly shorter than the rostrum. I have examined a female that is 44 mm long versus a maximum of 35 mm given by Corrêa. Also, in the table provided by Corrêa for comparison of *Upogebia affinis* with *U. omissa,* the distinction based on spines on the lower surface of the rostrum is not useful, as *U. affinis* from Venezuela lacks the spines. The protopods of the uropods bear two spines in *U. affinis* from Venezuela rather than one.

Table 3. Summary of the results of the meristic characters scored on samples from the following localities: A-E) *Upogebia affinis*. A) Wellfleet, Massachusetts. B) Beaufort, North Carolina. C) Miami, Florida. D) Mississippi Gulf Coast; Chandeleur Is., Louisiana; Rockport, Texas. E) Cumana, Venezuela. F-I) *U. omissa*. F) Limon Bay, Canal Zone, Panama. G) Forteleza Ceará, Brazil. H) Mamanguape Stone Reef, Brazil. I) São Paulo, Brazil. Consult Table 2 and Fig. 1 for explanations of characters and scores. A comma separating two character states indicates essentially equal frequency. A character state in parentheses is a low frequency alternate state. A plus sign means the character is present, a minus that it is absent.

Character	*U. affinis* locality					*U. omissa* locality			
	A	B	C	D	E	F	G	H	I
Ocular spines	1 (2)	1 (2)	1	1	1	1	1	1	1
Rostral spines	+ (−)	+ (−)	+	+ (−)	−	−	−	−	−
Epistomal spines	1 (0, 2)	1	1	1 (2)	1, 2	2	2	2 (1)	2
Cervical spines	1, 2	1, 2	1 (2)	1 (2)	1, 2	2, 3	2 (4)	2 (1)	2 (1)
Uropod edge serration	−	+	−	+, −	+	+	+	+	+
Uropodal spines	1, 2	1, 2	2 (1)	1, 2	2	2	2	2	2
Abdominal spines	−	−	−	−	−	+	+	+	+
Dactylar teeth	2	2	2 (5)	2 (1)	5	5	5	5 (2)	5 (2)
Fixed finger teeth	1, 2 (0)	2	1 (0, 2)	0, 2	2	2	4	2 (0)	2 (0)
Palm ridges	2	2	2	2	2	3	3	3	3
Carpal spines	2, 3	2, 3	3, 4 (2, 1)	3 (1, 2)	3, 2	1	1	1	1
Meral spines	+	+	+	+	+	+	+	+	+

THE SPECIES OF UPOGEBIA

On the basis of the analysis of *Upogebia affinis* and *U. omissa,* I selected characters that had little within-species variability while setting off at least one described species from the others. These characters, coupled with several useful characters from the literature, are presented as a diagnostic matrix showing the interrelationships among the species (Table 4). Characters based on measurements were not included, because the lack of specimens of other American species made it impossible to properly evaluate their variability, except that the ratio of P1 fixed finger length to dactylus length, which is routinely given in the literature, was included.

Table 4 reveals a portion of the interrelationship among the members of the genus in the Americas, and can be used to distinguish among the species. The information presented is from several sources: holotypes of *Upogebia annae* n. sp. and *U. jamaicensis* n. sp., paratypes of *U. omissa* and *U. rostrospinosa*, museum collections of *U. affinis*. The original descriptions of *U. noronhensis* Fausto-Filho 1969 and *U. brasiliensis* Holthuis 1956 were used. For *U. spinigera* (Smith 1871) the original description was supplemented by Holthuis' (1952) redescription. Similarly, for *U. pugettensis* (Dana 1852) de Man (1929) and Stevens (1928) were used.

Upogebia longipollex was described very incompletely and without figures by T. H. Streets (1871) from a Panamanian collection of J. McNeil. Lockington (1878) states that the material ". . . probably came from the Pacific coast of the isthmus." De Man (1928) speculated that *U. longipollex* might be a junior synonym to *U. spinigera* (Smith) if differences in spination of the pereopods were the result of differences of the ages of the specimens described. Holthuis (1952) synonymized *U. longipollex* with *U. spinigera* without comment.

The results of this study indicate that leg spination, particularly the P2 meral spine (ventral proximal spine of merus of pereopod 2), is diagnostic at the specific level. Streets, describing spination, states, ". . . third article [carpus] . . . armed with spine above at distal extremity; remaining pairs [of legs] unarmed." *U. spinigera* has a P2 meral spine as well as spines on P3 and P4. It cannot be the same species as *U. longipollex*.

Upobegia longipollex has been included in Table 4 as a good species and adjacent to *U. pugettensis* to which it seems to be most similar. It appears likely that after an adequate variational

Table 4. Summary of diagnostic differences for A) *Upogebia longipollex.* B) *U. pugettensis.* C) *U. affinis.* D) *U. jamaicensis.* E) *U. rostrospinosa.* F) *U. omissa.* G) *U. spinigera.* H) *U. noronhensis.* I) *U. brasiliensis.* J) *U. annae.* Consult Table 2 and Fig. 1 for explanations of the characters. A comma separating two character states indicates essentially equal frequency. A character state in parentheses is a low frequency alternative state. "P3 with spines" means that the third pereopod bears spines on any segment excluding the dactylus, basis, and coxa.

Character	A	B	C	D	E	F	G	H	I	J
Ocean	Pacific	Pacific	Atlantic	Atlantic	Pacific	Atlantic	Pacific	Atlantic	Atlantic	Atlantic
Overall length (mm)	28	38–54	27–60	40–50	28	27–60	40	25–30	14–30	32–40
Rostral spines	—	+, —	+, —	—	—	—	—	—	—	—
Ocular spines	1	1 (reduced)	1 (2)	4, 5	1	1	1	1	1	1 (2)
Cervical spines	?	many	1, 2	8–10	2, 3	1, 2	2, 3	1, 2	0	0
Epistomal spines	?	?	1, 2	1	3, 3	2	2	?	0	1, 2
Abdominal spines	?	—	—	—	+	+	—	—	—	—
Ratio: Fixed finger length to dactylus length	?.9	.5	.8	.3–.7	.7	.5	.7	.9	.9	.9
Dactylar teeth	5	5	2 (5)	2	5	5 (2)	5	2	5	0, 1, 3
Fixed finger teeth	2	1	1, 2	1 (2)	2	2 (0)	1, 2	1	1	2 (1)
P1 palm cross section	?	squared	squared	squared	ovoid	ovoid	ovoid	ovoid	?	ovoid
Palm ridges	0	2	2	2	3	3	3	3	2	0
P2 meral spine	—	—	+	+	+	+	+	+	—	—
P3 with spines	—	—	+	+	+	+	+	+	+	+
P4 with spines	—	—	—	—	—	+	+	—	—	—
P5 with spines	—	—	—	—	—	—	—	+	—	—
Uropodal spines	?	1	1, 2	1 (2)	2	2	2	2	1	1
Serration of uropod edges	?	+	+, —	+	+	+	+	+	+	+, —

study of *U. pugettensis* (1852) has been performed, *U. longipollex* (1871) will be synonymized under that species, but until the Pacific American upogebiids become better known, *U. longipollex* should be maintained.

American upogebiids seem to show examples of speciation by geographic isolation. In Table 4 are two cases where a pair of morphologically very similar species are separated by Central America. *Upogebia rostrospinosa* from El Salvador is most closely related to *U. omissa* from Panama and Brazil; *U. spinigera* from the Gulf of Panama to *U. noronhensis* from northern Brazil. *Upogebia rugosa* from the Gulf of California and *U. operculata* from Barbados are a third example. An interpretation of this evidence is that in each of these cases a single species existed in tropical waters before the close of the Central American seaway. After this event the Atlantic and Pacific populations no longer shared a common gene pool and evolved separately. Under somewhat different selective pressures each population became differentiated while retaining a basically similar morphology within a species-pair. Thus the model of speciation by geographic isolation appears to explain the occurrence of species-pairs in *Upogebia*.

Conclusions

A study of the variability within two species of *Upogebia* has shown measured characters to be of uncertain taxonomic value. Relatively invariant and taxonomically useful characters have been used to help demonstrate the distinctness of ten known species.

It is extremely likely that further collecting will lead to the discovery of additional species. Their description as well as a fuller understanding of the biology and distribution of each species will have to be achieved before one can come to a biologically real understanding of speciation in this group.

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APPENDIX

Upogebia jamaicensis n. sp.

Figure 4

Male holotype from Montego Bay, Jamaica. USNM #41748. The species is named for the type locality. Overall length is 50 mm.

Diagnosis. Upogebia with 4–5 ocular spines; 8–10 spines behind cervical groove laterally; rostral ventral surface unarmed; P2 with strong proximal ventral spine on merus; 1 epistomal spine. For relationships to American species see Table 4.

Upogebia jamaicensis is most closely related morphologically to *U. spinifrons* (Haswell, 1881) from Australia. Much of the cephalon spination is similar in the two species. Following de Man (1927), *U. spinifrons* has the rostral ventral surface armed, the dorsolateral extensions of the carapace without tubercles, and with 2 epistomal spines. *Upogebia jamaicensis* has the rostral ventral surface unarmed, tuberculate dorsolateral extensions, and 1 epistomal spine. There are differences in number of P1 palm ridges and P2 meral spines. No other described species has 4–5 ocular spines.

Description. A slash separating 2 measurements indicates the ratio of the first to the second. For a discussion of the use of ratios in taxonomy, see Hessler (1970: 7). LENGTH: 40–50 mm. CEPHALOTHORAX: Rostral basal width/rostral length is 0.6–0.8. Length rostral lateral teeth/rostral length is 0.3–0.5. Dorsolateral extensions of carapace with 10–12 spines (becoming spinules posteriorly). Eye length/rostral length is 0.5. ABDOMEN: Segmentation typical of genus. Sixth segment width/length is 1.4. Telson width/length is 1.0–1.2. Telson with proximal transverse carina, median groove, and wrinkled surface. PEREOPODS: P1: Fixed finger length/dactylus length is 0.3–0.7. Dactylus with large tooth laterally and lesser tubercles distally; large distal tooth on cutting edge with lesser teeth proximally. Fixed finger with 4–6 denticles on cutting edge. Palm width/length is 0.4–0.6. Palm ovoid in cross section. Palm spination: dorsally 2 ridges, outer of spines, inner of spinules. Exteriolateral surface with 6 spines; interiorly 1 distal spine. Carpal spines: 1 large ventrally, 1–2 exteriorly. Dorsally 1 major spine distally with row of 4–6 behind it; 2 exterior, 1–2 interior to it. Meral width/length is 0.3–0.5. Meral spines: 1 distodorsal spine, 6–7 spines on ventral margin. P2: Carpus with distal spine dorsally and ventrally. Merus with distodorsal and proximoventral spines. P3: Merus with 2 distodorsal spines: ventral margin with 4–6 spines, many tubercles. Ischium with 1 spine. P4: Merus of holotype with spine on ventral margin, absent in paratypes. PLEOPODS: Endite of 2–5 enlarged, squarish. UROPODS: 1 spine on interior protopod, tubercle on exterior protopod; distal edges denticulate.

In female, width rostral base/rostral length is greater, P1 dactylus shorter, cheliped less robust.

Range. Jamaica. Four specimens examined. Features of types are: holotype without left P4, right P2, P3. Paratype, female, USNM #138897, same locality, left of carapace damaged. Paratype, female, USNM #138896, same locality, right P1 missing.

Upogebia annae n. sp.

Figure 5

Female holotype: R/V OREGON, sta. 5421, Bahama Isl., lat. 20°54′N, long. 73°36′W, 125 fathoms (229 m). USNM #138892. The species is named for my wife, Anne. Overall length is 25 mm.

Diagnosis. Upogebia with 1, 2 ocular spines, no spines behind cervical groove, P1 fingers of claw equal, P1 with no ridges on dorsal surface of palm. P2, P3, P4 with elongate merus.

Upogebia annae is most closely related to *U. brasiliensis. Upogebia annae* differs in having no dorsal P1 palmar ridges and no epistomal spines. In *U. brasiliensis* the merus width/length ratio of P2 is 0.33, of P3 is 0.41, and of P4 is 0.30; in

U. annae that of P2 is 0.20, of P3 is 0.21, and of P4 is 0.22. See Table 4 for comparison to other American species.

Description. A slash separating 2 measurements indicates the ratio of the first to the second. LENGTH: 32–40 mm. CEPHALOTHORAX: Rostral basal width/rostral length is 0.8–0.9. Length rostrolateral teeth/rostral length is 0.2. Dorsolateral extensions of carapace with 10–12 spines (becoming spinules posteriorly). Eye length/rostral length is 0.1–0.3. ABDOMEN: Segmentation typical of genus. Sixth segment width/length is 1.0–1.2. Telson width/length is 0.9–0.10. Telson with proximal transverse carina, median groove, and wrinkled surface. PEREOPODS: P1: Fixed finger length/dactylus length is 1.0. Dactylar row of tubercles variable. Fixed finger with 4–6 denticles on cutting edge. Palm width/length is 0.3–0.5. Palm ovoid in cross section. Carpal spines: distally, one each ventrally, exteriorly, dorsally; dorsal spine with 3–5 above it, 2 interiorly, 2 exteriorly. Meral width/length is 0.3. Merus with distal dorsal spine, 4–6 spines on ventral margin. P2: Carpus with dorsal, ventral distal spines. Merus with distal dorsal variable tubercles on ventral margin. P3: Carpus, ventral distal spine, variable. Meral ventral margin with 2–3 spines, many tubercles. PLEOPODS with oval endite. UROPODS with small spine on protopod.

In female, uropodal exopod extends beyond telson. Males with robust P1, more highly calcified, uropod edges finely denticulate.

Range. Known only from types.

Features of types. Holotype discolored in branchial area. Male paratype, R/V OREGON sta. #5421, USNM #138893, same locality as holotype, left P3, right P5 damaged. Male paratype, R/V SILVER BAY sta. #5158, USNM #138894, Bahama Isl. lat. 19°55.5′N, long. 71°07′W, 100 fathoms (183 m), right P4, P5, left P3, P5 missing.

Upogebia rostrospinosa Bott 1955

Figure 6

Female holotype from Puerto el Triunfo, El Salvador. Senckenburg Museum #2116.

This redescription is based on an examination of one female paratype. Differences from the original description should be noted. No evaluation of variability is possible.

Diagnosis. Upogebia with 1 ocular spine, P2 meral spine, spinules on ventral surface of first abdominal segment, no spines on P4, spines on telson transverse ridge.

Upogebia rostrospinosa is most closely related to *U. omissa* on the basis of the ventral abdominal spines. *U. rostrospinosa* differs in having no spines on P4 while *U. omissa* lacks the spines on the telson. See Table 4 for comparison to other American species.

Description. A slash separating 2 measurements indicates the ratio of the first to the second. All measurements refer to the paratype. LENGTH: 28 mm. CEPHALOTHORAX: Rostral basal width/rostral length is 0.6. Length rostrolateral teeth/rostral length is 0.3. Dorsolateral extensions of carapace with 9–10 spines (becoming spinules posteriorly). Eye length/rostral length is 0.75. ABDOMEN: Segmentation typical of genus. Sixth segment width/length is 1.3. Telson width/length is 1.2. Telson with proximal, 8-spined transverse ridge. PEREOPODS: P1: Fixed finger length/dactylus length is 0.7. Palm width/length is 0.53. Palm ovoid in cross section, 3 dorsal rows of hairs, 1 external. Carpal spines: 1 ventral distal, 1 exterior distal, 1 dorsal distal with a row of 4 behind it. Meral width/length is 0.5. Merus with 1 distal dorsal spine, 3 on ventral margin. Ischium with 1 spine. P2: Carpus with distal spinule dorsally and ventrally. Merus with distal dorsal spine; proximal ventral spine. P3: Merus with 3 spines on ventral margin, 4 spinules on exterior proximal surface. PLEOPODS with elongate endite.

No males known.

Range. Known only from type locality.

Remarks. Bott (1955) mentions four paratypes (SMF #2117). I have examined these and three do not fit the description of the holotype. The discrepancies are in characters that I have found to be diagnostic, and I believe that these three specimens cannot serve as representatives of *Upogebia rostrospinosa.*

Figure 4. *Upogebia jamaicensis* n. sp. male holotype: A) habitus, B) A1, C) pleopod 2, D) sixth abdominal segment and telson, E) pereopods 1–5, F) female pleopod 1 (paratype), G) cephalothorax and right cheliped, H) A2. Hairs and setae omitted. Scale lines equal 2 mm.

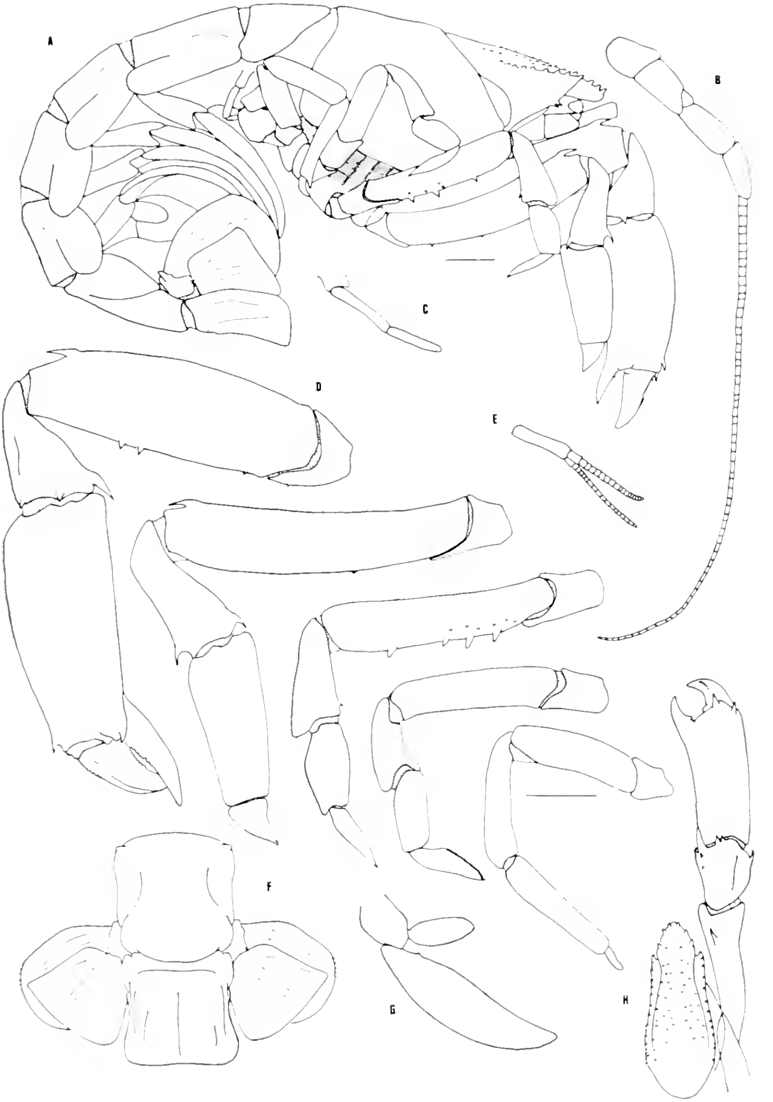

Figure 5. *Upogebia annae* n. sp. female holotype: A) habitus, B) A2, C) pereopods 1–5, D) female pleopod 1, E) A1, F) sixth abdominal segment and telson, G) pleopod 2, H) cephalothorax and right cheliped. Hairs and setae omitted. Scale lines equal 2 mm.

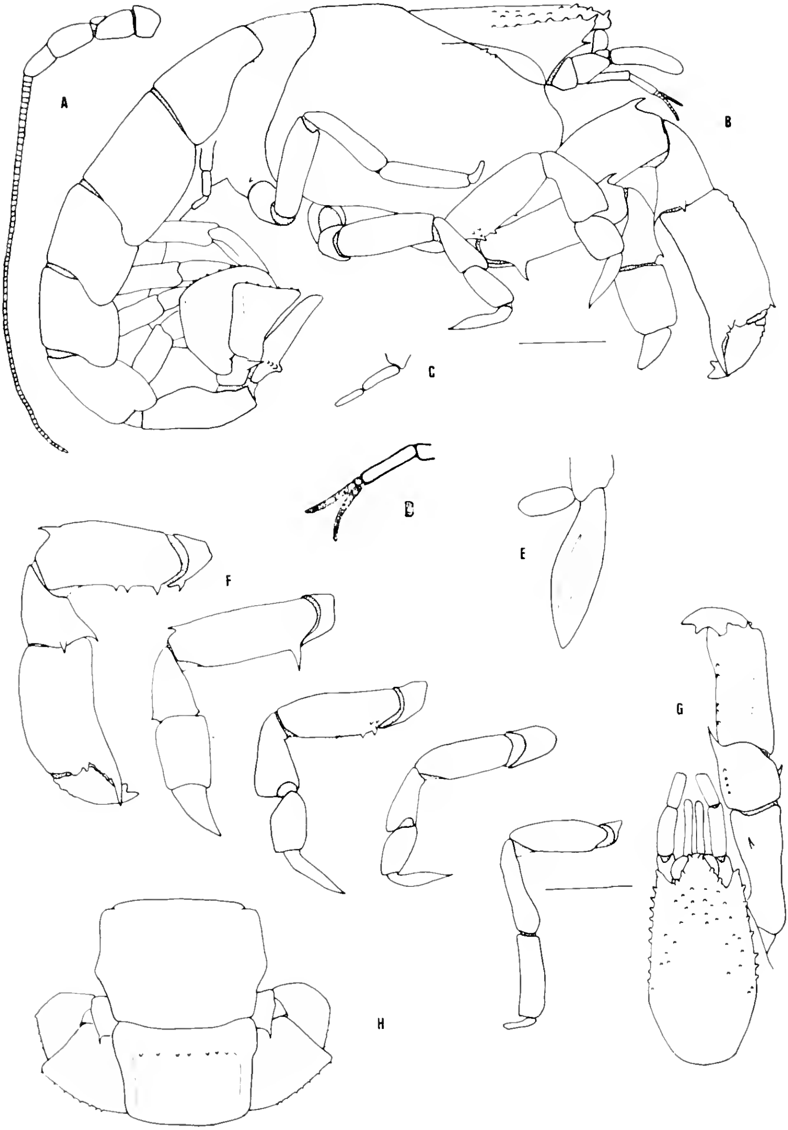

Figure 6. *Upogebia rostrospinosa* Bott female paratype: A) A2, B) habitus, C) female first pleopod, D) A1, E) pleopod 2, F) pereopods 1–5, G) cephalothorax and right cheliped, H) sixth abdominal segment and telson. Hairs and setae omitted. Scale lines equal 2 mm.

Key to the American Species of *Upogebia*

1\. a. Telson distal margin conspicuously wider than proximal margin .. 2
b. Telson essentially rectangular 3

2.*a. Rostrum armed dorsally with "two strong spines"; Caribbean .... *U. operculata*
b. Rostrum "beset with small tubercules and hirsute" dorsally; Pacific, Central America .... *U. rugosa*

3\. a. First abdominal segment spined ventrally 4
b. First abdominal segment unspined ventrally 5

4\. a. P4 with spines (see Table 4 caption); Atlantic, Panama to Brazil .... *U. omissa*
b. P4 without spines; Pacific, Central America .... *U. rostrospinosa*

5\. a. P2 with proximal meral spine 6
b. P2 without proximal meral spine 9

6\. a. P1 propodus with two ridges dorsally 7
b. P1 propodus with three ridges dorsally 8

7\. a. Having one or two ocular spines; Atlantic, widespread .. *U. affinis*
b. Having four or five ocular spines; Caribbean .... *U. jamaicensis*

8\. a. P4 with spines, P5 unspined; Pacific, Central America to Colombia .... *U. spinigera*
b. P4 unspined, P5 with spines; Atlantic, Brazil ...... *U. noronhensis*

9\. a. P3 with spines 10
b. P3 without spines 11

10\. a. Epistome spined, P2, P3, P4 with elongate merus; Caribbean .... *U. annae*
b. Epistome unspined; Atlantic, Brazil .... *U. braziliensis*

11\. a. P1 propodus with two ridges dorsally; Pacific, Alaska to Lower California .... *U. pugettensis*
b. P1 propodus with no ridges dorsally; Pacific, Central America .... *U. longipollex*

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*The present distinction between these two species is probably semantic; they are badly in need of redescription.

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THE CLASSIFICATION OF THE COTINGIDAE (AVES)

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ABSTRACT. The treatment to be given to the Cotingidae in Peters' *Check-list of Birds of the World* is discussed. Both the limits of the family and the best arrangement of the genera within it are problematical, and it is stressed that the system to be adopted must be regarded as provisional.

Previous attempts to classify the family are reviewed. Nine genera are discussed, whose allocation to the Cotingidae has been disputed. Four of these (*Laniisoma, Phoenicircus, Lipaugus* and *Rupicola*) are considered best retained in the family on available evidence, and five (*Attila, Casiornis, Laniocera, Rhytipterna* and *Xenopsaris*) are considered to belong to the Tyrannidae.

Doliornis and *Zaratornis* are not considered to be sufficiently distinct from *Ampelion* to be maintained as separate genera. Likewise, *Platypsaris* is merged with *Pachyramphus*, and *Erator* with *Tityra*.

The sequence of genera adopted indicates a general progression from unspecialized types to highly specialized, sexually very dimorphic frugivores; but it is emphasized that this may not represent an evolutionary progression. Within the genera, there is a marked tendency for closely related forms to replace one another geographically. Many of these are too distinct to be treated as races of one species; moreover, in two cases where there is slight geographic overlap the forms concerned apparently behave as distinct species although they are very similar. To take account of this general situation, liberal use is made of Mayr's concept of the zoogeographical species. On this basis the family is treated as containing 79 taxonomic species and 56 zoogeographical species.

Before his death in 1955, J. T. Zimmer prepared a rough manuscript of the Pipridae, Cotingidae, Tyrannidae, and related families, to constitute volume 8 of Peters' *Check-list of Birds of the World*. The section on the Cotingidae was reviewed in 1957 by James Bond, who made minor modifications, and it was this revised manuscript that was the basis of the classification adopted by Meyer de Schauensee (1966). Volume 8 of the *Check-list*, however, unfortunately remained unpublished.

Having been invited by Melvin A. Traylor, who has accepted responsibility for the final editing of this volume, to revise Zimmer's manuscript of the Cotingidae in the light of recent work, I here discuss the controversial points in the classification of this difficult family at the species level, in particular the affinities of the genera *incertae sedis,* the limits of some of the species, and the sequence to be adopted in the *Check-list.* Zimmer, as is well known, was a meticulous worker with subspecies, and his treatment was reviewed by Bond, as already mentioned. It has therefore seemed unnecessary to alter his arrangement of subspecies except where modification is called for in the light of more recent published reviews. Hence in what follows no mention is made of subspecies except where they are involved in questions of specific status.

The Cotingidae is a notoriously heterogeneous family, and successive systematists have despaired of producing a satisfactory classification of it. About half of the genera are monotypic, and several others are represented by a single superspecies. Many of these are such distinct forms that it is not possible to say to which other genera they are most closely related. Moreover, it has been doubted, by one worker or another, whether about a third of the genera should belong in the family at all. Recently there have been some very useful anatomical studies that have thrown new light on relationships within the family, and within the whole suboscine complex; but even so, it is not yet possible to make anything like a final classification of the family.

What we have to deal with, it seems, is a collection of very diverse evolutionary lines whose common ancestry lies far back in the stock of forest-inhabiting, insectivorous and frugivorous birds that gave rise to the present-day manakins and tyrant-flycatchers, as well as the present-day cotingas. There is no certainty, and probably never will be, that even the "best" cotingid genera may not be more closely related to birds that are now placed in one of the other two families than they are to some other "good" cotingas. Nevertheless, some arrangement has to be made, and it should be based on the best available evidence, and should be justified. It is the purpose of the present paper to justify the treatment to be given to the family in Peters' *Check-list.*

THE LIMITS OF THE FAMILY COTINGIDAE

Sibley (1970) has given a useful historical review of the attempts to classify the passerine birds, and it is not necessary to go over the same ground. For the present purpose it need only be said that, ever since the foundations of the present arrangement of the passerines were laid by Nitsch, Müller, Garrod, and others, and systematized by Sclater (1888), there has been great uncertainty as to where the dividing lines should be drawn between the three main suboscine families of the New World, the Cotingidae, Pipridae and Tyrannidae (with which are associated the two very small families, Phytotomidae and Oxyruncidae). Recently, moreover, Olson (1971) has widened the controversy by reviving Pycraft's contention that the Old World family Eurylaemidae may be the closest relatives to the Cotingidae. According to this view, the Eurylaemidae and Cotingidae are derived from the primitive suboscine stock, and the Tyrannidae, by implication, are the result of a more recent evolutionary radiation. It seems entirely possible, however, that much of the detailed resemblance between the specialized frugivorous members of the Eurylaemidae and Cotingidae, which Olson stresses, may be convergent; but whether the resemblance is the result of relationship or convergence, it does not resolve the difficulty under discussion, that among the less specialized members of the Cotingidae (as usually considered) there are genera that approach the tyrant-flycatchers and manakins more or less closely.

Olson's suggestion raises an important general point, that it may be incorrect to regard the specialized frugivorous cotingids as the culmination of the adaptive radiation of the family. Previous classifications of the cotingas have usually started with the apparently less specialized types, and have ended with the specialized frugivores such as the fruit-crows and bellbirds, and this is a convenient sequence which is followed here too (p. 13); but it must be admitted to be no more than a matter of convenience. The evolutionary interaction between specialized fruit-eating birds and the fruits to which they are primarily adapted, belonging mainly to a small number of plant families (Snow, 1971b), has obviously been a very long one; in fact, the evolutionary history of the frugivorous stocks may be older than that of the more specialized insectivorous types.

Previous classifications. Sclater, in the *Catalogue of Birds in the British Museum*, vol. 14 (1888), recognized 31 genera in the Cotingidae, dividing them from the Tyrannidae and Pipridae on the basis of tarsal scutellation. The relevant part of the key is as follows:

a. Tarsus exaspidean.
  a'. Toes nearly free (as in the *Oscines*).
    Bill incurved, hooked ...... 1. Tyrannidae

        Bill straight, pointed ...... 2. Oxyrhamphidae [=Oxyruncidae]
    b′. Toes more or less united. .... 3. Pipridae
b. Tarsus pycnaspidean.
        Bill elongated, compressed,
        not serrated .... 4. Cotingidae
        Bill short, conical,
        serrated .... 5. Phytotomidae

In this classification, all three families were distinguished from the Eurylaemidae by the conformation of the manubrium of the sternum, which, as Olson (1971) has since shown, may show considerable intrageneric variation in the characters that have been used to separate families. Although he was aware of the fact that the main artery of the thigh is the sciatic in *Rupicola* and the femoral in all the other cotingas studied, Sclater did not consider this to be of sufficient importance to justify removing *Rupicola* from the family. He placed it in a subfamily, including with it *Phoenicircus* (whose thigh arteries had not been studied and still have not been) for no very convincing reason.

Ridgway (1907), in prefacing his very detailed key to the family Cotingidae, pointed out that the nature of the tarsal scutellation was not so invariable within the families as Sclater supposed. He followed Sclater's arrangement almost exactly, however, the only changes being to replace *Laniisoma* in the family (placed in the Pipridae by Sclater), remove *Laniocera* to the Pipridae, and add to the family eight genera that are now generally considered to be tyrannid and a ninth, *Xenopsaris,* which has subsequently been bandied between the two families. In spite of his *caveat* on the variability of tarsal scutellation, all these changes from Sclater's treatment were made on the basis of this character, except for *Rupicola,* which Ridgway placed in a separate family on the basis of the arteries of the thigh. Ridgway also divided Sclater's *Tityra* into two genera, *Tityra* and *Erator,* largely on the basis of tarsal scutellation.

The next important classification of the family was that of Hellmayr (1929). Again, he followed Sclater and Ridgway closely as far as most genera were concerned. He agreed with Ridgway in including *Laniisoma,* but differed from him in also keeping *Laniocera* in the family. He removed the eight genera of small flycatcher-like birds that Ridgway had brought into the family, as well as *Xenopsaris.* Like Ridgway, he treated *Rupicola* as a separate family. He did not subdivide the genus *Tityra.*

These three classifications agreed in large part, in regard to the genera admitted into the family. Ridgway's sequence, however, departed radically from that of Sclater. Both sequences were simply the result of the keys which they devised, and they do not appear to have been intended to reflect any evolutionary development, such as from more primitive to more specialized types. Thus Ridgway began the family with the peculiar genus *Phoenicircus* and followed it with the very different genus *Laniisoma* simply because the first division of his key dealt with the union (or non-union) of the outer toe to the middle toe.

It is noteworthy that these three authors all questioned the correctness of placing *Attila* (and Sclater also *Casiornis*) in the Cotingidae rather than in the Tyrannidae. Ridgway expressed the same doubts about *Rhytipterna* and *Lipaugus* and the flycatcher-like genera, which he separated from the Tyrannidae "solely on account of the different character of the tarsal envelope."

Meyer de Schauensee (1966) followed Hellmayr fairly closely. He replaced *Xenopsaris* in the family, however, with a footnote indicating that it may be tyrannid, and he added the newly discovered genera *Zaratornis* and *Conioptilon,* and the recently described genus *Pseudattila.* In his later book (1970) he made a more important change. As a result of recent anatomical research, he removed five genera and placed them in the Tyrannidae. These were the controversial *Attila* (with *Pseudattila*), *Casiornis, Laniocera,* and *Rhytipterna.* He also modified Hellmayr's order of genera in two ways. He placed *Ampelion, Zaratornis,* and *Doliornis* later in the sequence, associating them with the other Andean genera *Pipreola* and *Ampelioides* rather than with the eastern Brazilian genus *Phibalura.* Secondly, he placed *Phoenicircus* at the end of the family, after *Procnias,* instead of at the beginning.

The debated genera. The eight genera that Ridgway alone included in the Cotingidae are now generally agreed to belong in the Tyrannidae, and they will not be discussed further (*Microtriccus, Ornithion, Tyrannulus, Idiotriccus, Elainopsis, Hylonax, Ramphotrigon, Syristes*). Apart from these, there are nine genera whose position has been debated.

LANIISOMA

Laniisoma was placed in the Pipridae by Sclater (under the name *Ptilochoris*) on the basis of its foot structure and tarsal scutellation. Ridgway replaced it in the Cotingidae, linking it with *Phoenicircus,* also on the basis of its foot structure. Curiously enough, among the other characters that he listed for these two genera, he gave for *Phoenicircus* "adult males with sixth and seventh primaries shortened, especially the seventh, which is strongly bowed . . .," and for *Laniisoma* "adult males with sixth and seventh primaries normal"; but in fact males of *Laniisoma* have the seventh primary modified, as Sclater noted, though to a much less extreme degree than *Phoenicircus.* Thus *Laniisoma* and *Phoenicircus* agree in structural characters of both wing and foot, though they are very different in plumage. *Laniisoma* has not been dealt with in recent anatomical studies, being rare in collections, and nothing is known of its behavior. Its distribution is similar to that of *Phibalura,* with a southeastern Brazilian population and restricted populations along the eastern slopes of the Andes. It also resembles *Phibalura* in some points of plumage.

On present evidence *Laniisoma* is best kept in the Cotingidae. It is in accordance with the little that can be inferred about its relationships to place it between *Phoenicircus* and *Phibalura,* but this creates difficulties, as discussed under Sequence.

PHOENICIRCUS

Phoenicircus seems to be a very isolated genus, in spite of the characters shared with *Laniisoma,* as noted above. All recent classifications have placed it in the Cotingidae, though Hellmayr (1929) remarked (footnote, p. 92) that it is "a genus of doubtful affinity, perhaps more nearly related to the *Rupicolidae* or constituting a family by itself." Sclater also linked it with *Rupicola,* in the subfamily Rupicolinae, but on what real evidence is not clear. In his key to the subfamilies the designation for the Rupicolidae, "Tarsi very strong; gressorial," refers only to *Rupicola;* in fact only the crest (very different in the two genera), the presence of modified primaries in the male (but different ones, and many cotingid genera show such modifications) and the general colour serve as a very tenuous link between the two genera.

The anatomy of *Phoenicircus* has not been investigated, and very little is known of its behaviour except that it appears to have some form of communal display (Olalla, 1943). The united toes, the colour of the plumage, and the communal display all suggest that it may be an overgrown manakin. At least, this possibility deserves as much consideration from future workers as the more usual idea that it is cotingid; but until more is known about the genus it is preferable to retain it in the Cotingidae.

ATTILA

Superficially, its narrow hooked beak, flycatcher-like plumage, general behaviour (Skutch, 1971), and habit of nesting in niches in tree trunks all tend to suggest tyrannid affinities for the genus *Attila.* Sclater, however, following Sundevall, placed it in the Cotingidae, forming a subfamily Attilinae with *Casiornis,* on the basis of the tarsal envelope. Although he expressed doubt about the correctness of this, subsequent authors all kept *Attila* as cotingid, though usually with reservations. Ridgway pointed out that the tarsus is not in fact typical of the cotingas. Meyer de Schauensee (1966) followed the conventional treatment in his 1966 work, but in 1970 transferred *Attila* to the Tryannidae, as a result of Warter's studies of the skull. (Warter's work is not yet published, although cited with a publication date of 1966 in Meyer de Schauensee, 1966: 314, footnote.) The more recent studies of the syrinx by Ames (1971) confirm the tyrannid character of *Attila,* whose syrinx is closely similar to that of *Myiarchus.* It may be noted that these two genera have the same kind of nest-site.

There is little doubt that *Attila* should be removed from the Cotingidae, and placed in the Tyrannidae near to *Myiarchus.* The anatomy of *Pseudattila* has not been studied, but it seems so close to *Attila* (not having been separated as a genus until 1936) that it may safely be placed next to it.

CASIORNIS

Most of what has been said about *Attila* applies equally to *Casiornis.* Structurally it is close to *Attila* (in tarsus, beak, and syrinx [Ames]), but little seems to be known about it in life and its nest has apparently not been found. On present knowledge is seems best to place it close to *Attila* and remove it from the Cotingidae.

LANIOCERA

Sclater placed *Laniocera* in the Cotingidae, while noting that in foot structure it resembles the Pipridae. Ridgway, on the basis of its foot structure (exaspidean tarsus and extensively coherent toes), placed it in the Pipridae, but it was replaced in the Cotingidae by Hellmayr in spite of its foot structure because of the general similarity of its appearance to *Lipaugus* and *Rhytipterna*. Recent studies of its osteology and syrinx, however, suggest strongly that its correct place is in the Tyrannidae, presumably close to *Attila*. The genus is little known in life, and no nest has been found.

RHYTIPTERNA

There was general agreement in placing *Rhytipterna* in the Cotingidae, close to *Lipaugus*, until Meyer de Schauensee removed it to the Tyrannidae along with the genera *Attila* and associated genera, as the result of recent studies of the osteology and syrinx. This anatomical evidence seems too strong to be set aside.

The very peculiar tarsal scutellation of *Rhytipterna* separates it from all other genera, whichever family it is placed in. Nothing seems to be known of the genus in life, but it may be guessed that the spiky tarsal scutes are in some way connected with its nest-site or even its roosting behaviour. In the former case they might be analogous to the horny processes on the plantar surface of the tarsi of some hole-nesting non-passerines such as jacamars (in which case there would be a further link with *Attila*, a niche-nester), or in the latter case to the tarsal serrations of the tree-roosting *Tinamus*. Field observations on all the genera that are here thought to be close to *Attila* are badly needed.

LIPAUGUS

There has been consistent agreement among systematists that *Lipaugus* is a cotinga, but on the basis of his syringeal studies Ames (1971) has recently suggested that "*Lipaugus* may later be added to this group" (*Attila* and related genera, which must be transferred to the Tyrannidae). The only specimen available for study, however, was damaged, and no firm conclusion was possible.

The two closely related species *L. vociferans* and *L. unirufus* seem to be typical cotingas, so far as they are known in life. Males of *L. vociferans* display in leks (the advertising display being vocal, not visual), and the nest (*L. unirufus*, Skutch, 1969;

L. vociferans, Willis, personal communication) is a minute stick platform such as other medium-large cotingas (*Xipholena*, *Procnias*) build, but no tyrannids so far as known. Moreover, in spite of the dull grey, brown, or greenish plumage of most of the species, L. *streptophorus* has a brilliant magenta collar encircling the anterior part of the body, and Völker (1952) has shown that the pigment in these feathers, as in the red feathers of other cotingids, changes to orange under mechanical pressure.

In summary, the evidence, though scanty, suggests that *Lipaugus* should be retained in the Cotingidae. The peculiarities of the syrinx may well be related to the extraordinary development of vocal display in the genus, and may thus be a specialization rather than an indication of relationship. In this connection it would be interesting to examine the syrinx of a species that has not been reported to have an unsually loud voice, e.g., *L. streptophorus*.

It is not surprising that Hellmayr was impressed by the general similarity of *Lipaugus*, *Laniocera*, and *Rhytipterna*. In addition to their general resemblance they show a remarkable parallelism in geographical variation. In each genus there is a grey form widespread in South America east of the Andes, which is replaced by a chestnut-brown form in Central America and South America west of the Andes.

Xenopsaris

Sclater placed this genus in the Tyrannidae, as did most authorities of his time, although the single species, *X. albinucha*, was originally ascribed to the cotingid genus *Pachyramphus*. Ridgway placed it in the Cotingidae, noting that its tarsus is not exaspidean, thus not conforming to his main criterion for the Tyrannidae. Hellmayr removed it again to the Tyrannidae, and Meyer de Schauensee replaced it in the Cotingidae. This genus has thus been switched back and forth four times. As Meyer de Schauensee notes, "anatomical investigation is needed to settle the disputed status of this genus," but it is not abundant in collections and its anatomy is still unknown.

If it is a cotinga, it is unique in its habitat; no other member of the family is found primarily in reedbeds and other riverine vegetation, but many tyrannids are. The evidence for the tyrannid affinities of *Attila* and related genera shows that undue reliance should not be placed on tarsal characters alone. The evidence is clearly inadequate for a proper decision, but on balance it seems best to place *Xenopsaris* in the Tyrannidae.

RUPICOLA

As mentioned above, Sclater kept *Rupicola* in the Cotingidae in spite of the fact that the main artery of the thigh is the sciatic (as in the Tyrannidae) and not the femoral (as in the other cotingas studied). It is uncertain what weight should be given to this character until the thigh arteries of all the cotinga genera have been studied, but it should be noted that there is apparently no other character which links *Rupicola* with the tyrant-flycatchers rather than with the cotingas. On the basis of the thigh arteries, Ridgway placed *Rupicola* in a separate family, and Hellmayr followed him presumably for the same reason. Subsequent authors have not been consistent: for instance, Meyer de Schauensee (1966) maintains the family Rupicolidae, while Sibley (1970) has replaced *Rupicola* in the Cotingidae.

Sibley's decision was made before any evidence from egg-white proteins was available. Since then, he has analysed the proteins from a fresh egg that I sent him from southern Guyana (Snow, 1971c), and he writes as follows: "Your fine specimen has been 'run' at least three different times with different comparisons, both in isoelectric focusing and also in the standard type of net charge electrophoresis. In all of these it was compared with excellent specimens of *Pachyramphus*, with *Phytotoma*, *Manacus*, at least one or more tyrannid flycatchers, an ovenbird, and an antbird. Without any question, in all of these comparisons, *Rupicola* agrees most closely with *Pachyramphus*. Thus I think it is entirely in keeping with the egg white evidence, which seems to me satisfactory, to include *Rupicola* in the Cotingidae."

If *Rupicola* is retained in the Cotingidae, its isolated position in the family can be given recognition by placing it at the end of the sequence of genera, after the very difficult bellbirds (*Procnias*). The two genera thus represent two distinct types of specialized frugivores, in which the pure fruit diet is associated with marked sexual dimorphism and the evolution of elaborate courtship display.

RECOGNITION OF DEBATED GENERA

Most cotingid genera are so distinct that there has been general agreement about their recognition, even though their affinities may be in doubt. There are, however, a few genera that have been recognized by some authorities but not by others, and these are discussed below. In a family like this, where relationships are so hard to detect and the ratio of genera to species is so high, it seems far more satisfactory to use generic names, when possible, to indicate affinity rather than to emphasize minor differences between forms that are certainly quite closely related.

AMPELION, DOLIORNIS AND ZARATORNIS

Taczanowski in his original description admitted the nearness of *Doliornis* to *Ampelion*, but it was maintained as a separate genus apparently without dissent until Bond (1956) suggested that both it and *Zaratornis* should be merged with *Ampelion*. *Ampelion* and *Doliornis* are both Andean, occurring at high altitudes; they share the same plumage colours (greys and chestnut-browns), and they agree closely in their concealed red-brown nuchal crest. The main structural difference is that *Doliornis* has a narrower and less hooked beak than *Ampelion*. There has been no study of the internal anatomy of *Doliornis*, of which only two specimens are known from a single locality in Peru. It seems most likely that *Doliornis sclateri* has been derived from an isolated fragment of *Ampelion* stock, and the maintenance of the monotypic genus seems unnecessary.

The best treatment of *Zaratornis* is more difficult to decide. Bond recommended merging it with *Ampelion* because of the general similarity of its plumage, especially to that of *A. rufaxilla*. The red-brown nuchal patch is present, though reduced. Its relict distribution in the Andes, like that of *Doliornis*, suggests an offshoot from early *Ampelion* stock. According to J. Farrand, Jr. (personal communication), it is very like *Ampelion* in general behaviour. Farrand writes: "I spent several days at Zarate in the Department of Lima with the late Dr. Maria Koepcke in 1964, and saw the species daily. In its general behavior it is very like *Ampelion rubrocristata*. In a manner very reminiscent of that species it often 'pops up' suddenly onto a dead snag and sits upright, looking about rather nervously. The flight of *Zaratornis* is very similar to that of *Ampelion*, and both species approach a perch flying low and making a final upward sweep, rather like that of a shrike or kestrel." On the other hand, Lowery and O'Neill (1966) state that its skull, which they have examined, is "so distinct as to preclude making *Zaratornis* congeneric with *Ampelion*." Nevertheless, they place its skull next to that of *Ampelion* in what they describe as a "nicely graded series" of six genera, and the exact differences are not specified. Without knowing to what extent skull structure can be modified in response to differences in feeding behaviour in otherwise closely related forms, it is not possible to weigh the skull differences against the other evidence that suggests close relationship to *Ampelion*. Provisionally, I recommend merging *Zaratornis* with *Ampelion*.

PACHYRAMPHUS AND PLATYPSARIS

The closeness of these two genera has been obvious to everyone who has studied them, though nobody has liked to take the step of formally merging them. Ridgway gave as distinguishing characters the greater size of *Platypsaris*, the less extreme specialization of the modified ninth primary in the male, and the more cylindrical, less broad, beak. These hardly seem to warrant the recognition of a separate genus in view of the diversity of size and other characters within the genus *Pachyramphus*. Moreover, the partly concealed white scapular feathers characteristic of *Platypsaris* are also present in *Pachyramphus surinamus*. Both genera build gobular, bulky nests, with a side entrance, but that of *Platypsaris* is typically suspended from the tip of a drooping branch, while that of *Pachyramphus* is typically supported in a vertical or horizontal fork.

The four species of *Platypsaris* are almost completely allopatric (see later, p. 21). They overlap widely with several species of *Pachyramphus*, and their greater size is presumably one of the means by which they avoid competing with them. None of the distinctions seem great enough for generic separation, and they are best united under *Pachyramphus*, the older name, as Bond (1959) has already recommended.

TITYRA AND ERATOR

At first glance the three species in this group (*cayana*, *semifasciata*, and *inquisitor*) seem very close to one another. Ridgway, who laid stress on structural characters that might be used to separate genera, placed the last-named species in *Erator* on the basis of its feathered lores and orbital region.

taxaspidean (not pycnaspidean) tarsus, and broader and flatter bill. Hellmayr and most subsequent authors have preferred to recognise a single genus, although Wetmore (1926, 1927) has upheld *Erator* for the reasons given by Ridgway. It is almost inconceivable that this group of hole-nesting cotingas, whose plumage, modified ninth primary, general proportions, behaviour, and calls are so similar, are not closely related and monophyletic. The presence or absence of areas of bare skin clearly need not be considered of generic importance in the Cotingidae (cf. *Cephalopterus*, *Procnias*); beak shape is presumably adapted to feeding habits (though exactly how in these species is not known); while the difference in tarsal scutellation must be taken to indicate that variation in this character may evolve relatively easily without major modification of other characters.

THE SEQUENCE OF GENERA

As is true for all diverse families, no linear order can express relationships satisfactorily. This would be true even if the relationships were perfectly understood. In the Cotingidae we have a large number of isolated genera whose affinities are quite uncertain, and it seems best to use a sequence that keeps as close as possible to what has been customary while taking account of the more well-based conclusions from recent studies.

Sclater's sequence, as already mentioned, followed directly from his key, and subsequent advances in the systematics of the family make it obsolete. Ridgway's sequence also followed directly from his key, and although it is to this extent artificial it has been generally followed. The reason for this is probably that it seems a more or less natural sequence — except that it starts with *Phoenicircus,* but this genus would be anomalous in any position except the beginning or the end. After this awkward start, the sequence proceeds with five genera (*Laniisoma, Phibalura*, *Heliochera* (=*Ampelion*), *Tijuca*, and *Ampelion* (=*Carpornis*)) which are undoubtedly cotingid but unspecialized — that is to say, not specialized towards the large, frugivorous, highly dimorphic types that seem to be the culmination of evolution in the family (but see the *caveat* on p. 3). They are not very specialized in beak shape, and have plumages in which yellows, greens and greys predominate. Moreover, these apparently unspecialized genera are distributed peripherally to the main lowland forest region, which is the headquarters of most of the specialized frugivores. It is reasonable to regard these genera as closer to the early cotingid stock than the larger, brilliantly coloured fruit-crows and other bizarre forms that are placed towards the end of the generic sequence.

Four genera follow (*Porphyrolaema*, *Cotinga*, *Xipholena* and *Carpodectes*), which consist of medium-sized specialized frugivores with striking colours (purple, wine-red, blue or white) in the male plumage and duller-coloured females. There then follow (omitting the genera that have been placed in the Tyrannidae by all other authors) three genera of small or very small frugivorous forms (*Pipreola*, *Iodopleura*, *Calyptura*), the attiline genera and *Lipaugus*, the tityrine genera, and finally the large and diverse fruit-crows with the very specialized bell-birds (*Procnias*) placed at the extreme end.

Obviously the sequence in which the middle groups should be placed is to a large extent arbitrary, but this order does broadly represent an advancing sequence along the line of specialization for which the family is noted. Probably for this reason, Hellmayr followed it almost exactly (except in so far as he exluded or included the debated genera). Meyer de Schauensee also followed it, except for one major change: he placed *Ampelion* and the two related genera *Doliornis* and *Zaratornis* (the latter not described when Hellmayr wrote) somewhat later in the sequence, before *Pipreola* and after the recently discovered *Conioptilon*.

I believe that the basis of Hellmayr's sequence can be retained, but that some changes are needed in order that it should reflect as far as possible the most likely relationships in the light of recent knowledge. The suggested sequence, with annotations and justification of changes, follows: —

Phoenicircus	retained at the head of the list because it is so isolated but, so far as it shows affinities with other genera, may be linked with *Laniisoma*.
Laniisoma *Phibalura* *Tijuca* *Carpornis*	these four genera appear to be products of the same evolutionary centre (the SE Brazilian highlands, from which the first two have spread to the eastern slopes of the Andes)
Ampelion (including *Doliornis* and *Zaratornis*	shares some characters (especially nuchal crest) with *Phibalura*

Pipreola *Ampelioides*	almost certainly closely related: perhaps an offshoot from Andean stock sharing a common ancestry with *Ampelion*, and more remotely with the four preceding SE Brazilian genera.
Iodopleura *Calyptura*	of uncertain status; small forest birds not obviously related to each other nor to any other genera; syrinx of *Iodopleura* of tyrannid type (Ames 1971)
Lipaugus *Chirocylla*	probably belong together; not obviously related to other genera
Pachyramphus (including *Platypsaris* *Tityra*	probably fairly closely related (plumage colours, modified ninth primary of males, beak shape): not obviously related to other genera
Porphyrolaema *Cotinga* *Xipholena* *Carpodectes*	medium-sized specialized frugivores, sharing some plumage and structural characters; listed together in this sequence by Ridgway and later authors. *Xipholena* and *Carpodectes* appear to be closely related, on some characters (Snow, 1971); but Ames has found marked differences in syringeal structure and puts *Carpodectes* in a different group from the other three, with *Querula*. Further evidence is needed before upsetting the existing order, which seems satisfactory in other respects.
Conioptilon	resembles *Carpodectes* in skull characters, and seems to form a link between the above group and *Gymnoderus*, which it resembles especially in the great development of powder down (Lowery and O'Neill, 1966).
Gymnoderus *Haematoderus* *Querula* *Pyroderus* *Cephalopterus* *Perissocephalus* *Procnias*	large, mainly frugivorous cotingas, including the so-called fruit-crows. The sequence is the same as that adopted by Ridgway and followed by all later authors, except that *Gymnoderus* is placed first instead of near the end. This enables *Conioptilon* and *Gymnoderus* to be placed together, and does not violate any other known or presumed affinities. The position of *Procnias* at the end is in accord with its highly distinct syrinx.
Rupicola	

SPECIES LIMITS

A rather large proportion of all genera of cotingas consists of groups of parapatric forms (mainly or entirely allopatric forms that replace one another geographically). The differences between the allopatric populations range from very slight to very marked, thus posing problems of every degree of difficulty in the often arbitrary decisions that have to be made about specific limits. Each case needs to be treated on its own merits, but in fact there is too little evidence in nearly every case to allow a reasoned decision to be made. It is noteworthy, however, that in two cases where very similar forms come together (*Phoenicircus carnifex* and *P. nigricollis*, *Xipholena punicea* and *X. lamellipennis*) they appear to behave as good species, admittedly on very slender evidence (Haffer, 1970). The members of these two pairs are more alike than the members of most other allopatric pairs or groups of cotingas whose specific status is debatable. This should lead to caution in lumping allopatric forms into single species when only an arbitrary decision is possible. It is also very difficult, once one starts to lump allopatric forms, to know where to stop; and awkward situations occur. Logically, if closely related allopatric forms are to be treated as conspecific, *Xipholena atropurpurea* should be treated as conspecific with one of the very closely related species which replace it geographically; but with which? As far as one can tell, it is somewhat intermediate between *punicea* and *lamellipennis* and there is no good reason to link it with one rather than with the other.

For these reasons, I have been conservative in my treatment of allopatric forms, retaining specific status for them unless there seems to be particularly good reason to merge them; and even this involves subjective judgment with which it is easy to disagree. In order to make the classification given in Peters more useful for zoogeographic analysis, groupings of zoogeographic species and possible alternative taxonomic treatments will be indicated in footnotes, where appropriate.

PHOENICIRCUS. The two very similar species, *P. carnifex* and *P. nigricollis*, meet in the region of the lower Tapajos and perhaps the lower Xingu and Tocantins (Haffer, 1970). It seems that they must exclude each other from their respective ranges, but information is quite inadequate to decide the point. There is no evidence for intergradation between them. On present evidence they are best kept as separate species.

PIPREOLA RIEFFERII *and* P. INTERMEDIA. These two species are closely related, differing chiefly in the terminal tail markings of *intermedia*, which are absent in *riefferii*, and, less strikingly, in other plumage characters. *P. riefferii*, which has a wide range in northern parts of the Andes, is replaced by *intermedia* in Bolivia and most of Peru. Hellmayr (1929) treated them as specifically distinct, since specimens of both, showing no signs of intermediacy, have been collected near to each other in the Department of Libertad, *intermedia* at 2400 m and *riefferii* at 1200 m. Altitudinal data from elsewhere do not show *intermedia* as occurring consistently higher than *riefferii*, and in fact 1200 m is an exceptionally low altitude for either species; in the Department of Amazonas in northern Peru *riefferii* has been collected at 2300–2800 m, while further south *intermedia* had been recorded mainly at 2500–3000 m. Further information is needed on the distribution of these two species where they approach one another, but Hellmayr's opinion regarding their specific status appears sound.

Pipreola arcuata is almost certainly a derivative of the *riefferii-intermedia* stock, from which it differs chiefly in its large size and barred underparts. It now overlaps extensively with them.

PIPREOLA AUREOPECTUS, P. LUBOMIRSKII, P. JUCUNDA, *and* P. PULCHRA. The last three of these obviously form a natural group, as Hellmayr recognized. *P. aureopectus* is more distinct, but *pulchra* forms a clear link between it and the other two. The male of *pulchra* is almost exactly intermediate in its crown colour, and the female is almost exactly like the female of *aureopectus* except for the lack of white apical margins to the wing feathers. All four species agree in the unique combination of red beak, yellow iris, and olive-grey feet. They replace one another from north to south in the Andes, in the order listed, with no overlap so far as known. It seems clear that they should be treated as conspecific.

PIPREOLA FRONTALIS *and* P. CHLOROLEPIDOTA. The males of these two species at first sight appear very different, since the underparts of *chlorolepidota* are darkish green apart from the throat-patch, and those of *frontalis* are yellow. But the former species retains a small yellow area lateral to the throat-patch, where the feathers are brightest yellow in *frontalis*, and the two species agree in the colour of the soft parts (in the adult male, white or yellow iris, orange or red beak and feet). Moreover, the females are almost identical in plumage. Although they appear to be mainly allopatric, so far as can be told from the limited records, they overlap in southeastern Ecuador and probably northeastern Peru, and so cannot be considered conspecific; but they have probably speciated comparatively recently.

IODOPLEURA FUSCA *and* I. ISABELLAE. These two forms replace one another, so far as known, but there are wide areas where neither has been found. *Fusca* has been found at five localities in Guyana, one in Surinam, and one in eastern Venezuela on the upper Caroni River; the nearest records for *isabellae* are from the upper Orinoco region, the Rio Negro and the middle Amazon (Obidos). Until more is known of the situation in the intervening areas it seems premature to treat them as conspecific, as Hellmayr and others have suggested; they certainly differ more than do *Phoenicircus carnifex* and *P. nigricollis.* It may be noted that *Iodopleura pipra,* the only other species in the genus, which occurs in southeastern Brazil, is also known from two specimens from Guyana. The possibility of long-distance migration by these small aerial cotingas of the treetops cannot be excluded.

LIPAUGUS VOCIFERANS, L. UNIRUFUS *and* L. LANIOIDES. These three forms replace one another geographically. Hellmayr considered *lanioides* probably conspecific with *vociferans,* but did not go so far as to merge them. No systematist has merged *vociferans* and *unirufus,* although they are almost certainly more closely related than *vociferans* and *lanioides.*

L. vociferans and *L. unirufus* between them occupy almost the whole of the lowland tropical forest region of Central and South America. *L. vociferans* occupies the greater part of the South American range, but does not occur north of the Orinoco (except near its mouth). *L. unirufus* does not extend east of the Magdalena Valley in Colombia. There is thus an area in eastern Colombia and western Venezuela, containing some lowland forest, where neither occurs. The two species are very different superficially, since *vociferans* is all grey and *unirufus* all rufous-brown, but in behaviour and ecology the little evidence there is suggests that they are rather similar, and the colour difference could be based on a small genetic difference. For the reasons given in the introduction to this section I prefer, however, not to treat them as conspecific.

At first sight, *L. lanioides* differs from *vociferans* less than does *unirufus,* but the differences are in fact probably more numerous and important. It is larger, with a browner rump and underparts, and brownish (not grey) wings and tail. It replaces *vociferans* in southeastern Brazil south of 20° S. The separation at this point involves habitat as well as range, as *vociferans* occurs in lowland tropical forest while *lanioides* is found mainly in subtropical montane forest (but has also been recorded near sea-level, perhaps as a result of vertical migration). Further, although little is known of *lanioides* in life it is hard to believe that it could utter the kind of piercingly loud calls, in leks, that are so characteristic of *vociferans* wherever it occurs. It seems more likely that *lanioides* and the other montane species of *Lipaugus* (*streptophorus*, *fuscocinereus*, *cryptolophus* and *subalaris*) are comparatively quiet birds, with a different social organization from *vociferans* and *unirufus*. Hellmayr's suggestion that *lanioides* and *vociferans* are conspecific thus receives no support in the light of more recent knowledge.

The genus Pachyramphus. With 11 species usually recognized (15 if *Platypsaris* is included), *Pachyramphus* is easily the largest cotingid genus. It is also unique in the family in the amount of geographical overlap between species; in extensive areas up to five or even six species may occur close together, even if not in exactly the same habitats. Some of the species can be placed in groups that constitute zoogeographical species. The arguments for and against recognizing larger specific units than are currently recognized are discussed below.

Pachyramphus castaneus *and* P. cinnamomeus. *P. castaneus* differs from *P. cinnamomeus* principally in its smaller beak and in the presence of a narrow grey stripe separating the chestnut of the crown from the paler brown sides of the head and neck. Otherwise they are closely similar, and are the only two species in which male and female are alike in plumage. Moreover, both are characteristically found in lowland tropical forest, a habitat avoided by most of their congeners. *P. castaneus* also ranges up into the subtropical zone.

Between them, these two species apparently occupy most of the tropical forest area of South and Central America. In northwestern Venezuela and eastern Colombia, their ranges approach closely: *P. castaneus* occurs in the coastal mountains of northern Venezuela, and is replaced by *P. cinnamomeus* round Lake Maracaibo and in the mountains south of Lake Maracaibo. Further south, the potential habitats of the two species are widely separated by savanna country west of the Orinoco, except in the west where a corridor of forest along the eastern foothills of the Andes connects the main forest areas occupied by the two species. *P. cinnamomeus* has apparently occupied this corridor from the north, as it has been recorded from near Villavicencio, while *P. castaneus* occurs not far to the south, in the forest of the Sierra Macarena.

This geographical replacement suggests that the two species are potential competitors. The morphological differences between them, though slight, seem too clear-cut to warrant treating the two forms as conspecific.

PACHYRAMPHUS RUFUS *and* P. SPODIURUS. Hellmayr pointed out the similarity of these two species and suggested that *spodiurus* might well prove to be the Pacific representative of *P. rufus*. *P. spodiurus* is larger, with a slenderer bill; the male is much darker than *rufus*, but the female plumage is closely similar. The little that has been reported on habitat preference suggests that *rufus* avoids heavy forest, preferring wooded savanna and open woodland; it nevertheless occurs in areas dominated by rain-forest. *P. spodiurus* is also a bird of open woodland, and the absence of records from the very humid coastal forest of northwestern Colombia suggests that it is absent from this area, which thus effectively isolates it from *rufus* to the north.

This is a case much like several others, where two allopatric forms are clearly closely related and it must remain a matter of judgment whether or not they should be treated as conspecific. On balance, and in the absence of any real evidence, it seems that consistency demands that *rufus* and *spodiurus* should receive the same treatment as *castaneus* and *cinnamomeus* and should provisionally retain their specific status.

PACHYRAMPHUS MARGINATUS *and* P. ALBOGRISEUS. These two species agree in many points of plumage, the most conspicuous difference being in crown pattern: the male of *albogriseus* has extensive black on the crown and nape, and the female a brown crown bordered posteriorly with black, forming a patch of the same extent as the male's black; whereas *marginatus* has a small black crown-patch in the male and a brown crown with no black border in the female.

P. marginatus is a bird of lowland tropical forest, east of the Andes. *P. albogriseus* replaces it in limited areas of the Andes, west of the Andes, and in Central America, being found in a variety of habitats, tropical and subtropical. Where the two species approach one another, on the eastern slopes of the Andes of Peru and Ecuador and in northern Venezuela, *P. albogriseus* occurs only at high altitudes and *P. marginatus* in the lowlands.

Again, it seems clear that these two are related, but the little evidence available does not justify treating them as conspecific.

PLATYPSARIS. The close affinity of *Pachyramphus* and *Platypsaris*, and the reasons for merging the two genera, have already been discussed. *Platypsaris* consists of five forms, usually treated as species, which are almost completely allopatric. Four of these forms between them occupy almost the whole of tropical and subtropical America except some montane and unwooded areas. They clearly constitute a zoogeograpical species, but the status of the constituent members is not clear. It is convenient, however, in discussing them to use the four specific names that are in general use. (Unfortunately, the specific name *rufus* is in use in both *Pachyramphus* and *Platypsaris*, and when the genera are merged it will be available only for the species currently known as *Pachyramphus rufus*, which has priority.) The fifth form, *P. niger*, occurs only in Jamaica and is rather distinct. The following discussion concerns only the four mainland forms.

P. minor, the central form, occupies the whole of the tropical forest of the Amazon basin and upper Orinoco system. To the south and east, *P. rufus* occurs in a wide variety of more seasonal wooded habitats, tropical and subtropical. These two differ in a number of plumage characters in the male, and less strikingly in the female; they differ also in size. There appears to be no intergradation between them, and moreover their ranges overlap in two areas, in northern Pará and Maranhão in northern Brazil and along the base of the Andes in Peru and Bolivia. These are areas where lowland tropical forest comes into contact with more open vegetation types (N Brazil) or with lower montane woodland (base of Andes). Their ranges also approach closely, and may even interdigitate, along the southern fringe of the main Amazonian forest in central Brazil.

To the northwest, *P. minor* is isolated from *P. homochrous*, also a forest bird, by the savannas of Venezuela and eastern Colombia. Neither species is found in the forested coastal mountains of northern Venezuela. These two forms differ slightly but constantly in both male and female plumage, and are much alike in size.

In Central America *P. homochrous* and *P. aglaiae*, both inhabiting forest or more open woodland according to the habitats available, are separated by a gap between central Panama and central Costa Rica in which neither seems to occur. The populations on either side of this gap are very alike in male plumage, and in size. The females are more distinct, but some specimens of *aglaiae* resemble female *homochrous* closely. *P. aglaiae* is geographically and individually a very variable species. Webster (1963), in a recent review of its variation, considered it conspecific with *homochrous* by modern standards, and the judgment seems sound.

The evidence does not, however, warrant any further lumping within this group. It is obviously necessary to give specific status to *minor* vis-à-vis *rufus.* No critical test is possible of the status of *minor* vis-à-vis *homochrous,* but the constant plumage differences in both sexes suggest a similar degree of differentiation to that between such species as *Lipaugus vociferans* and *L. unirufus,* whose ranges are also similar to those of *minor* and *homochrous.* It has been argued above that in the absence of evidence to the contrary it is best to give specific status to such forms.

The genus COTINGA. Six of the seven species usually recognized in this genus replace one another geographically: the Central American and northwest South American *amabilis, ridgwayi* and *nattererii; maynana* of the upper Amazon basin; *cotinga* of the lower Amazon-Guiana region; and *maculata* of eastern Brazil. (The seventh species, *cayana,* is more distinct morphologically and overlaps extensively with *maynana* and *cotinga.*) The first three are very similar to one another, and considered in isolation from the others might reasonably be treated as conspecific. *C. cotinga* and *maculata* are also very similar to one another, and Hellmayr suggested that they might be conspecific. They differ most conspicuously from the Central American forms by the deeper (not turquoise) shade of blue in the male and the more extensive purple below. The sixth form, *maynana,* is at first glance rather distinct from the others. Hellmayr made the rather surprising suggestion that it might prove to be conspecific with the Central American forms, apparently on the basis of its similiar shade of turquoise blue.

A more detailed analysis shows that these six forms exhibit a mosaic of characters that link one with another in many different ways (Table 1). The Central American group forms a unit, having in common six of the characters considered, and the two eastern forms constitute another unit, with seven common characters. *C. maynana* is certainly the most distinct form, having four peculiar characters, while none of the others has any character not found in at least one other form. In wing formula, however, *maynana* is closer to *nattererii* than the latter

TABLE 1

Characters of males of six allopatric *Cotinga* species.

	amabilis	*ridgwayi*	*nattererii*	*maynana*	*cotinga*	*maculata*
Shade of blue	turquoise	turquoise	turquoise	turquoise	deep blue	deep blue
Distribution of purple	throat and belly (two patches)	throat and belly (two patches)	throat and belly (two patches)	small throat patch	extensive patch, throat to belly	throat and belly (two patches)
Colour of feather bases	black	black	black	pinkish purple	black	black
Under-wing	black	black	black	extensive white	black	black
Secondaries and greater coverts	blue-edged	blue-edged	blue-edged	blue	black	black
Wing tip: —						
Length of 7th primary	abbreviated	normal	normal	normal	abbreviated	abbreviated
primaries 7–10	unmodified	9th attenuated, 10th slightly so.	notched	7th and 8th slightly notched	9th and 10th attenuated	9th and 10th attenuated
Eye colour	brown	brown	brown	yellow	brown	brown

is to the other two of the Central American group. Similarly, *amabilis* of the Central American group resembles the two eastern forms, *cotinga* and *maculata,* in its abbreviated 7th primary, while *ridgwayi,* the remaining member of the Central American group, approaches them in the modification of its two outer primaries (but not in its 7th primary, which is normal).

It seems probable that the common ancestor of these six forms — perhaps during a period of contraction of the forests — was divided into a number of isolated populations, which evolved a number of small but consistent differences to which no obvious adaptive significance can now be attributed. The forest refuges suggested by Haffer (1970) provide obvious origins for five of the forms: *amabilis* in the Caribbean (Costa Rica) refuge, *nattererii* in the Chocó refuge, *maynana* in either the Napo or the East Peru refuge, *cotinga* in the Guiana refuge, and *maculata* in the southeastern Brazilian refuge. The sixth form, *ridgwayi*, presumably evolved in a small forest refuge on the Pacific coast of Costa Rica and Panama, to which it is still confined. The rather exact geographical replacement of one form by another, and lack of any evidence of morphological intergradation, suggest that they have reached specific status to the extent of being reproductively isolated, but that they are still not able to penetrate one another's ranges.

In spite of the unequal differentiation of these forms, and the fact that they fall into two groups, with one isolated form, it is probably best to treat all six as species, as has been the usual practice.

The genus XIPHOLENA. The status of the three forms has already been discussed, with the reasons for keeping them as three separate species.

The genus CARPODECTES. This genus consists of three allopatric forms, of which two (*nitidus* and *antoniae*) are very similar to one another while the third (*hopkei*) is a good deal more distinct. There is no doubt that together they constitute a zoogeographical species, but it is less clear whether they should be treated as one, two or three species. All three courses have been adopted or advocated. Slud (1964), however, gives some reasons for keeping *nitidus* and *antoniae* separate, and if this is done *hopkei* must also be given specific rank. Such a treatment is in accord with the general policy adopted for other groups, as discussed above.

The genus CEPHALOPTERUS. In accord with the general policy adopted, as discussed above, the three allopatric forms of umbrellabirds should be kept as separate species. The differences between them are at least as great as the differences between the overlapping forms of *Xipholena* and *Phoenicircus*.

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APPENDIX

Annotated species list of the Cotingidae; treatment to be adopted in Peters' *Check-list of Birds of the World.* (Zoogeographical species bracketed)

⎡ Phoenicircus carnifex	See discussion, p. 16
⎣ Phoenicircus nigricollis	
Laniisoma elegans	
Phibalura flavirostris	
Tijuca atra	
Carpornis cucullatus	
Carpornis melanocephalus	
Ampelion rubrocristata	
Ampelion rufaxilla	
Ampelion sclateri	Formerly *Doliornis sclateri*
Ampelion stresemanni	Formerly *Zaratornis stresemanni*
⎡ Pipreola riefferii	See discussion, p. 17
⎣ Pipreola intermedia	
Pipreola arcuata	
Pipreola aureopectus	Includes *lubomirskii, jucunda* and *pulcha* (p. 17)
⎡ Pipreola frontalis	See discussion, p. 17
⎣ Pipreola chlorolepidota	
Pipreola formosa	
Pipreola whitelyi	
Ampelioides tschudii	
⎡ Iodopleura fusca	See discussion, p. 18
⎣ Iodopleura isabellae	
Iodopleura pipra	
Calyptura cristata	
Lipaugus subalaris	
Lipaugus cryptolophus	
Lipaugus fuscocinereus	
⎡ Lipaugus vociferans	See discussion, p. 19
⎣ Lipaugus unirufus	
Lipaugus lanioides	
Lipaugus streptophorus	
Chirocylla uropygialis	
Pachyramphus viridis	
Pachyramphus versicolor	

Pachyramphus spodiurus	See discussion, p. 20
Pachyramphus rufus	
Pachyramphus castaneus	See discussion, p. 20
Pachyramphus cinnamomeus	
Pachyramphus polychopterus	
Pachyramphus marginatus	See discussion, p. 20
Pachyramphus albogriseus	
Pachyramphus major	
Pachyramphus surinamus	
Pachyramphus aglaiae	Includes *homochrous;* see discussion, p. 21
Pachyramphus minor	
Pachyramphus validus	
Pachyramphus niger	
Tityra cayana	
Tityra semifasciata	
Tityra inquisitor	
Porphyrolaema porphyrolaema	
Cotinga amabilis	Possibly the first six species could be considered as one zoogeographical species (p. 22).
Cotinga ridgwayi	
Cotinga nattererii	
Cotinga maynana	
Cotinga cotinga	
Cotinga maculata	
Cotinga cayana	
Xipholena punicea	See discussion, p. 24
Xipholena lamellipennis	
Xipholena atropurpurea	
Carpodectes nitidus	
Carpodectes antoniae	See discussion, p. 24
Carpodectes hopkei	
Conioptilon mcilhennyi	
Gymnoderus foetidus	
Haematoderus militaris	
Querula purpurata	
Pyroderus scutatus	
Cephalopterus glabricollis	See discussion, p. 25
Cephalopterus ornatus	
Cephalopterus penduliger	
Perissocephalus tricolor	
Procnias tricarunculata	All four *Procnias* species are closely related and replace one another almost completely (Snow, in press)
Procnias alba	
Procnias averano	
Procnias nudicollis	
Rupicola rupicola	
Rupicola peruviana	

Total: 79 taxonomic species
56 zoogeographical species