Postilla

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THE CRESTED LIZARD HAWK (*AVICEDA JERDONI*) IN THE PHILIPPINES

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The genus *Aviceda* contains about five species of small hawks distributed through the Old World tropics. Two forms of this genus have been described from the Philippines: *Hypticopus magnirostris* Kaup, 1847, and *Baza leucopias* Sharpe, 1888. The latter was based on a single specimen from the island of Palawan. The application of these two names to the Crested Lizard Hawks of the Philippines has varied. Modern authors agree that the Philippine birds belong to the Indo-Malaysian species *Aviceda jerdoni*. Peters (1931: 196) used the name *A. j. magnirostris* for the populations of Luzon and Mindanao, and attributed those of the islands of Romblon, Samar, and Palawan to a subspecies to which he attached Sharpe's name *leucopias*. He was followed in this treatment by Hachisuka (1934: 34-35) and Swann and Wetmore (1936: 294-295); the former author adopted the emendation to "*leucopais*" published by Whitehead (1890: 43) at Sharpe's request.

The most recent manual on Philippine birds (Delacour and Mayr, 1946: 40) abandons the concept of two subspecies, using the name *magnirostris* for the birds of all five islands (Palawan, Luzon, Romblon, Samar, and Mindanao) from which *Aviceda* has supposedly been recorded. The description of the "immature" *A. j. magnirostris* given by Delacour and Mayr, however, is based on the unique type of *leucopias*, which was described as a "young female" by Sharpe.

I have examined the type of *leucopias*, now in the American Museum of Natural History (Rothschild Collection), which remains to this writing the only specimen of *Aviceda* known from Palawan. It is my belief that this bird (figured in color by Whitehead, 1890: pl. 2) is albinistic, and that there is no definite evidence that the *leucopias* coloration represents a normal "immature" plumage of *magnirostris* as described by Delacour and Mayr. Truly "immature" specimens of *Aviceda* of any species are rare in collections, and examination of the entire series of this genus in the American Museum suggests that this is because such plumages are held very briefly, unlike the situation in many other Accipitridae. Two juvenile specimens of *A. jerdoni ceylonensis* in the American Museum are similar to definitively plumaged adults, but have the feathers of back, crown, wing coverts, etc., edged with white, and the upper breast streaked longitudinally. It seems very unlikely that *A. j. magnirostris*, of which the adults rather closely resemble other subspecies, would have a juvenal plumage as radically different as that represented by *leucopias*. As mentioned above, other *Aviceda* hold the juvenal plumage only briefly; the type of *leucopias* is, in part, badly worn and bleached to an extent that juvenile *Aviceda* would not normally have time to attain before molting. It thus seems probable that the type of *leucopias* represents a "dilute" or albinistic adult female. The fate of the name depends on whether a case can be made for two subspecies of *Aviceda jerdoni* in the Philippines.

The presence of the small island of Romblon in the list of Philippine localities from which *Aviceda* has been taken rests on the record of Bourns and Worcester (1894: 33), who reported "*Baza leucopais* Sharpe" from Romblon and Samar. These authors had not seen the unique type of *leucopias*, and identified their specimens from descriptions only. Their single Romblon specimen is now in the collection of Carnegie Museum (no. 137904). It is not an *Aviceda* at all, but an immature female *Spilornis cheela*, collected September 7, 1892, just seven days before Bourns and Worcester collected an adult female

(C.M. 137902) of the same species on Romblon. The very small size of these two specimens (flattened wing 308, 305 mm) and the pale color of the adult incidentally confirm Rand's identification of his single Romblon specimen as *Spilornis cheela panayensis* (Rand, 1951: 578). The island of Romblon may thus be removed from the known range of *Aviceda jerdoni* in the Philippines.

For many years the status of *Aviceda* on the island of Samar was precisely like the Romblon status described above, resting on a single Bourns and Worcester specimen. This bird was collected at Catbalogan, Samar, on August 12, 1892, and is now in the collection of the Minnesota Museum of Natural History, University of Minnesota (no. 11416). It, too, is an immature *Spilornis* cheela (male, wing 312 mm). There is, however, a bona fide record of *Aviceda jerdoni* from Samar; an adult male was collected by D. S. Rabor on Mt. Capoto-an, May 9, 1957. The statement of Rand and Rabor (1960: 374) that *A. j. magnirostris* had been "collected previously [on Samar] by Bourns and Worcester" is thus erroneous, and theirs is the first specimen from that island.

Leaving out of consideration the single problematical Palawan specimen (the type of *leucopias*), we are left with three islands from which *Aviceda jerdoni* is alleged to have been recorded: Luzon, Samar, and Mindanao. The name *Hyptiopus magnirostris* Kaup was based on *Baza magnirostris* Gray, (List Bds. Brit. Mus., 1844: 19), a *nomen nudum*, which in turn was based on a single specimen received by the British Museum in 1842 among some 175 Philippine specimens collected by Hugh Cuming. Mr. R. W. Sims has kindly examined this type specimen for me, and writes as follows (letter of July 16, 1960): "Cuming never tied collectors' labels on his specimens, hence the only label is that secured in the time of G. R. Gray. The information there reads: 'Baza magnirostris, locality Philippines, ex. coll. Cuming.'" At some later date (apparently), the additional locality "Island of Manilla, South" was entered against this specimen in the British Museum Register (Sharpe, 1893: 555). The source of this additional locality information is problematical. It is highly unlikely that it was supplied by Cuming, the collector; Mr. S. P. Dance of the Mollusca Section of the British Museum, who is working on the life and collections of Hugh Cuming, informs me that Cuming never, to his knowledge, employed the expression "Island of Manilla," whereas "Island of Luzon" was frequently used by Cuming. Mr. Sims, of the Bird Room, writes, "I gather from Mr. Dance that in his later years Cuming employed a secretary to do all his writing for him so it is possible that somewhere either on the part of the secretary or perhaps on the part of G. R. Gray there was an error in transcription and that the type of *magnirostris* was collected at some other locality." Mr. Dance (letter of August 29, 1960) says that he "should be inclined to treat any label on a Cuming specimen with circumspection . . ."

Sharpe (1893: 556) pointed out that nobody since Cuming's time had recorded *Aviceda* from Luzon, and this statement is equally true 68 years after Sharpe's words were printed. Although new species are still being discovered on Luzon, it seems highly unlikely that a bird the size of an *Aviceda* would escape detection on this, the most heavily populated Philippine Island, particularly since most Luzon birds collected in Cuming's time, some 130 years ago, came from the vicinity of Manila. In view of the great uncertainty attached to the validity of the locality "Island of Manilla, South," I would suggest that the type locality of *Hyptiopus magnirostris* Kaup be designated as Davao, Mindanao, a source of some early Philippine collections and a locality at which the species is definitely known to occur. A precedent for such an action with respect to a Cuming specimen was set by Rand and Rabor (1960: 429).

An additional published record of *Aviceda jerdoni "leucopais"* must be mentioned here. Hachisuka (1941: 72) lists five "light creamy birds" from Mr. Hirazawa's collection as "*leucopais*." As these were collected in Mindanao, where *magnirostris* is also known to occur, Hachisuka stated that the two forms must be separate species unless further investigation should prove them to be age or individual variants within a species. One would suspect that this might serve to confirm Delacour and Mayr's identification of the *leucopias* type as the "immature" plumage of *magnirostris*. This is not the case, however. One of the Hirazawa specimens was obtained by

Hachisuka, and is now in the personal collection of S. Dillon Ripley at the Peabody Museum, Yale University, where I have examined it. This specimen (Hachisuka 3751, SDR 337) was collected near Davao, Mindanao, sometime in 1927-1928. It is neither *Aviceda* nor *Spilornis*, but a pale, very worn example of *Pernis celebensis steerei*! The latter species of Honey Buzzard, incidentally, is highly variable in color, as is its congener *P. ptilorhynchus*, as amply illustrated by the series in the Peabody Museum collection; one would not suspect this variability from the description given by Delacour and Mayr (1946: 42).

An additional specimen in the Hachisuka collection (Hachisuka 3752, SDR 338) was collected at Bitogan, Sigaboy, Mindanao in 1930 (no date given). It was first identified as *Spizaëtus limnaeetus*, then reidentified as *Aviceda jerdoni magnirostris*. It is, in fact, another specimen of *Pernis celebensis steerei*. I do not know that Hachisuka ever specifically referred to this specimen in print. As for the rest of the Hirazawa series of "*leucopais*," I have been unable to learn of their present whereabouts, if, indeed, the Hirazawa collection survived World War II. One can but assume that all five specimens were of one species, in which case they were not *Aviceda* but *Pernis*, as illustrated by the example seen.

Rand and Rabor (1960: 374) stated that their one Samar specimen of *Aviceda jerdoni magnirostris*, a male, had a definitely shorter wing than two females and an unsexed specimen from Mindanao. There probably is no geographic significance in this difference. The Samar male has a flattened wing of 294 mm; measurements of a Mindanao series run as follows: male 299, 311; female 298, 299, 308, 314, 321, 324. It would appear that males average slightly smaller than females. There is a spread of 26 mm between the smallest and largest females measured, and only 12 mm between the two Mindanao males. The Samar male would undoubtedly fall within the range of variation in size of a larger series of Mindanao males.

The unsexed specimen from Mindanao mentioned by Rand and Rabor is readily identified as a female on the basis of plumage color. Although this is not suggested in the description by Delacour and Mayr (1946: 40), *Aviceda jerdoni* is markedly sexually dimorphic in color. The difference is well described for *A. j. jerdoni* by Stuart Baker (1928: 174), but the dimorphism of *magnirostris* does not appear to have been correctly described. The descriptions of the "nearly adult female" and "adult male" given by McGregor (1909: 236-237) and Hachisuka (1934: 34) are copied directly from Sharpe (1874: 356), with and without credit, respectively. But, as Sharpe himself pointed out (1893: 555-556), the "nearly adult female" proved to have been a victim of a labeling error, and was not in fact from the Philippines at all. The figure in Delacour and Mayr (1946: 41) may be a composite of the two specimens in the American Museum of Natural History, as it partakes of the characteristics of both sexes. In males the upper breast is more or less clear gray; in females this area is mixed with rufous. The broad brown bars of the posterior underparts are a darker, less rufescent brown in males. The cheeks of males are gray with black shaft-streaks; this area in females is buffy or pale rufous with darker-brown shaft-streaks. Females are much more rufescent dorsally; this is most striking on the crown and nape, which have bright rufous feathers with darker centers. In males the crown is virtually black, with narrow, paler feather-edges, and the nape nearly lacks rufescence. On the outer rectrix of males, the dark bars of the outer web are approximately opposite those of the inner web, whereas in females the dark bars are offset from one another, sometimes to the degree that (as in C.N.H.M. 184011) the dark bars of the outer web are opposite the *light* bars of the inner web. Incidentally, the figure in Delacour and Mayr (1946: 41) shows the outer rectrices with only a narrow pale tipping, whereas there is actually a rather broad pale terminal band (20-28 mm).

The four Mindanao females now before me are rather uniform in dorsal color, making allowances for relative wear and museum age. Only two males are at hand, one of which is the Samar bird reported by Rand and Rabor (1960: 374). This specimen differs slightly in color from a single Mindanao male in being of a darker, colder tone of brown dorsally, lacking almost completely the rufescent tinge on the nape of the latter bird. The Samar specimen also has dark-gray rather than dark-brown edgings to the black feathers in the center of the crown. Further material must be compared before any geographical significance can be attached to these differences.

The Crested Lizard Hawk is a rare bird in the Philippines. Dr. Rabor writes me (letter of September 17, 1960) that the Samar male is the only specimen he has taken in 26 years of collecting. I have attempted a census of Philippine specimens of *Aviceda jerdoni*, and have managed to locate the following:

British Museum (Natural History)

♂ "Philippines," Cuming coll. (type of *magnirostris*).
♀ Davao, Mindanao, February, 1905.

American Museum of Natural History

♀ Kalusian, Palawan, October 5, 1887 (type of *leucopias*).
♂ Davao, Mindanao, May 17, 1889.
♀ Davao, Mindanao, September 8, 1903.

Chicago Natural History Museum

[♀] Culamen, Caburan, Davao, Mindanao, January 25, 1947.
♀ Mt. Busaw, Caburan, Davao, Mindanao, January 28, 1947.
♀ Mati, Digos, Davao, Mindanao, February 9, 1947.
♂ Mt. Capoto-an, Samar, May 9, 1957.

University Zoological Museum, Copenhagen, Denmark

♀ Talacogan, Upper Agusan, Mindanao, March 8, 1952.
♀ Pulangi River, Bukidnon, Mindanao, November 20, 1952.

National Museum of the Philippines, Manila

♂ Limot, Mati, Davao, Mindanao, April 10, 1949.

[♀ Bunauan, Agusan, Mindanao, December 17, 1909: McGregor, 1910. This specimen was lost with the destruction of the Museum in 1945.]

These thirteen specimens (one lost) are the only examples of *Aviceda* to have been collected in the Philippines to my present knowledge. I have examined the seven now in museums in the United States.

Lint and Stott (1948: 42) published sight records of this species from three localities in Zamboanga, western Mindanao, all in October, 1945. In view of the rarity of *Aviceda jerdoni*, however, the possibility must be considered that some similar species was involved (several Philippine raptors have similar patterns), particularly as a "bare tree within half a mile of the center of the city of Zamboanga" seems a most unlikely situation for a species usually described as a shy resident of original forests. The species has not been collected in Zamboanga.

It is obvious that the principal Philippine range of this rare bird is central Mindanao; only two specimens are known to have been collected elsewhere. It is just possible that a recognizable subspecies may inhabit Samar, but the status of the Palawan population cannot be determined from the single specimen known, which appears to be a freak individual.

ACKNOWLEDGEMENTS

Specimens were borrowed through the kind cooperation of Dr. A. L. Rand of the Chicago Natural History Museum, Dr. Dean Amadon of the American Museum of Natural History, and Mr. Robert W. Dickerman of the University of Minnesota. Mr. Dickerman and Dr. Dwain Warner were instrumental in arranging the exchange of a portion of the Bourns and Worcester Philippine collection to the Carnegie Museum. Specimens were examined at the Peabody Museum of Natural History, Yale University, through the courtesy of Drs. S. Dillon Ripley and Philip S. Humphrey. Data on specimens in the British Museum (Natural History) were supplied by Mr. R. W. Sims, and information about Cuming's collecting localities by Mr. S. P. Dance. Data on specimens in the National Museum of the Philippines were sent by Mr. Telesforo Oane, and on those in the University Zoological Museum, Copenhagen, by Mr. Arne Nørrevang.

SUMMARY

The Crested Lizard Hawk, *Aviceda jerdoni*, is known from the Philippines by thirteen or more specimens of the endemic subspecies *A. j. magnirostris*. The type locality "Luzon" generally given for this subspecies is almost certainly erroneous, and Davao, Mindanao is substituted. A second supposed race, *A. j. leucopias*, is based on a single specimen from Palawan which is probably an aberrant individual. Other records of "*leucopias*" from Romblon, Samar, and Mindanao are based on misidentified specimens. All but two specimens of known origin of *magnirostris* are from Mindanao; these are the type of "*leucopias*" from Palawan and one from Samar which may represent a recognizable race. Sexual dimorphism in *magnirostris* is described for the first time, and all known specimens listed.

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AEGEAN BIRD NOTES I

DESCRIPTIONS OF NEW SUBSPECIES FROM TURKEY

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Introduction

In the course of gathering material for a study of the Aegean avifauna, I was able to collect during March and April, 1960, in south and west Asia Minor. The areas visited extended from Tarsus, Içel, and Pozantı, Seyhan, along the south coast to Muğla and up the west coast to Bursa. Some of the regions visited have been little collected during the early spring. This fresh material revealed that the populations of some species in this area were markedly different from other known populations nearby. Therefore, the following descriptions of new subspecies are presented. The distinctness of some of these populations suggests that biogeographic studies of the Asia Minor avifauna may be rewarding in terms of elucidating eastern Mediterranean late Pleistocene refugia (cf Kosswig, 1955, *Syst. Zool. 4:* 49-73, 96).

I

Prinia gracilis

The population of the Streaked Prinia inhabiting south coastal Asia Minor was found to be consistently different from its nearest geographical relatives and warranted description as a new subspecies. This difference was suggested by the information available to Hartert (1910, *Vög. der pal. Fauna:* 609) and Zedlitz (1911, *Journ. f. Orn. 59:* 610) but overlooked by them. I therefore propose the name:

Prinia gracilis akyildzi subsp. nov.

Type: Adult ♂ (Y.P.M. No. 59196) collected in Antalya, Turkey, March 31, 1960, by George E. Watson.

Diagnosis: Nearest to *P. g. deltae* and *P. g. palästinae* but darker above, with even broader dark-brown shaft-streaks on the back; underparts brighter and more suffused with buff. This character is most noticeable in fresh unworn plumage, but even in late March south Asia Minor birds are separable from spring specimens from Palestine, Syria, and the Nile of Egypt. Brown shaft-streaks are present on the feathers at the sides of the upper breast and form an indistinct necklace. On some specimens shaft-streaks are also present on the flanks. This character clearly separates this race from all others of the species except *P. g. deltae* in which side and breast-streaking is present in some specimens. Tail with less well-defined and narrower black subterminal bars than either *P. g. palästinae* or *P. g. deltae*; tip buffish not whitish as in *P. g. palästinae*. In the reduced width and lack of definition of the subterminal bars this form resembles *P. g. irakensis*, but the back-streaking is far more emphasized and the general color tone is darker, more brown. The culmen averages markedly shorter than in any of the other three races.

Measurements: Type, wing, 44; tail, 66; culmen (from skull), 10.6 mm; weight, 6.5 gr. Six other specimens from Antalya, Tarsus, and Adana, south Turkey: 2 ♂♂ wing, 42, 42; tail, 65, 60; bill, 11.2, 11 mm; weight, 6.7 gr; 4 ♀♀ wing, 41, 41, 39, 37.5; tail, 59, 55, 56, 55; bill, 10.5, 11, 11, 11 mm; weight, 6.7, 6.5, 6.5 gr.

COLOR OF SOFT PARTS: Iris light red-brown, light-brown, or cream; bill flesh or upper mandible brown, lower mandible cream or yellow-cream; feet buffish-flesh or flesh. Apparently the bill color in this species changes to black during the breeding season.

The type series consists of six specimens, two males and four females collected between March 2 and March 31, 1960, at Antalya, and Tarsus, Içel, in south Turkey. In addition, a single male from the American Museum collected in nearby Adana, January 1, 1879, was also examined. A male collected on March 3 is renewing feathers on the center throat. None of the specimens had gonads enlarged for breeding, but males were calling loudly from exposed perches.

RANGE: This race is confined to the coastal fringe of southern Turkey. It extends on the west as far as Antalya and on the east to Adana and probably as far as the Arsuz plain where Kizil Dağ (Mount Amanus) may form a barrier between this race and *P. g. palästinae.* The species has been seen a little farther north at Osmaniye (Danford, 1880, *Ibis 22:* 84); two American Museum specimens from Kara Suleiman, "Syria" (=Karasüleyman, Maraş, Turkey?), approach this form in darker-brown upperparts, broad shaft-streaks, short bill, and reduced black subterminal tail bar; the underparts, however, are very pale, as in *P. g. irakensis.*

REMARKS: This population, the darkest, brownest, and most heavily streaked of the species, is also the northernmost: Antalya is the farthest west that the species has been found in Asia Minor. The population, therefore, comprises the end points of east-west and south-north clines of increasing color saturation from India and Arabia. Another saturated brown population, *P. g. deltae,* occurs along the lower Nile and toward Suez. Southern Turkey is also the western end point of the populations which have narrow or indistinct subterminal tail bars. These range from the Brahmaputra westward across India, Pakistan, southern Afghanistan, southern Iran, southeast Arabia, Iraq, northern Syria (?) to south coastal Asia Minor.

This new race is named for Zubeyir Akyildiz who shared in my explorations of southern Turkey.

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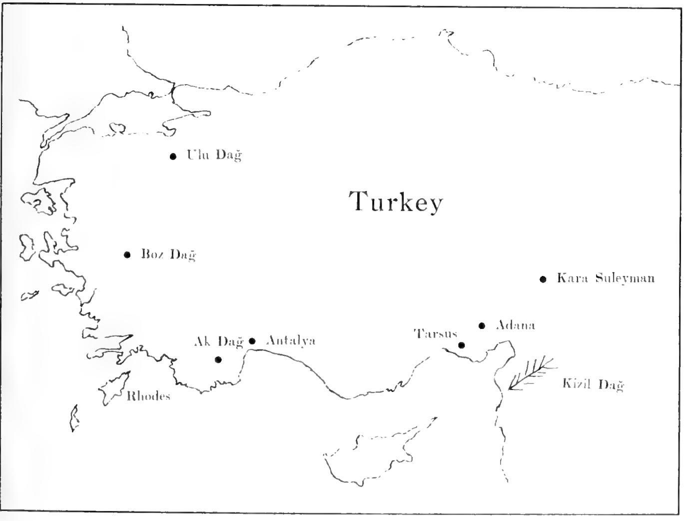
In studying the Asia Minor population of *Prinia gracilis*, I had the opportunity to examine some specimens from Arabia, including the type of *P. g. anguste* Ripley from Bahrein Island and part of the type series of *P. g. carpenteri* de Schauensee and Ripley from Oman. *P. g. anguste*, based on a single worn July specimen, is said to differ from *P. g. hufufae*, the population of the adjacent mainland, in being darker and more brownish-gray with narrower shaft-streaks. The only specimens of *P. g. hufufae* available to me are five freshly molted November birds of the Cox-Cheeseman type series in the American Museum of Natural History. I can find no character in the type of *P. g. anguste* compared with this series which I would not attribute to the birds being collected at different times of the year. Meinertzhagen (1954, *Birds of Arabia:* 219) states that a specimen he collected on Bahrein is identical with mainland birds.

P. g. carpenteri from Muscat, Oman, is a well-marked race. It differs sharply from *P. g. hufufae* to the north in its narrower and less distinct subterminal tail bars; from *P. g. yemenensis* to the west in its more distinctly cross-rayed tail and more finely pencilled head and back-streaking; and from *P. g. irakensis* from Iraq and southwestern Iran and *P. g. lepida* from southern Iran, Afghanistan, and northwestern India in its darker back coloration and more prominent subterminal tail bars. I cannot agree with Meinertzhagen (*ibid:* 220) and lump Oman specimens with *P. g. lepida.*

II

Erithacus rubecula

The Robin varies clinally and occasionally markedly over its continental Palearctic range. As shown by Lack (1946, 1947, *Bull. Brit. Orn. Cl. 66:* 55-65; *67:* 51-54; and 1951, *Ibis 93:* 629-30), there is a widespread north and central European form (*E. r. rubecula*) with olive-brown upperparts, brownish tail and upper tail coverts, and reddish-orange throat and breast. To the east, populations occur in Caucasia (*E. r. caucasicus*) and Iran (*E. r. hyrcanus*) with darker backs and breasts and with a strong rufous tinge to the sides of the tail and upper tail coverts. In the Urals there breeds a somewhat reddish-tailed, but strikingly pale gray-backed form (*E. r. tataricus*). In Spain and Italy Robins tend to be darker, approaching the north African form (*E. r. witherbyi*). An isolated slightly grayish-backed population (*E. r. atlas*) is found in northwest Morocco. On the other hand, a different clinal tendency starts in Yugoslavia. Extending through southern Greece and across Bulgaria to Asia Minor, Robins are markedly gray above and paler below, but even Turkish specimens have the brownish tail of the European populations.



Lack refrained from giving this southeast population a name but noted its existence, especially pronounced in Bulgaria, although he later (1951, *Ibis 93:* 629-630) believed that the grayishness was merely due to wear rather than valid geographic variation. Stresemann (1920, *Avifauna Macedonica:* 179-180) also noted gray spring specimens in Macedonia. Examples of the gray form have been found near Bursa in northwest Turkey by Mrs. Scott-Neuhauser (1948, *Senckenbergiana 28:* 177), but she collected what appears to be *E. r. caucasicus* in Rize. Koller (1948, *Senckenbergiana 28:* 177) collected a dark specimen ("*E. r. xanthothorax*" = *E. r. caucasicus* on passage towards the Aegean?) in Bolu.

The lack of a nomenclaturally recognized population breeding in Asia Minor has led to confusion about the identity and origin of the wintering populations of the Aegean (e.g. what to do with *E. r. xanthothorax*). The very marked gray character of Asia Minor birds and the reddish tail and upper tail coverts of Caucasian and other eastern populations makes them both equally separable from the brownish-backed and tailed European populations. The nomenclatural recognition of this Balkan gray cline will perhaps lead to more meaningful discussion of geographic variation in the eastern part of the species range and will certainly make the nomenclature better balanced, since all other clinal trends are named or overnamed. Therefore, the most extreme population of this gray cline is given the name:

Erithacus rubecula balcanicus subsp. nov.

TYPE: Adult ♂ (Y.P.M. No. 59198) collected on Boz Dağ, Odemis, Izmir in western Turkey at 4,200 feet on April 20, 1960, by George E. Watson.

DIAGNOSIS: Differs sharply from all other subspecies in its concolorous olive-gray back and rump, brownish flanks, pale-orange underparts, and grayish brown-edged rectrices. The grayish upper tail coverts are most diagnostic of this form. The population tends toward nominate *E. r. rubecula* in northern Yugoslavia and is grayest in north and west Asia Minor.

No difference from the nominate form in length of wing, tail, and culmen, or weight.

Measurements: Type, wing, 70; tail, 56; culmen, 15 mm; weight, 17.5 gr; 2 ♂♂ wing, 71, 71; tail, 59, 58; culmen, 14, 14.5 mm; weight, 18.3, 18.7 gr; 4 ♀♀ wing, 70, 68, 71.5, 71.5; tail, 56, 56, 56, 58; culmen, 15.2, 14.2, 13.8, 14 mm; weight, 22 (laying), 21.5 (laying), 17, 17.

The type series consists of seven specimens, one breeding male and two laying females from Boz Dağ (March 20, 21), and four wintering specimens from Antalya, south Turkey, and the Aegean islands of Icaria and Andros (February and March). In addition, nine breeding and wintering specimens were examined from Bosnia and Herzegovina.

Range: Breeds from northern Yugoslavia south through the Balkans to southernmost peninsular Greece (rare in the Peloponnesus) and across Bulgaria to northern and western but apparently not southern Asia Minor. At the eastern limits of its range in Asia Minor it may meet a reddish-tailed population of *E. r. caucasicus* probably near Samsun or Trabzond, but breeding specimens are lacking from this area. In the southern part of its range, breeding is confined to the mountains, both in conifer (*Abies*) and deciduous forests and open woods. In winter, individuals move to lower altitudes, and some birds may spread into the Aegean islands (Andros, Icaria) and to the south coast of Turkey (Antalya).

Remarks: It is possible that a discontinuity exists between the birds of southern Bulgaria and those of northwest Asia Minor. Nothing would be gained, however, in further separating the cline on this slight difference. In the Aegean islands and in the southern Balkan Peninsula *E. r. rubecula* is also found wintering. See below for a discussion of "*E. r. xanthothorax.*"

This Balkan cline probably results from the northwestward post-glacial expansion of an isolated forest population from the Mediterranean "pluvial" refuge into which the birds retreated during the Würm glacial advance.

I propose this new subspecies fully aware of the "tyranny of subspecific names" (Lack 1946, *Bull. Brit. Orn. Cl. 66:* 63) in the Robin. Partially following Dr. Lack's admonition, I have given this population the most appropriate geographic name available for the entire range.

* * * * * * *

Many authors have questioned the validity of *E. r. xanthothorax* Salvadori and Festa (1913, *Bull. Mus. Zool. Anat. Comp. Torino 28:* 15). This name is based on a series of five birds collected during February and March in Rhodes in the south Aegean. The characters cited in the description clearly mark the birds as belonging to a reddish-tailed southeastern form. Robins are common on Rhodes during the winter. Most had left but I located a few on March 30, 1959; following that date no more were seen. A Rhodian forest guard, who was well aware of the identity of the bird, told me that no Robins would be seen again until October. The type series in Turin is too old and dirty to distinguish much color definition, but on the basis of the type description and the following measurements (personally taken) including the type, the series belongs with the shorter-billed Caucasian birds, rather than with the Iranian form: 1 ♂ (type) wing, 72; tail, 51; culmen, 14.5 mm; 2 ♀ ♀ wing, 71, 70; tail, 53.5, 53.5; culmen, 15, 14.5 mm; 1 o wing, 69; tail, 53; culmen, 14.5 mm; I therefore endorse Vaurie's (1958, *Birds Pal. Fauna:* 376) decision in synonomizing the name *E. r. xanthothorax* with *E. r. caucasicus.*

III

Prunella modularis

A very dark gray population of Hedge Sparrow breeds in the fir forest up to the tree limit on Ulu Dağ above Bursa in northwest Turkey. The two males collected necessitated comparison with series from nearby breeding localities. This comparison revealed that the Asia Minor birds differ sharply from nearby Balkan and Caucasian and Iranian birds and further suggested that the Balkan population *P. m. meinertzhageni* Harrison and Pateff is merely the extremely dark end point on a continental cline of increasing grayness.

There are two well-marked groups of populations of Hedge Sparrows in southeast Europe and southwest Asia. The grayish nominate group *modularis*, with black back-spotting, breeds over most of Europe down to southern Bulgaria and northern Greece (Peus, 1957, *Mitt. Zool. Mus. Berlin 33:* 275). The browner *obscura* form, with brown back-spotting breeds in the Caucasus and northern Iran.

The Balkan population *meinertzhageni* is an extreme form of the *modularis* group. The gray of the underparts is darker and more extensive than in the nominate race; whitish flecking is reduced or absent. Above, the bird is a trifle grayer with larger darker spots. Most wintering Hedge Sparrows from the Aegean are separable into two categories. Most of those collected in the north, in Epirus and Macedonia and in the Asia Minor islands, belong to the *meinertzhageni* population, and most of those from the south and in the Cyclades are northern European *P. m. modularis.* Iranian and Caucasian birds differ from each other mainly in degree. Caucasian birds are darker and the gray of the underparts is more extensive.

On the other hand, the two breeding males from Ulu Dağ show some blending of characters but differ from both these forms in several characters and I therefore propose the name:

Prunella modularis euxina subsp. nov.

Type: Adult ♂ (Y.P.M. No. 59297) collected on Ulu Dağ (= Asiatic Mount Olympus of some authors), Bursa, northwest Turkey, April 29, 1960, by George E. Watson.

Diagnosis: Head light ashy-gray heavily streaked with brown; superciliary buffy-gray; back light reddish-brown with darker-brown spots; rump and upper tail coverts brownish-gray; underparts dark ashy-gray with white on the center of the abdomen, some of the lower breast feathers tipped with white, sides of upper breast washed with brown; flanks moderately streaked with the same brown as the back; under tail coverts gray-brown. In dorsal coloration, this form is closest to *P. m. obscura* in having brown not black spotting, but it differs from eastern birds mainly in its grayer and darker underparts and the lesser extent of white on the abdomen. It is even darker gray below than the darkest individuals of *P. m. modularis* from the Balkans. From both subspecies it differs in having gray, not brown rump and upper tail coverts and in having the flanks much less strongly marked with brown.

	P. m. modularis	*P. m. euxina*	*P. m. obscura*
Crown	gray with brown streaks	light ashy-gray with light-brown streaks	gray-brown with brown streaks
Superciliary	dark-gray	buffy-gray	gray-buff
Dorsal spotting	black	brown	brown
Rump and upper tail coverts	brown	gray	brown
Underparts	gray	dark-gray	light brownish-gray
Flanks	heavy brown streaks	restricted streaking	heavy brown streaks
Under tail coverts	dark brownish-gray	light-gray	brownish-gray

Measurements: Type and one other ♂ : wing, 69, 68.5; tail, 57, 56; culmen (from skull), 13, 14 mm; weight, 22, 21 gr.

Range: Mountainous fir forests of northern Asia Minor. Eastern limits of range unknown but probably meets *P. m. obscura* in Transcaucasia or Turkish Armenia. Probably somewhat migratory (wing length and formula same as other migratory populations) but winter range unknown.

Remarks: Although there is some introgression of characters of the eastern populations into this north Asia Minor population, the much darker-gray underparts and gray rump suggest that it is on a separate evolutionary line, one that has perhaps developed *in situ* in the thick fir forests of the rainy north coast. The fact that the Bursa population is also so sharply different in several characters from the Balkan form further suggests that this population is isolated from the

European birds as well. And in fact there are no high coniferous forests in European Turkey. The Ulu Dağ population therefore constitutes the end point of an Asia Minor cline running westward from the Caucasus.

In habitat the north Asia Minor population differs somewhat from northern and especially western European birds. It is found confined to the fir forest and tree line scrub in Turkey, but the same species is a bird of deciduous gardens and hedgerows in western Europe, and also open conifer woods in north central Europe. Northern birds wintering in the Aegean are usually to be found in lowland macchia or open woods undergrowth.

A single female collected March 7, 1960, above Tarsus in the foothills of the Cilician Taurus Mountains is clearly a wintering example of the nominate race from northern Europe. It is impossible to separate from the paler winter specimens from the Aegean. Danforth also collected winter *P. m. modularis* in the Taurus in 1879 (*Cat. Birds Brit. Mus. 7:* 652). Apparently, only light-colored migrants with white-flecked breasts were collected in northern Asia Minor by Kummerlöwe and Niethammer (1935, *Journ. f. Orn. 83:* 40), Rössner (1934: *Akad. Wiss. Wien math-natur. Klasse Sitz.* 1944: 307), and Mrs. Scott-Neuhauser (1948, *Senckenbergiana 28:* 178), although the first pair of collectors undoubtedly earlier observed breeding birds. The new subspecific name is derived from the classical epithet for the present-day Black Sea which marks the northern limit of this population.

IV

Montifringilla nivalis

Three well-marked groups of populations of Snow Finch occur in the Palearctic. The *nivalis* group of southern Europe has brown upperparts and a gray head; the variable *alpicola* group of central Asia has a brown head and back; and the *henrici* group of Tibet is uniform brown above but washed with gray-brown below. Nine specimens from south Asia Minor belong to the *alpicola* group, in which there are four fairly well-marked races. *M. n. alpicola* has an extensive range from the Caucasian Mountains south into Turkish Armenia, where the exact western limits of the range are unknown, and eastward across northern Iran towards Afghanistan and into the Tian Shan range. In southern Iran, in the Zagros, a markedly paler race *M. n. gaddi* occurs; in Mongolia another pale race *M. n. groum-grzimaili* is found. These three races are long-billed. A very pale-sandy and short-billed race *M. n. kwenlunensis* occurs in the Kun Lun and Astin Tagh ranges. The south Asia Minor population, which is isolated from these four populations, differs in being lighter in color and showing characters which approach the European *nivalis* group. For this isolated southern population I propose the name:

Montifringilla nivalis fahrettini subsp. nov.

Type: Adult ♂ (Y.P.M. No. 59445) collected at 6,400 feet on Ak Dağ, Kaş, Antalya, southern Turkey on March 25, 1960, by George E. Watson.

Diagnosis: Closest to *M. n. gaddi* but much paler and grayer on the back, less reddish-tan and with a pronounced grayish tinge on the crown, whereas Zagros birds have the head essentially the same color as the back. Wing and bill in the spring adult much shorter than in the Zagros population at the same season. Differs from *M. n. alpicola* in its markedly lighter and less brown upperparts and in having a shorter bill and wing. Differs from *M. n. nivalis* in much lighter upperparts, less distinctly gray head, shorter wing, and lighter weight.

Measurements: Type, wing, 112; tail, 68; bill from skull, 14.5 mm; weight, 33 gr, 4 ♂ ♂ wing, 111, 117, 115, 115, (mean of 5: 114); tail, 68, 71, 69, 70 (69); bill, 13.5, 14, 14.5, 14.1 (14.1); weight, 31, 33, 34, 35.5 (33.3); 4 ♀ ♀ wing, 110, 111, 116, 106, (111.3); tail, 65, 62, 73, 64 (66); bill, 14, 14.5, 14, 14 (14.1); weight, 32.5, 32.5, 33, 28.5 (31.6).

M. n. nivalis (Greece), 4 ♂ ♂ wing, 116-120 (119); tail, 67-72 (69.5); bill, 13.5-14 (13.6); weight, 37-40 (38.1); 1 ♀ wing, 116; tail, 64; bill, 13.5 mm; weight, 37 gr.

M. n. alpicola, 10 ♂♂ wing, 117-112 (118.9); 7 ♂♂ tail, 66-71 (68.9); 10 ♂♂ bill, 16-17.5 (16.4); 4 ♀♀ wing, 110-115 (112); 3 ♀♀ tail, 62, 66, 72 (66); 4 ♀♀ bill, 15-16.5 (15.88).

M. n. gaddi, 19 ♂♂ wing, 116-126 (119.3); 18 ♂♂ tail, 68-76 (71.5); 18 ♂♂ bill, 15-17.5 (16.2); 4 ♀♀ wing, 112-116 (114.3); 5 ♀♀ tail, 65-71 (68.5); 5 ♀♀ bill, 15-16 (15.6). Measurements of *M. n. alpicola* and *M. n. gaddi* are taken from Vaurie (1949, *Amer. Mus. Novitates 1406:* 29).

Summer collected specimens of this species tend to have shorter and more worn bills than winter birds (Stegmann 1932, *Journ. f. Orn. 80:* 99). This is perhaps related to a change in diet from insects picked off snow to seeds picked and scratched from bare rocky soil. It should be pointed out, however, that late March *M. n. fahrettini* were compared with late March *M. n. gaddi*. The bills were found to be markedly longer and more attenuated in the Zagros birds. A young January specimen from the north Zagros does have a short bill, but not as short as that of the longest-billed Asia Minor bird. Furthermore, Vaurie's measurements were taken on birds collected at all times of the year, including January and February as well as spring and summer. His shortest measurements for *M. n. gaddi* and *M. n. alpicola* do not overlap at all the longest measurements of the Asia Minor population. Taking the bill measurements of five examples of each of the four populations (data from Vaurie *ibid.: 28*) and of the two populations *M. n. gaddi* and *M. n. fahrettini* and comparing them gives the following variance ratio table:

	df	ss	ms	VR
Between				
4 groups	3	25.8	8.6	21.5
2 groups	1	7.9	7.9	46.6
Within				
4 groups	16	6.5	.4	
2 groups	8	1.4	.17	
Total				
4 groups	19	2.27		
2 groups	9	9.3		

Had all the measurements available for *M. n. alpicola* and *M. n. gaddi* populations been taken during the same season, the statistical results would have been even more striking.

The type series consists of nine birds collected on March 25 and 29 at from 6,000 to 7,300 feet on Ak, Kohu, and Mancarli Dağlari near Elmali, Antalya, in south Turkey. The gonads were little enlarged and the birds were still feeding in flocks.

Range: Occurs on the highest mountain tops in the Bey and Taurus mountain ranges of south Turkey and probably on Mounts Lebanon and Hermon; resident but descending to about 6,000 feet in winter.

Remarks: The only other record of this species from south Turkey is that of Danford (1878, *Ibis 20:* 23) who included the species in his list "with some hesitation" on the basis of a sight record on Anaş Dağ in the Taurus north of Adana. Snow Finches were observed by Tristam (1868, *Ibis 10:* 208) on the peaks of Mounts Lebanon and Hermon. I failed to find the species on Boz Dağ, Izmir (*ca.* 7,100 feet), or Ulu Dağ (Bursa 8,343 feet) in mid- and late April. It is doubtful whether there are any other mountains in western and northwestern Asia Minor high enough to support breeding populations of Snow Finches, so that *M. n. fahrettini* is separated from the European populations of the species. On the other hand, it may well occur through the anti-Taurus and in Kurdestan and therefore be continuous with the Iranian populations, but it has not yet been found in southeastern Turkey or northern Iraq.

Five adult and two juvenal specimens of Snow Finch, *M. n. nivalis*, from Greece constitute only the second record of this species from that country verified by specimens. Reisor (1895, *Ornis Bal. 3:* 23) found the bird on Vardusia, Makatsch (1950, *Die Vögelvelt Macedoniens:* 117) probably saw the bird on Olympus, and Flach (*in litt.*) recorded Snow Finches on Parnassos. The specimens are from Vardusia and Parnassos. The species was not found on any of the Peloponnesian mountain tops in spite of repeated searches.

In their distribution the populations of Snow Finches show the type of disjunction common to glacial relicts. It is possible that when the climate of the Eastern Mediterranean was more rigorous during the retreat of the Würm glaciation, many of the mountains throughout the Aegean basin may have harbored populations of these Snow Finches. As the climate grew warmer and the snow disappeared from all but the highest peaks, extensive suitable habitats disappeared and the disjunct distribution of today came about. The south Turkey population, which shares the tendency toward a grayish head and a short bill with the European population, is evidence that such must have been the past history of the species in the eastern Mediterranean.

The new subspecies is named for Fahrettin Özgecil of the Turkish Forest Department, who accompanied me on my travels in the western sector of his country.

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Postilla

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THE SKULL OF *SCIURAVUS NITIDUS*, A MIDDLE EOCENE RODENT

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Primitive rodents of the family Sciuravidae are known primarily from the Eocene of western North America, with the genus *Sciuravus* itself ranging from late early Eocene (Gazin, in press) through the late Eocene (Wilson, 1949b, pp. 81-82). The type specimen of *Sciuravus nitidus* Marsh, 1871, the type species, is an incomplete maxilla with M^{1-3} from the middle Eocene Bridger formation of Wyoming. The type specimen is from the lower Bridger, but specimens referred to *S. nitidus* occur throughout the Bridger formation (Wilson, 1938, pp. 130-132). The skull of *S. nitidus* was described briefly by Matthew (1910, pp. 59-60). More recent collections from the Bridger have yielded more complete specimens of this species than were available to Matthew. These specimens allow an amplified description to be made of the skull of *S. nitidus*, the only Bridger sciuravid whose essentially complete skull is known.

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Sciuravus nitidus; to Drs. J. T. Gregory and E. L. Simons for access to the collections and for facilities for study in the Yale Peabody Museum (Y.P.M.); to Drs. C. C. Black of the Carnegie Museum (C.M.) and M. C. McKenna of the American Museum of Natural History (A.M.N.H.) for the loan of specimens. Plates I, III, IV, and V, figure 1 are prepared from photographs furnished by courtesy of the Smithsonian Institution, and plate V, figure 2 is from a photograph by J. Howard, Yale Peabody Museum. This study, supported by National Science Foundation Grant G14254, was completed while the author was a Research Associate of the Division of Vertebrate Paleontology, Yale Peabody Museum.

DESCRIPTION

The following description of the skull and lower jaw of *Sciuravus nitidus* is based in large part on U.S.N.M. No. 22477, a nearly complete skull with associated lower jaw and postcranial fragments from near Millersville, Wyoming. The specimen was collected by C. L. Gazin and F. L. Pearce in 1946. The skull is distorted by some anteroposterior compression and the left side is pushed forward relative to the right. Tooth wear indicates that the individual was adult. Other specimens used are: U.S.N.M. No. 18100, partial skull and jaws of a young individual having dP^4; A.M.N.H. No. 12551, skull flattened dorsoventrally and jaws figured by Matthew (1910, figs. 13-15); A.M.N.H. Nos. 12531 and 13101, partial skulls. Less complete specimens include Y.P.M. No. 13458, C.M. No. 9683, U.S.N.M. Nos. 17697 and 17700. All specimens are from the lower Bridger.

Skull. The overall appearance of the skull is that of a rather generalized, primitive rodent. Postmortem distortion of the specimens prevents an entirely clear picture of the skull shape. Thus, the doming of the parietals in U.S.N.M. No. 22477 is due at least in part to anteroposterior compression, A.M.N.H. No. 12551 is flattened dorsoventrally, U.S.N.M. No. 18100 and A.M.N.H. No. 13101 are compressed transversely.

Viewed dorsally (pl. I) the skull widens from the anterior tips of the nasals to the anterior zygomatic roots, has its greatest width across the zygomatic arches, which essentially parallel one another, and is narrower posterior to the arches. The nasals are slightly convex dorsally, especially anterodorsally, and extend farther forward than the anterior surface of the incisors. The nasals terminate posteriorly about on a line with the anterior orbital border. The frontals exhibit a distinct interorbital constriction, anterior to which there is a protrusion on each side possibly similar to the "rudiments of processes" in *Pseudocylindrodon* (Burke, 1938, p. 260). The protrusion is less in evidence in A.M.N.H. No. 12551 and U.S.N.M. No. 18100 than in U.S.N.M. No. 22477. The large interparietal, shown in Nos. 12551 and 18100, has a convex anterior margin and widens posteriorly. Lateral to it the parietal extends to the occipital bone. There is no sagittal crest. The squamosal is incomplete in all specimens but seems to have had a narrow dorsal exposure. The occipital bone extends onto the dorsal skull surface for a very short distance, and the nuchal crest on that bone forms the posterodorsal margin of the skull.

Maxillary, jugal, and squamosal components form the zygoma. The jugal contacts the maxilla and lacrimal anteriorly, tapers posteriorly, and terminates bluntly below the posterior edge of the zygomatic process of the squamosal.

The anterior surface of the anterior zygomatic root is essentially vertical and is in a line anterior to P^3 (pls. III, IV). The root is farther forward relative to the cheek teeth than in *Paramys delicatus* (Matthew, 1910, fig. 2). The rounded infraorbital foramen, which is situated in the maxilla medial to the anterior zygomatic root, is relatively a little larger than in *Aplodontia*. From a ventromedial knob of bone on the anterior root a ridge passes laterad, curves backward and upward onto the lateral surface of the jugal, and continues toward the posterior end of that bone, diminishing posteriorly. As preserved in U.S.N.M. No. 22477, the outer surface of the zygoma faces laterally above and ventrolaterally below the ridge. The origin of the masseter muscle seems to be limited to the zygoma, the "primitive sciuromorph" or "protrogomorph" condition. There is no indication that any of the masseter muscle originated on the rostrum anterior to the anterior zygomatic root. The ridge on the zygoma probably marks the dorsal edge of the origin of the masseter lateralis muscle. That the anterior part of the masseter may have been strengthened is suggested by the ventromedial knob and the ridge, which is more distinct anteriorly.

The orbit is moderately good-sized, about comparable in proportions to that in *Cavia* but relatively smaller than in *Cynomys*. The lacrimal bone forms part of the anteromedial orbital border. The surface of this bone is lightly pitted where it extends onto the face anterior to the orbit. The most complete orbital wall occurs in U.S.N.M. No. 18100, although cracking obscures details. The frontal forms most of the anteromedial orbital wall. Near the dorsal rim of the orbit and posterior to the supraorbital protrusion is a small foramen. The sphenopalatine foramen (terminology of foramina follows Hill, 1935) is ventromedian in the orbit, approximately in line with M^2, and is bounded anteriorly, dorsally, and ventrally by the maxilla. Boundaries of the palatine bone are not clear, and either this bone or the maxilla borders the sphenopalatine foramen posteriorly. Several foramina are present in the maxilla posterolateral to the sphenopalatine foramen. A plate of bone posterior to the maxilla and frontal in the orbit seems to be the orbitosphenoid. More posteriorly, in a line behind M^3, the posteromedial orbital wall is depressed and overhung by more dorsal parts. A dorsoventrally elongated slit in the depression may be the sphenoidal fissure. The alisphenoid borders the slit posterolaterally. Anterodorsal to the slit and partly separated from it by a bony bar is a rounded gap. It is suggested tentatively that the optic foramen may be in the gap. Parietal and squamosal form part of the posterior wall of the orbit.

On the palate (pls. II, III) the elongate incisive foramina are separated from one another by a median septum and are within the premaxilla except posteriorly, where they are bounded by the maxilla. A slight concavity of the maxilla occurs anterior to P^3. The two rows of teeth essentially parallel one another. Between them the palate is nearly flat.

The palatine extends forward about to a line with the anterior or middle of M^1, where the jagged maxilla-palatine suture crosses the palate transversely. The foramen for the palatine artery is present approximately in line with the anterior half of M^2. The posterior margin of the palate, about opposite the middle of M^3, has a posteriorly directed median projection, on each side of which a small flange of bone projects anteroventrally below the palatal surface.

The region of the pterygoid plates is incompletely preserved in all specimens but can be reconstructed in part. A ridge extends posterad from behind M^3, becomes thicker, and leads into entopterygoid and ectopterygoid plates. A shallow pterygoid fossa is enclosed by the plates. The specimens suggest that the entopterygoid plate lacked a contact with the bulla, but the ectopterygoid plate continues posteriorly and contacts the lateral side of the bulla. In *Paramys delicatus* (Matthew, 1910, fig. 2) the ectopterygoid plate is absent, and the pterygoid fossa is less distinct than in *S. nitidus.* A small foramen between the plates in A.M.N.H. No. 12551 may represent the posterior opening of the sphenopterygoid canal. Posterolateral to this foramen is a second foramen, probably the foramen ovale. The ectopterygoid plate forms a bridge across this foramen, which resembles the foramen ovale in *Paradjidaumo* (Wilson, 1949a, pp. 38-39 and fig. 1C) and in *Cynomys.* The position of another foramen is indicated by a notch in the basisphenoid at the anteromedial edge of the tympanic bulla.

The tympanic bulla in *Sciuravus nitidus* is ossified but seems to have been loosely attached. Out of seven otic regions, in U.S.N.M. Nos. 22477 and 18100 and A.M.N.H. Nos. 12531 and 12551, the bulla is in place in two cases, on one side in Nos. 22477 and 12531. A suture seems to be traceable between bulla and periotic, and where the bulla is missing there is no clear broken area on the periotic. The rounded bulla is not dissimilar in general appearance to that in *Neotoma.* The bulla has a large opening but lacks an elongated bony meatus. The anterodorsal lip of the opening is thickened. The bulla in A.M.N.H. No. 12531 may have been incomplete dorsally, and a process of the squamosal curves down over this possibly incomplete closure. Viewed ventrally, the bulla has a short anteromedial protrusion. The bulla does not completely cover the petrosal, which is exposed medial to the bulla. A somewhat similar exposure of the petrosal has been reported in *Paradjidaumo* (Wilson, 1949a, p. 39). Where absence of the bulla exposes the periotic, the auditory prominence appears as a distinct, raised structure. The fenestra vestibuli faces dorsolaterally and the fenestra cochleae posterolaterally. The mastoid process is short and blunt, and the stylomastoid foramen seems to be represented by a notch medioventral to the process.

Between the bullae the basioccipital exhibits a distinct longitudinal ridge. The elongate jugular foramen is between basioccipital and periotic, posteromedial to the bulla. The hypoglossal foramen pierces the condyle posterior and medial to the jugular foramen.

The occipital surface (pl. V, fig. 1) is convex dorsally. The nuchal crest leads into two ridges, one on the lateral surface of the mastoid and the other along the mastoid-exoccipital contact. The mastoid is exposed on the occipital surface near the dorsal part of the latter ridge. The short paroccipital process does not contact the bulla.

Lower jaw. On the lateral surface of the horizontal ramus (pl. IV) a large mental foramen is present about in line with the anterior wall of P_4. A smaller foramen or foramina occur slightly farther posteriorly. The masseteric fossa is bounded by dorsal and ventral ridges that meet in a line approximately between M_1 and M_2. The masseteric fossa in *Paramys delicatus* does not extend so far anteriorly (Matthew, 1910, fig. 1). The nearly complete lower jaw of C.M. No. 9683 shows that the coronoid process rises steeply and hooks backward toward the lower condyloid process. The lateral surface of the coronoid process is slightly concave for the insertion of the temporalis muscle. On the medial surface of the jaw (pl. V, fig. 2) a ridge extends posterodorsad from the posterior end of the row of cheek teeth toward the condyle. The dental foramen is in the dorsal side of the ridge, approximately in a line below the posterior edge of the coronoid process. Ventral to the ridge is the concavity for insertion of the internal pterygoid muscle; unfortunately, the area for pterygoid insertion is not completely preserved in any of the specimens. A slight concavity dorsal to the ridge on the condyloid process probably marks the insertion of the external pterygoid muscle.

Measurements (in millimeters) of U.S.N.M. No. 22477:

Greatest length of skull	39.4
Anterior width across zygomatic arches	21.5
Posterior width across zygomatic arches	22.2
Height occiput	12.8
Length diastema, posterior of I to P^3	8.1
Length right P^3-M^3	9.6
Length left P_4-M_3	9.5
Outside depth of lower jaw at M_1	6.2

DISCUSSION

Sciuravids have been suggested, mostly on the basis of dental characters, as possible ancestors for various later rodent groups including muroids and geomyoids (Wilson, 1949a, p. 47, 1949b, pp. 97-98; Wood, 1959, p. 358). As described here the skull of *Sciuravus nitidus* does not seem to add much in the way of positive evidence on relationships. Primitive features include the large jugal, zygomasseteric structure, seemingly shallow pterygoid fossa, ossified but loosely attached bulla, short paroccipital processes. The incomplete medial covering of the petrosal by the bulla may also be primitive, a feature that *S. nitidus* shares with *Paradjidaumo*, an eomyid. The masseter muscles may have been somewhat better developed for gnawing than in some contemporary paramyids, such as *Paramys delicatus*. This is suggested by the more anterior position of the anterior zygomatic root and of the mandibular masseteric fossa, and by the distinct anterior knob and ridge on the zygoma. A more distinct pterygoid fossa than in *P. delicatus* suggests some strengthening of the pterygoid muscles as well. The zygomasseteric structure is still, however, that of a primitive sciuromorph. Whether the indications of muscle strengthening show that the sciuravids were experimenting along lines leading toward more advanced zygomasseteric conditions remains a matter of speculation. At any rate, the skull of *S. nitidus* seems to lack any specializations countering the suggestions that sciuravids gave rise to some of the advanced rodent groups.

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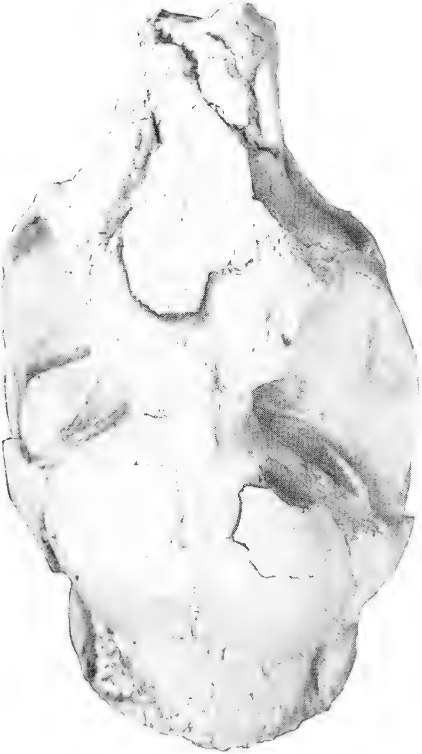

Plate I

Dorsal view of skull of *Sciuravus nitidus*, U.S.N.M. No. 22477, approx. x 3.

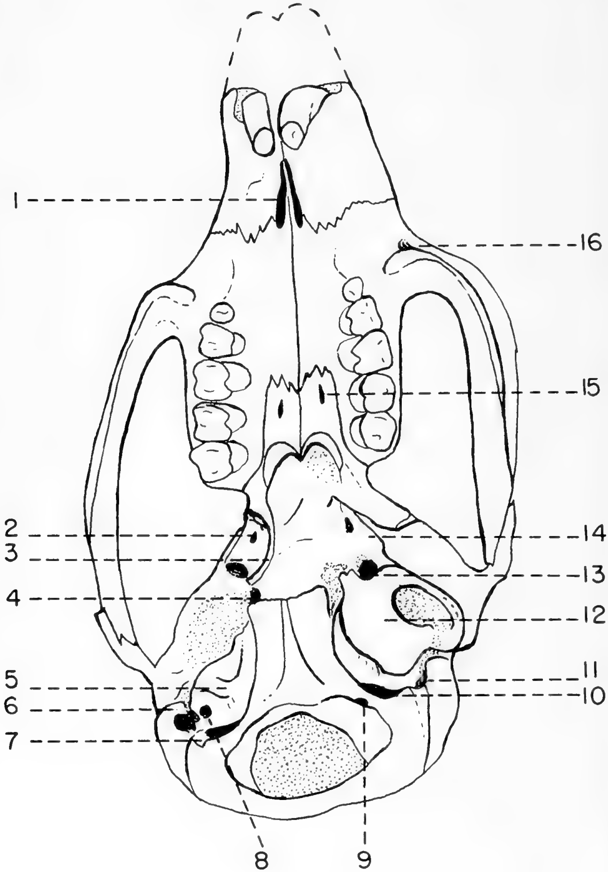

Plate II

Ventral view of skull of *Sciuravus nitidus,* approx. x 3. Based on U.S.N.M. No. 22477; restored in part from A.M.N.H. Nos. 12551 and 12531. 1, incisive foramen; 2, sphenopterygoid foramen; 3, entopterygoid plate; 4, foramen in basisphenoid; 5, auditory prominence; 6, mastoid process; 7, paroccipital process; 8, fenestra cochleae; 9, hypoglossal foramen; 10, jugular foramen; 11, stylomastoid foramen; 12, tympanic bulla; 13, foramen ovale; 14, ectopterygoid plate; 15, foramen for palatine artery; 16, infraorbital foramen.

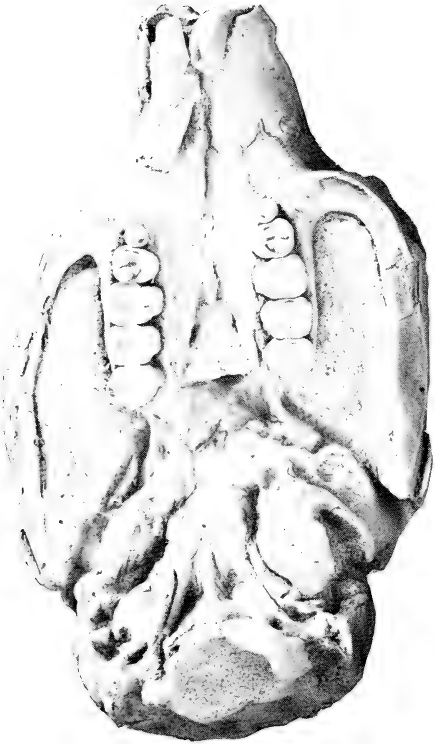

Plate III

Ventral view of skull of *Sciuravus nitidus*, U.S.N.M. No. 22477, approx. x 3.

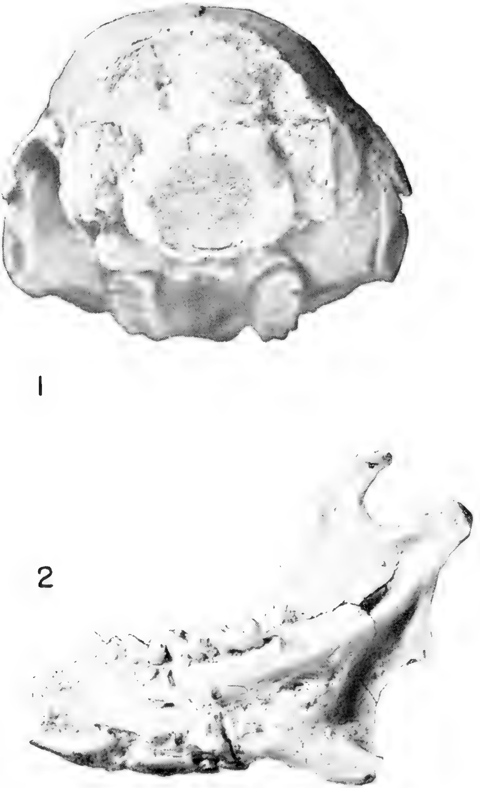

Plate IV

Lateral view of skull and lower jaw of *Sciuravus nitidus,* U.S.N.M. No. 22477, approx. x 3.

Plate V

Sciuravus nitidus, approx. x 3. Figure 1. Occipital view of skull, U.S.N.M. No. 22477. Figure 2. Medial view of right lower jaw, C.M. No. 9683.

Postilla

YALE PEABODY MUSEUM

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THE DENTITION OF *OURAYIA*: —ITS BEARING ON RELATIONSHIPS OF OMOMYID PROSIMIANS

ELWYN L. SIMONS

Gazin (1958) has established for the North American anaptomorph, or so-called "tarsioid" prosimian Primates two families: the Anaptomorphidae, containing seven early and middle Eocene genera; and the Omomyidae, to which eleven Eocene and one early Oligocene genera are assigned by him. It has long been recognized that members of these two families differ distinctly from the more clearly lemur-like North American prosimians of the subfamily Notharctidae, which has been suggested, originally by Leidy (1873:90) and more recently by W. K. Gregory (1921:220), as being plausibly the group from which the South American platyrrhine Primates arose. Recently, however, the candidacy of *Notharctus* and its allies for such an ancestral position has been increasingly questioned. This is because, although generalized in many ways, notharctids already show a number of features that are unlike Platyrrhini. The greater expression of the hypocone and mesostyle, together with a tendency toward doubling of the outer cusp of the fourth upper premolar — all non-platyrrhine features, but seen in the successively later species of *Notharctus*—indicate a dental pattern that was diverging from, and not approximating that which typifies the Platyrrhini. Moreover, both *Notharctus* and *Smilodectes* exhibit upper third molars that, relative to the other cheek teeth, are much larger and more complex than those of the earliest known notharctine, *Pelycodus*, as well as of those of Oligocene-Recent South American Monkeys.

Some current students regard omomyid prosimians as alternative, or better, candidates for the ancestry of Ceboidea; for instance, see Gazin (1958:100). This idea appears to have had its origin in comments by J. L. Wortman (1904:242) in his imaginative but often overlooked studies on Eocene Primates at the Yale Peabody Museum. Probably the main reason the case for a possible ancestor-descendant relationship between omomyids and ceboids has not previously been considered in detail is that no really complete dentitions of members of this prosimian family have been described. Without better knowledge of the anterior dentition most of those acquainted with the problem appear to have hesitated in expressing opinions as to the phyletic relationships of this group. The completeness of the dentition in one omomyid, a specimen of *Ourayia uintensis*, described below, largely obviates this difficulty.

ACKNOWLEDGMENTS

The writer is greatly indebted to Dr. Glenn L. Jepsen of the Department of Geology, Princeton University, who generously made available for study and description here the unequalled specimens of *Ourayia* in his charge collected for Princeton by J. B. Hatcher, O. A. Peterson [both formerly associated with the Yale Peabody Museum], and by later field expeditions of Princeton University. Thanks are also due Dr. M. C. McKenna of the American Museum of Natural History for making available for study the type specimen of *Ourayia uintensis* (Osborn) and to Dr. C. L. Gazin of the U.S. National Museum for kindly discussing with me some problems relating to the Omomyidae. Figures were prepared by Margaret E. Freeman of New Haven and the early completion of this paper was facilitated by a grant from the Wenner-Gren Foundation for Anthropological Research of New York.

ABBREVIATIONS

A.M.N.H.	American Museum of Natural History, New York.
C.M.	Carnegie Museum, Pittsburgh.
P.U.	Princeton University, Princeton
Y.P.M.	Yale Peabody Museum, New Haven

DESCRIPTION AND RELATIONSHIPS OF OURAYIA

The single species of this genus, *Ourayia uintensis*, is apparently retricted to Uinta (B) horizon of the late Eocene. It was originally described by Osborn (1895:77) as a species of *Microsyops*. Later, Osborn recognized that the assignment of this species to *Microsyops* was in error, remarking (1902:202): "Its nearer reference is either to the Anaptomorphidae or to some member of the Notharctidae." A further, but incomplete, step in the direction of a more correct taxonomic assignment for this prosimian species was made by Wortman (1904:232) who referred it to the genus *Omomys*. However, it remained for Gazin (1958:70) to recognize that this species belongs to a distinct omomyid genus for which he coined the name *Ourayia*, after the village of Ouray to the north of the "White River pocket," Utah, from which it seems most, if not all, known specimens of this species have been recovered. Gazin (1958) noted that this genus is close to later Eocene omomyids such as *Washakius*, *Hemiacodon*, and *Stockia* and pointed out that the species differs greatly from any assigned to *Notharctus* which it resembles only in its comparatively large size. The specimens from the Princeton collections, described here, are much more complete than the American Museum materials available to Gazin and further serve to emphasize the distinctness of the dentition of *Ourayia* from that of any notharctid. In view of the completeness of the specimen P.U. 16431 it is now possible to define much more adequately the structure and relationships of this primitive prosimian.

Order **PRIMATES** Linnaeus 1758

Suborder PROSIMII Illiger 1811

? Infraorder LEMURIFORMES Gregory 1915

Family Omomyidae Gazin 1958

Subfamily Omomyinae Wortman 1904

OURAYIA Gazin, 1958

Type species: *Ourayia uintensis* (Osborn), 1895.

Included species: *Ourayia uintensis.*

Distribution: Late Eocene, Uintan stage; White River pocket, Uinta Basin, Uintah County, Utah.

Generic distinctions: In addition too having lower and more anteroposteriorly elongated trigonids and comparatively larger talonid basins than in *Hemiacodon,* as mentioned by Gazin (1958-71) for *Ourayia,* the hypoconid is less anteroposteriorly conpressed than in *Hemiacodon* and does not project as far laterally from the main body of M_1 as it does in *Stockia* and *Hemiacodon.* M_{1-2} hypoconulids are not distinctly set off as in *Hemiacodon* and *Washakius.* Resembles *Hemiacodon* and differs from *Washakius* in lacking molar metastylids. In *Ourayia* the apices of molar paraconids are situated somewhat more internally than in *Stockia* and M_3 hypoconulids are comparatively smaller than in *Hemiacodon* and *Washakius.* Second and third molars above and below are larger compared to first molars than in *Washakius* and *Hemiacodon. Ourayia* agrees with species of these two genera in having crenulate tooth surfaces, but unlike *Washakius* has only a single metaconule. Differs from *Hemiacodon* in having a much less sharply broken crest between para- and metacones and no appreciable development of P^4 parastylar cuspule. Anterolingual cingular region of M^{1-2} shows a pericone variably present as is the case also in *Hemiacodon* and *Omomys* among omomyids and in the living platyrrhine *Samiri sciurea.*

Discussion: One difference between *Ourayia* and *Hemiacodon,* noted by Gazin (1958:71), that the M_2 paraconid of the former is nearly obscured in the anterior trigonid crest, is now seen to be a feature of the type specimen alone. The M_2 paraconid on both sides in P.U. 11236 and P.U. 16431 shows distinctly. This difference, together with slightly smaller size and less oval M_2 outline in the latter two specimens might suggest a species distinction for the Princeton materials were they not from the same horizon and area as the type. Gazin pointed out that the lower dentition of this primate does not resemble *Notharctus.* This conclusion is amply confirmed in the upper dentition of *Ourayia* where, apart from basic differences in cheek tooth crown patterns, the upper incisors are seen to be comparatively huge and the canine much reduced. These features, together with the loss of $P\frac{1}{1}$, are in marked contrast to the situation in notharctines which have small upper incisors and long canines. The difference here is of the same order of magnitude as that separating Malagasy lemur from loris dental patterns and amply justifies reference of *Ourayia* and *Notharctus* to different families.

As regards the phyletic position of *Ourayia* among omomyids I suspect that the genus may have been derived directly from *Hemiacodon*, particularly since the M_2 paraconid is not as unlike that of *Hemiacodon* as was supposed from the type specimen alone.

Possible relationships with the early Oligocene *Macrotarsius montanus* are less certain, but direct derivation of this species from *Ourayia* is not out of the question. Crenulations of the enamel resembling those of both *Hemiacodon* and *Ourayia*, although less pronounced, are evident in the talonid basins of the Oligocene form. Paraconids are situated slightly more laterally than in species of the latter two genera, but this difference need not rule out a close relationship between them and *Macrotarsius*. Present knowledge of the relative size, number and positioning of the anterior lower teeth in several omomyid genera, *Omomys*, *Washakius*, *Chlororhysis*, *Hemiacodon*, and *Ourayia* strongly suggests that Clark (1941:562) was correct in interpreting the lower dental formula in this Oligocene omomyid as 2.1.3.3, the typical formula for the group. If P_1 is lost and P_2 single-rooted as in other Omomyidae, then the small anteriormost remaining tooth in *Macrotarsius* must be the base of a reduced canine (see fig. 1). This canine, however, is not less prominent than in any other omomyid as Clark suggested, although the lateral incisors do appear to reach an extreme of reduction, judging from the alveolus. In *Ourayia*, moreover, the lower incisors are more procumbent. To the extent that the species of *Hemiacodon*, *Ourayia*, and *Macrotarsius* are in, or close to, a single progressing phylum, the suggested trends, apart from size increase, were toward deepening and shortening of the ramus mandibuli, together with a size reduction and more vertical implacement of the lower incisors. Perhaps the latter changes are to be correlated with increasing use of the hands in feeding and with facial foreshortening.

OURAYIA UINTENSIS (Osborn), 1895

Figures 1, 2, 3.

Microsyops uintensis Osborn 1895, Bull. Amer. Mus. Nat. Hist. No. 7, pp. 77, fig. 1.

Omomys uintensis Wortman 1904, Amer. Jour. Sci. 4th Ser., Vol. 17, pp. 134, 135.

Ourayia uintensis Gazin, 1958, Smithsonian Misc. Coll. Vol. 136, No. 1, pp. 70-72, pl. 13, fig. 8.

Type of genotypic species: A.M.N.H. No. 1899; left mandibular ramus with P_3-M_2.

Type locality: Late Eocene, Uinta (B), White River, Utah.

Hyopdigm: Type and A.M.N.H. 1900, mandibular fragment with right M_1; P.U. 11236, left and right mandibular rami with left P_3-M_3 (lacking trigonid of M_2, alveoli of P_2; right P_4-M_3 (trigon of M_1 missing), alveoli of I_2-P_3; P.U. 11288, edentulous right mandibular ramus; P.U. 16431, maxillae with upper dentition excepting left P^2, mandibular fragments with left I_1, P_{3-4}, damaged M_1, M_2-M_3; right I_1, damaged P_3, M_1-M_2, trigonid of M_3.

Horizon and locality: Lower Uinta [B], upper Eocene, White River Pocket, Utah. P.U. 16413, Section 2, T. 9 S., R. 20 E. Uintah County, Utah; P.U. 11236, 11288 Uinta [B], Kennedy's Hole, White River, Utah.

Specific diagnosis and description:[1] A moderate sized prosimian; comparable parts approximately within the size range of the living *Perodicticus potto*. Dental formula $\frac{2.1.3.3}{2.1.3.3}$; I_2 spatulate, and somewhat procumbent, posteriorly with median vertical ridge and basal cingulum rising internally halfway toward crown; I_3 smaller than I_2 (alveolus); $\overline{C}$ probably smaller than I_2 (root), no diastema; P_2 single-rooted; P_3 with internal cingulum lacking on P_4; P_{3-4} of equal height, paraconid, metaconid, and external cingulum present in P_4, -lacking in P_3, heel of P_{3-4} with single cusp situated laterally. Surfaces of cheek teeth, particularly, bearing wrinkled or crenulate patterns. M_2 slightly larger and more oval in outline than M_1. Molar paraconids distinct (except in M_2 of type), situated only slightly less laterally than metaconids and connected with protoconids by an arcuate crest. Hypoconulids not sharply set off on M_{1-2}. M_3 hypoconulid not as

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[1] I fail to grasp fully the logic behind the increasingly popular practice of neglecting to distinguish between generic and specific diagnoses in treatments of monospecific genera. Generic characters, in this case, are those features which prevent reference of such species to other genera; the specific, those attributes which, combined, characterize a given, and no other, species. The two suites of features are not indistinguishable, although I suspect that the failure to see that they are not may be one prime contributor to the production of unnecessary or invalid genera.

large as in most earlier omomyids. Upper incisors large, I^{2-3} sub-equal in size, spatulate; upper canine reduced, premolariform, smaller than P^2; P^2 small, lacking lingual cusp; P^{3-4} with single inner and outer cusps. M^{1-3} with para- and metaconules, varying expression of cuspules on lingual protocone cingulum in positions of hypocone and pericone, pronounced labial cingula with cuspule not seen in *Hemiacodon* in position of mesostyle.

Discussion: *Ourayia uintensis* is of greater size than are other known omomyids except for the considerably younger species *Macrotarsius montanus* of Chadronian age, which is about ten percent larger in comparable parts. Among omomyids earlier or contemporary with *Ourayia*, *Hemiacodon gracilis* most nearly rivals it in size, being about eighty-five percent as large in most measurements. The remote possibility that canines were lost in *O. uintensis* and that there were actually four premolars above and below in this species has been considered but rejected. In spite of its premolariform appearance, the upper canine apex is directed forward while that of P^2 has a distinct backward tilt which can hardly be due to crushing. Moreover, occlusion of the teeth in P.U. 16431 shows that the lower canine (which has a larger root than the teeth adjacent to it) lies in front of the upper canine, as would be expected.

The maxillae of P.U. 16431 are crushed, but some features of interest are still to be observed (see fig. 2). Much of the premaxilla of the right side is preserved, and a wavy suture just in front of the canine and arching backward is indicated on both sides. Both narial margins of the premaxillae are evident anteriorly. The thin, fairly long right nasal has dropped down between the premaxillae. In the orbital region the jugal is missing and the orbital border of the right maxilla much eroded, so that it is not possible to determine whether the malar contacted the lachrymal. However, it is difficult to avoid the conclusion that the orbit was quite large relative to the size of the rostrum. This possibility is also indicated by a specimen of *Hemiacodon* figured by Gazin (1958: pl. 4, fig. 4) in which the supraorbital border of both orbits is preserved. Since this specimen and P.U. 16431 are the only individuals of any species of omomyid primate which preserve part of the skull other than maxillae or dentaries, they deserve special comment. It appears that in *Ourayia* the depth of the rostrum above the canine was greater than the horizontal distance from the narial to orbital borders, so that this primate shows the progressive feature of being comparatively short snouted, evidently much more so than in *Smilodectes* or *Notharctus*. On the other hand, this "advanced" omomyid feature is balanced by the presence of a metopic suture between the frontals in *Hemiacodon* figured by Gazin as is generally the case in "primitive" or non-tarsioid prosimians.

The reduced upper canine of *O. uintensis*, taken together with possession of a lower canine root that is hardly larger than P_2 in cross-sectional area, indicates a small, premolariform lower canine. Both Matthew and Granger (1915: fig. 24) and Gazin (1958: pl. 8) illustrated specimens of the closely related *Hemiacodon gracilis* which preserve broken lower canines that are indeterminate as to the height of this tooth. A specimen of *H. gracilis* recently located in the Yale collections, Y.P.M. 16253 from Henry's Fork, Wyoming, shows that the entire tooth was extremely premolariform and only barely higher than P_2 (see fig. 1). In view of an overall similarity in general size and proportions of the other teeth between *O. uintensis* and *H. gracilis*, the reduced upper canine of the former almost certainly opposed a premolariform tooth below. In earlier omomyids, *Omomys* and *Chlororhysis*, the lower canine is relatively larger (fig 1). Such canine reduction in the later omomyids practically eliminates them from consideration as being ancestors of any Ceboidea.

Although *O. uintensis* may be derived from *H. gracilis*, reference of the former species to the genus *Hemiacodon* seems out of the question. The primary distinctions between these two genera have been cited in the diagnosis given above (page 4), and they are considerably greater than those which have been proposed as separating the genera *Omomys*, *Loveina*, and *Chlororhysis*. No doubt, known omomyid species could be lumped under fewer genera, but in the fragmentary state of present knowledge concerning them, limited almost entirely to dentitions, this would serve no useful purpose and in any event cannot be attempted here.

Curiously, wear on $M\frac{1}{1}$ of *O. uintensis*, P.U. 16431, is distinctly less than on $M\frac{2}{2}$. That this could be due to misinterpretation of the dental formula, with molariform $P\frac{4}{4}$ and loss of one of the molars seems impossible, particularly because in the closely related *H. gracilis* the normal sequence of molar wear can be established for numerous specimens.

MEASUREMENTS IN MILLIMETERS OF *OURAYIA UINTENSIS*

LOWER DENTITION

		P.U. No. 16431	P.U. No. 11236	A.M.N.H. 1899
Length I_2 — M_3		27.6	....	....
Length P_3 — M_3		18.0	18.8	....
Length P_3 — M_2		13.0	14.6	15.0
Depth of jaw below M_1		6.2	6.8	7.6
Transverse diameters:	I_2	2.0	1.9	....
	I_3	...	....	....
	C	...	....	....
	P_2	1.1(?)	...	....
	P_3	2.0	2.3	2.3
	P_4	2.7	2.5	2.6
	M_1 (trigonid)	3.0	2.8	2.9
	M_2	3.1	3.1	3.4
	M_3	2.9	3.0	...
	M_1 (talonid)	3.5	3.3	3.6
	M_2	3.6	3.3	3.8
	M_3	3.2	3.0	
Anteroposterior diameters:				
	I_2	2.3	2.1	
	I_3	...	....	....
	P_2	1.8(?)	.	....
	P_3	2.9	3.1	3.2
	P_4	3.1	3.7	3.7
	M_1	4.0	4.2	4.6
	M_2	4.2	4.2	4.5
	M_3	5.2	4.6	...

UPPER DENTITION

		P.U. No. 16431
Length I^2 — M^3		28.9
Length P^3 — M^3		17.5
Transverse diameters:	I^2	1.7
	I^2	1.7
	C	1.4
	P^2	1.4
	P^3	3.1
	P^4	3.8
	M^1	4.8
	M^2	5.2
	M^3	4.8
Anteroposterior diameters:		
	I^2	3.4
	I^3	3.1
	C	2.2
	P^2	2.3
	P^3	3.1
	P^4	3.0
	M^1	3.8
	M^2	4.1
	M^3	3.8

Measurements for a possibly associated right P_2 of P.U. 16431 have been given above. Although there is no definite contact between this tooth and the right mandibular fragment, it is the proper size and shape for an omomyid P_2, judging from morphology of P_2 in *Omomys* and *Hemiacodon.*

RELATIONSHIPS OF THE OMOMYIDAE

The hypothesis that omomyid prosimians may be near the ancestry of the platyrrhine monkeys is based on several points of direct and indirect evidence, most of which are rather equivocal, as is often the case with such phyletic conjectures. For those who do not favor a notharctid derivation for platyrrhines these small Primates remain as the only other group now known in North America which contains members that are early and generalized enough to admit of such a relationship. Other early Cenozoic families of North American Primates including Plesiadapidae, Carpolestidae, Anaptomorphidae, Phenacolemuridae, and Paromomyidae (if the latter two are regarded as distinct) exhibit extreme tooth specialization or reduction which entirely eliminates their known members from any ancestral relation to the South American Monkeys. It is clear, however, that if the dental form and arrangement of *Ourayia uintensis* was at all typical of the later Omomyidae as a whole, it would require a reversal of the trend toward reduction of the canines, seen in this species in order to reach the condition typical of the ceboid monkeys. Such a possibility seems at best rather unlikely.

The question of the ancestry of the platyrrhine monkeys bears rather crucially on the interpretation of a number of more general assumptions inherent to the currently accepted higher categories of Primates, particularly the concept of the suborder Anthropoidea, as well as to the widely accepted succession of grades, from lemuroid to tarsioid, to monkey and etc., through which the ancestors of man and the other Higher Primates are commonly supposed to have passed. Perhaps the problem is largely semantic, resulting from the all too human tendency to superimpose an idealistically subdivided terminology on what are actually continua of evolving lineages. Nevertheless, most of the various named higher categories of Primates have been, and presumably will continue to be, useful in talking about evolutionary relationhips within the order. One possible reaction might be to suspend judgement or discussion of relationships between early and late Cenozoic Primates in view of the partial and fragmentary evidence now available, but within the framework that has been set up by previous research it seems advisable to follow out some earlier suggestions to their logical conclusion. For instance, if platyrrhine monkeys were actually derived from anything like the *Notharctus* group or even from the omomyid prosimians, it is difficult to see how they could have passed through a grade of organization that need be qualified as tarsioid. If either of these groups are actually ancestral to the South American Monkeys, but not to the Old World Higher Primates, then it is also necessary to conclude that those features which are shared by Old and New World Higher Primates are the result of parallel evolution and that these two groups were independently derived from the Prosimii.

In the latter case the taxon Anthropoidea consists of a grade in the sense of Huxley (1958) rather than a clade, in which the common ancestor of subsequent derivative stocks shares something of the definition which justifies the association of such subsequent groups within a single taxon. If Catarrhini and Platyrrhini were derived from independent stocks of Prosimii, then Anthropoidea have a polyphyletic origin, even if such stocks belonged to the same major division of prosimians.

When considering the various alternatives for the derivation of the Platyrrhini it may be noted that latest species of the genus *Notharctus*, and of *Smilodectes* as well, are rather large prosimians, having approximately the body size range seen in species of the living Malagasy genus *Lemur* or in the domestic cat. It seems implausible, although not impossible, that forms such as the pigmy marmoset could have descended from ancestors of the size range of known notharctids. The smallest notharctids, species of the early Eocene genus *Pelycodus*, in comparable parts, have about twice the linear dimensions of the smaller species of *Callithrix* and are even larger compared to *Cebuella*, should the latter genus be sustained as distinct from *Callithrix* [*Hapale*]. Inasmuch as known species of *Pelycodus* give every evidence of being close to the origin of the taxon Notharctidae, there is little reason to posit that there ever were unknown smaller members of this subfamily from which marmosets such as *Cebuella* might more plausibly have been derived without marked size decrease at some intermediate period. One is therefore faced with the supposition that, if Notharctidae are in or near the ancestry of platyrrhines, marmosets have undergone a size reduction since their initial differentiation. This view has sometimes been put forward, but to date there is no paleontological evidence for it.

In conclusion, it is possible to say that in spite of the fact that late Eocene and Oligocene omomyids were specializing along distinct lines of their own, not foreshadowing Platyrrhini, it seems probable that *Omomys* and its immediate forebears are the most likely early Cenozoic prosimians to have a direct relationship to the rise of the South American Monkeys. Among principal evidences supporting this view are the observations that *Omomys*, or one or more forms allied to it, was smaller than any known ceboids, had suitably unspecialized molar crown patterns together with small third molars, shared with some ceboids the otherwise nearly unique possession of a pericone cusp, and belongs to a group showing trends away from the primitive prosimian condition toward foreshortening of the rostrum, orbital enlargement, and vertical incisor emplacement. Moreover, Omomyidae are the only known family of ancient and undoubted Primates now known which possessed exactly the same dental formula as do the living Cebidae. Nevertheless, only in earliest omomyids are relative sizes of respective tooth types reasonably satisfactory for derivation of the tooth morphology characteristic of Oligocene-Recent South American Monkeys.

Figure 1.

Diagrammatic reconstructions of a sequence of representative omomyid species, approx. x 3. Dotted outlines hypothetical.

These species may not represent a single phylum, but each is typical of the successive Epoch substage to which it belongs. Specimens on which this chart is based are as follows: *Macrotarsius montanus* (type) C. M. 9592 (reversed); *Ourayia uintensis*, P.U. 16431 (P_1 and M_1 reversed from right ramus): *Hemiacodon gracilis* (composite), part A—A.M.N.H. 12037, part B—Y.P.M. 16253, part C—Y.P.M. 12987-1; *Omomys carteri* (composite), part A—A.M.N.H. 12600, part B—Y.P.M. 16287 (reversed), part C—Y.P.M. 13219-2 (reversed).

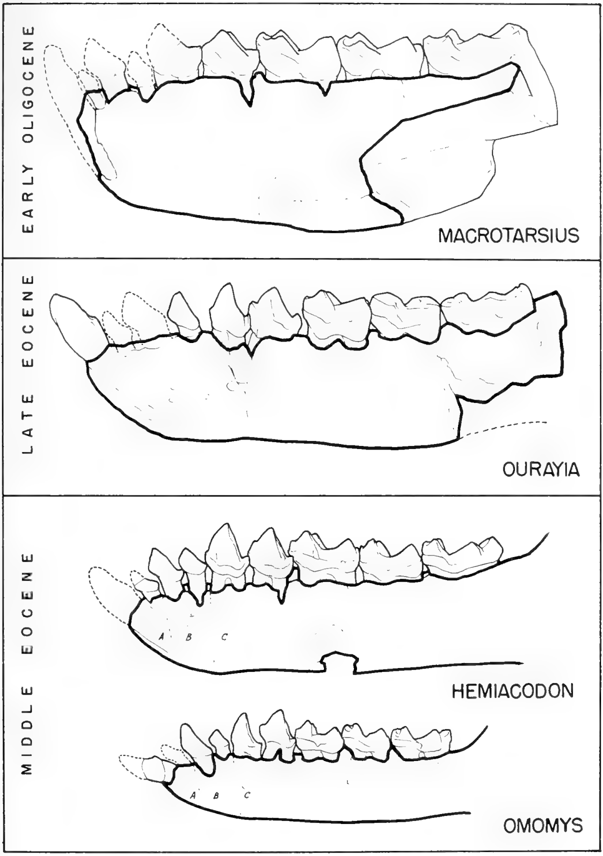
EARLY OLIGOCENE
MACROTARSIUS
LATE EOCENE
OURAYIA
MIDDLE EOCENE
A
B
C
HEMIACODON
A
B
C
OMOMYS

Figure 2.

Occlusal views of right upper, and left lower dentitions of *Ourayia uintensis*, P.U. 16431, (M_1 reversed from right side), approx. x 5.5.

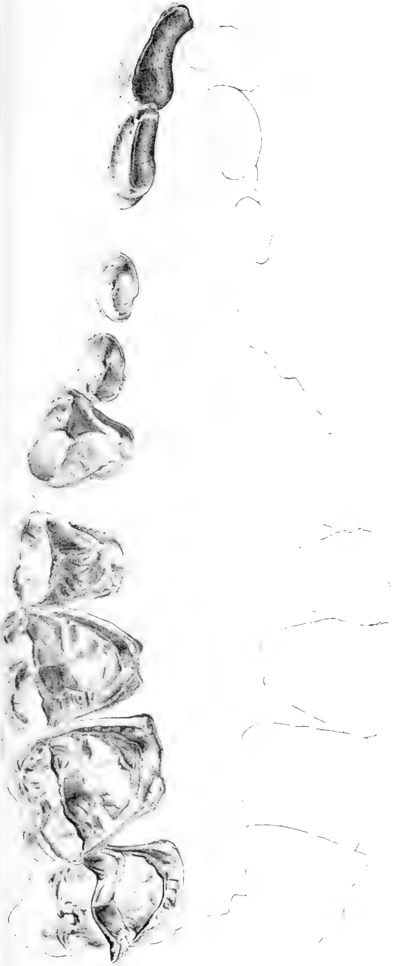

Figure 3.

Lateral view of right maxilla of *Ourayia uintensis,* P.U. 16431, approx. x 5.5.

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Postilla

YALE PEABODY MUSEUM
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NOTES ON *SAGITTA FRIDERICI* RITTER-ZÁHONY COLLECTED OFF PERU*

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In a paper on the chaetognath fauna off Peru, Bieri (1957) remarks, "In the 1941 Peru material a complete set of intergrades exists between *S. friderici* to the south and *S. tenuis* to the north. The same situation has been observed by the author in samples taken off Lower California except that there the *tenuis*-like form is to the south and the *friderici*-like form to the north" (pp. 261-262, fig. 13). He showed that *Sagitta bipunctata* described by Michael (1911) was identical with the *friderici*-like form and that *S. tenuis* and *S. friderici* were ecotypic variants of a single interbreeding population or species (p. 261). The smaller *tenuis*-form was considered a warm water form at that time.

In Bieri's 1952 material, however, only the larger *friderici*-form was found at stations as far north as the Gulf of Guayaquil. He then changed his opinion, admitting the validity of *S. friderici* and characterizing it as neritic or nearshore. He noted that the "distribution of *Sagitta friderici* off California,

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* Contributions from the Seto Marine Biological Laboratory, No. 359.

Peru and Chile, and North and South Africa, is correlated with upwelling and suggested that temperature and salinity are related to the distribution pattern of this species" (Bieri, 1959, pp. 14-18, fig. 17). He re-examined the specimens of Michael's *S. bipunctata* collected off California and found that they were in fact *S. friderici* (p. 14, footnote). The northernmost record of *S. friderici* in the eastern Pacific is evidently Monterey Bay where Bigelow and Leslie (1930) found Michael's *S. bipunctata* to be common (pp. 552-553). While there is no published record of *S. friderici* in Chilean waters, Bieri believes that the distribution of this species extends to the waters off Chile.

Sund (1959a) considers *S. friderici* as a synonym of *S. tenuis* and showed during the Eastropic Expedition (1959b) that *S. tenuis* occurred in only a limited area of the Gulf of Panama.

I have examined *S. tenuis* from Scammon's Lagoon and Manuela Lagoon, Baja California, and *S. friderici* collected in the blue-green water along the southern California coast near San Diego (1959). I have also found many specimens referable to *S. friderici* in collections of the Transpac and Shellback expeditions. Most of them were identified without any hesitation as *S. friderici*, but some doubtful specimens from the offshore waters in the Shellback Area were placed in Groups A and B (pp. 360-364, table 7, fig. 5). As these specimens were mostly found in more or less imperfect states of preservation, I could not examine the exact structure of the seminal vesicle or the corona ciliata.

Fortunately, however, I have had a chance to examine some excellently preserved specimens referable to *S. friderici* from the collection of the 1953 Yale Peruvian Expedition which were submitted to me for examination by Dr. G. B. Deevey of the Bingham Oceanographic Laboratory, Yale University, to whom I want to express my hearty thanks for her kindness.

These specimens include ten individuals, 8.9 mm - 13.3 mm in length, collected on April 2 at Station 34, 4° 3′ S. Lat., 81° 10′ W. Long.; and 12 individuals, 10.0 mm - 13.5 mm in length, collected on April 14 at Station 81, 3° 36′ S. Lat., 80° 47′ W. Long. Measurements of the specimens from the two stations are given in tables 1 and 2 and resemble each other closely except for the TC value (ratio of anterior part of the posterior fin along the trunk to posterior part of the posterior fin along the caudal segment times 100). All the morphological characteristics mentioned below are common to the specimens from both stations.

TABLE 1

Sagitta friderici, armature formulae of individuals from Sta. 34.

Body length	Caudal segment in per cent*	Hooks	Anterior teeth	Posterior teeth	TC-value
8.9 mm	27.0	8 - 9	6 - 6	15 - 16	81.6-84.7
11.7	26.4	7 - 7	9 - 9	20 - 21	80.4-88.9
11.9	25.6	7 - 7	9 - 9	22 - 22	73.3-80.0
11.9	26.4	7 - 7	8 - 9	20 - 20	87.4-87.5
12.0	26.4	7 - 7	9 - 9	18 - 21	86.9-88.7
12.3	25.2	7 - 8	8 - 9	20 - 20	76.9-82.7
12.5	25.8	7 - 7	8 - 8	21 - 22	78.6-83.2
12.7	25.3	7 - 7	9 - 10	20 - 20	84.7-85.9
13.0	27.4	7 - 7	9 - 10	21 - 23	69.5-75.8
13.3	25.7	7 - 7	8 - 8	20 - 21	80.5-84.8

* Caudal fin included.

TABLE 2

Sagitta friderici, armature formulae of individuals from Sta. 81.

Body length	Caudal segment in per cent*	Hooks	Anterior teeth	Posterior teeth	TC-value
10.0 mm	25.5	9 - ?	8 - 8	18 - 19	67.3-76.8
10.6	26.6	8 - 8	8 - 8	18 - 19	67.5-71.4
11.1	26.6	7 - 8	8 - 8	19 - 19	77.8-83.3
11.3	27.4	8	8	18	78.6-80.7
11.6	26.2	7 - 7	9 - 10	20 - 22	83.8-87.0
11.7	27.4	7 - 8	10 - 10	23 - 23	87.3-91.4
11.9	26.7	7 - 7	10 - 10	22 - 23	83.1-85.2
12.0	26.5	8 - 8	8 - 9	21 - 21	64.2-76.5
12.3	26.9	7	11	23	85.7-91.1
12.4	25.4	8 - 8	8 - 8	21 - 22	70.9-79.5
12.6	27.1	7 - 8	9 - 9	21 - 22	79.5-80.0
13.5	26.7	7 - 8	9	22	66.4-71.0

* Caudal fin included.

DESCRIPTION

Length up to 13.5 mm; the tail segment occupies 25.2% to 27.4% of the whole body length including the caudal fin, with an average of 26.4% for 22 measurements. The body is moderately rigid or rather soft and so translucent that the whitish and opaque intestine can be seen. It is usually widest in the posterior part of the trunk in the region of the posterior fins; there is no constriction at the trunk-tail septum. The anterior fin usually begins at the level of the posterior end of the ventral ganglion, although in a few specimens there may be a short distance, less than half of the ganglion's length, between the posterior end of the ventral ganglion and the anterior end of the anterior fin. The posterior fin is very slightly shorter than the anterior one; the ratio for anterior fin to posterior fin times 100 is 86-113, with an average of 105 for 22 individuals. The value is slightly higher in individuals from Sta. 34 than in those from Sta. 81, namely 100-113 (with an average of 108 for ten individuals) compared with 86-113 (with an average of 102 for 12 individuals). The fin is widest behind the trunk-tail septum. Both anterior and posterior fins are fully rayed; the rays are set vertically to the base in a small anterior part of each fin. The TC value is 69.5-88.9, with an average of 82.1 for ten individuals from Sta. 34; while it is 66.4-91.4, with an average of 78.6 for 12 individuals from Sta. 81. The distance between the anterior and posterior fins is highly variable, with an average value of 1/3.75 of the length of the anterior fin for 22 individuals; the distance is slightly shorter in individuals from Sta. 81 than in those from Sta. 34, the denominator being 3.1-6.0 (an average of 4.18 for 12 individuals) as against 2.3-4.1 (3.23, average for ten individuals). The collarette is distinct around the neck and diminishes in thickness posteriorly, reaching one half to two thirds of the distance from the neck to the ventral ganglion. The eye pigment (figs. 5-6) is small to medium, roundish or oval in shape, and the eyes are situated rather widely apart. The distance between the eyes is 24.7%-36.8% (average, 32.7% for five specimens) of the width of the head at the level of the eyes. The corona ciliata (figs. 2-4)* is

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* Heydorn (1959) described the corona ciliata as starting just behind or in front of the eyes in South African specimens, but I have never seen any specimen with the corona beginning just behind the eyes.

elongate. It begins just behind the brain and extends posteriorly for two-thirds of the distance from the neck to the ventral ganglion, or for one and one-half to three times and most frequently two and a half times the head length (see fig. 1). The corona has a pair of very prominent sinuses behind the eyes, but posteriorly it is only slightly sinuous. Usually six pairs of tufts of large tactile setae are found along the corona, although they fluctuate in number from five to seven. Intestinal diverticula are absent. Hooks number seven or eight, rarely up to nine; anterior teeth number six to ten, rarely up to 11; and both rows meet each other at an acute angle. There are 15 to 23 posterior teeth.

The 8.9 mm specimen from Station 34 is devoid of ovaries and seminal vesicles, but all others are provided with these structures in various stages of development. The anterior end of the ovary is situated most frequently near the anterior end of the posterior fin, but it may occur a considerable distance from this level; in five individuals the ovaries extend far beyond the anterior end of the posterior fin and attain the level of the middle of the anterior fin. Immature ova are only 83 μ in long diameter for an average of 11 measurements, whereas mature ones are 210-240 μ in long diameter. The seminal vesicle (figs. 7-14) is situated just at the base of the caudal fin; the posterior fin also ends very close to the vesicle. In earlier stages of development, the anterior glandular portion, which is somewhat rounded and walled with a tall epithelium that secretes the mucus for agglomerating sperm, is very prominent as compared with the low and inconspicuous saccular portion. However, the saccular portion becomes very prominent in advanced stages when it swells outwards more than the anterior glandular portion. The rupture seems to occur along the lateral side of the glandular portion at maturity.

REMARKS

The difference in TC value between the specimens from Station 34 and Station 81 is 3.5 when average values are compared. However, the value varies considerably since it is much

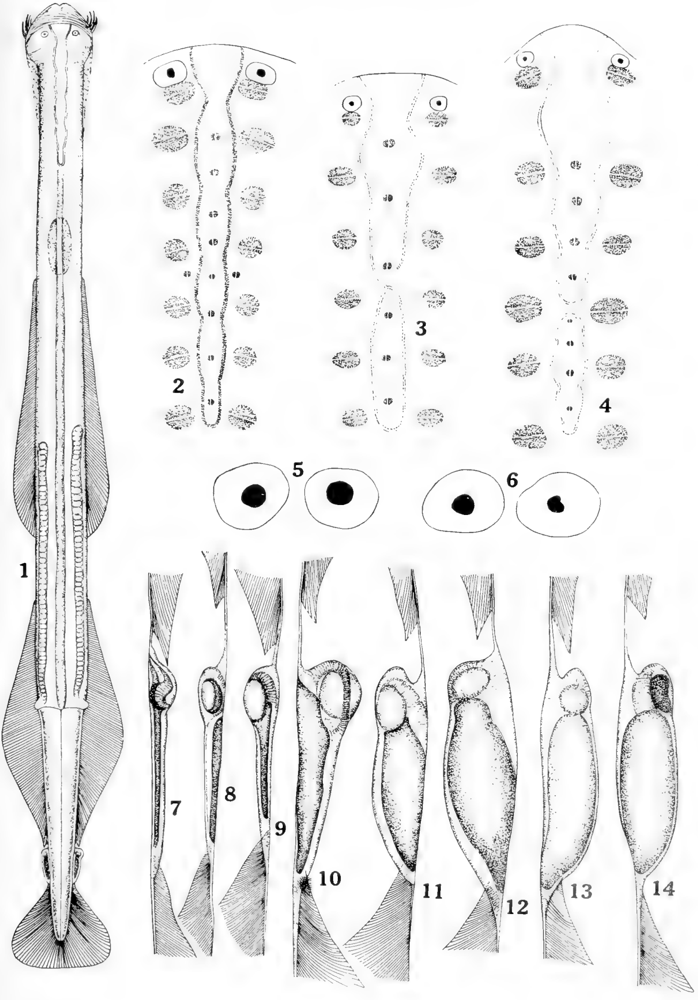
EXPLANATION OF PLATE

Sagitta friderici Ritter-Záhony from Peruvian waters.

1. Dorsal side of specimen 12.3 mm in length from Sta. 81.
2. Corona ciliata of the same individual.
3. Aberrant corona ciliata of specimen 10.6 mm in length from Sta. 81.
4. Aberrant corona ciliata of specimen 11.3 mm in length from Sta. 81.
5. Eyes of specimen 11.9 mm in length from Sta. 81. 300x.
6. Eyes of specimen 12.0 mm in length from Sta. 81. 300x.

7-14. Seminal vesicles arranged in order of developmental stages. 100x.

   7. Specimen 12.0 mm in length from Sta. 34.
   8. Specimen 11.7 mm in length from Sta. 34.
   9. Specimen 12.3 mm in length from Sta. 34.
   10. Specimen 13.0 mm in length from Sta. 34.
   11. Specimen 12.5 mm in length from Sta. 34.
   12. Specimen 10.0 mm in length from Sta. 81.
   13. Right vesicle of specimen 11.9 mm in length from Sta. 34; dorsal view.
   14. Left vesicle of same individual; ventral view.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affected by contraction or bending of the body. Even for the same individual, the value can be different between the right and left sides. For the 22 specimens examined here, the difference in value found between the two sides of the same individual fluctuates from 0.1 to 12.3, most frequently in the range from 1 to 7; and the average difference is 4.7. This is clearly greater than the difference noted between the samples from the two stations and suggests that the difference in TC value found for these specimens is insignificant. Thus, individuals from Station 34 may be considered to be identical with those from Station 81, and all these are identical with those of my Group A (Tokioka, 1959, p. 361). The latter vary up to 13.8 mm in body length, are armed with seven to nine hooks, have up to 11 anterior teeth and up to 25 posterior teeth, and show a TC value fluctuating from 80 to 91.1 (average, 86.3). The differences between Group A and Group B mentioned in the same paper are too great for these groups to be merged.

The appearance and structure of the specimens from the Bingham Oceanographic Collection resemble closely those of *Sagitta friderici* as described repeatedly in many previous papers, except for the armature formulae. The maximal numbers of anterior teeth (11) and posterior teeth (23) exceed those known previously for *Sagitta friderici.* Thus it is necessary to review the previous descriptions of *S. friderici* in order to establish the range of variation. There follows a list of dimensions for *S. friderici* published by previous authors. As the species was established by Ritter-Záhony (1911) and examined and described most exactly by Faure (1952) and Furnestin (1957), I shall begin with the data of these authors.

Ritter-Záhony (1911)

Loc.: The surface layer off South-West Africa and Cape Verde.

Body length: up to 13 mm.

Hooks: 8 - 9.

Anterior teeth: up to 9.

Posterior teeth: up to 22.

Faure (1952)

Loc.: The neritic waters off Morocco.
Body length: up to 15 mm.
Hooks: 5 - 9, most frequently 7 - 8.
Anterior teeth: up to 8, most frequently 6.
Posterior teeth: up to 21, most frequently 12 - 13.

Furnestin (1953)

Loc.: Israel.
Body length: up to 10.2 mm.
Hooks: 6 - 8.
Anterior teeth: 4 - 8.
Posterior teeth: 8 - 14.

Furnestin (1956)

Loc.: Tangier Bay and the west entrance to the Gibraltar Straits.
Body length: up to 12.5 mm.

Furnestin (1957)

Loc.: The neritic waters off Morocco.
Body length: up to 15.1 mm.
Hooks: 5 - 9, most frequently 7 - 8.
Anterior teeth: up to 8.
Posterior teeth: up to 17.

Michael (1911), as *Sagitta bipunctata*

Loc.: San Diego region.
Body length: up to 17 mm.
Hooks: 7 - 8.
Anterior teeth: 5 - 7.
Posterior teeth: 12 - 14.

Scaccini and Ghirardelli (1941)

Loc.: Rio de Oro.
Body length: 7 mm - 10 mm.
Hooks: 7 - 8.
Anterior teeth: 6 - 8.
Posterior teeth: 14 - 20.

Vannucci and Hosoé (1952)

Loc.: Near Trinidad in the South Atlantic.
Body length: 8.2 mm - 8.5 mm.
Hooks: 8.
Anterior teeth: 7.
Posterior teeth: 12.

Colman (1959)

Loc.: Eastern Central Atlantic.
Body length: 6.8 mm and 12.7 mm.
Hooks: 7 - 8.
Anterior teeth: 6 - 8.
Posterior teeth: 12 - 18.

Heydorn (1959)

Loc.: The neritic waters off South West Africa.
Body length: up to 18 mm.
Hooks: up to 9.
Anterior teeth: up to 8.
Posterior teeth: up to 20.

Tokioka (1955)

Loc.: The neritic waters off Morocco.
Body length: up to 11.6 mm.
Hooks: 7 - 9.
Anterior teeth: 5 - 7.
Posterior teeth: 11 - 17.
TC value: 71.1 - 91.0; av. 82.0.

Tokioka (1959)

Loc.: Blue-green water off lower California.
Body length: up to 19 mm.
Hooks: 7 - 9.
Anterior teeth: up to 6.
Posterior teeth: up to 12.
TC value: 83.3 - 134.0; av. 107.1.

Tokioka (1959), Group B

Loc.: The waters off central and northwestern South America.
Body length: up to 9.4 mm.
Hooks: 5 - 6.
Anterior teeth: 6 - 9.
Posterior teeth: 13 - 19.
TC value: 88.4 - 114.3; av. 96.6.

The present specimens and Tokioka's Group A are characterized by the following data:

Loc.: The waters off central and northwestern South America.
Body length: up to 13.8 mm.
Hooks: 7 to 9.
Anterior teeth: up to 11.
Posterior teeth: up to 25.
TC value: 78.6 to 86.3.

As nine anterior and 22 posterior teeth are already recorded for *Sagitta friderici*, the existence of 11 anterior and 25 posterior teeth is not unreasonable; these may be accepted as the upper limits in the species. Group B is characterized by fewer hooks than usual, but this low number of hooks is shared by some specimens from neritic waters off Morocco and Israel. Thus Group B may most probably be included in *S. friderici* as an unusual group. The maximum body length is 19 mm, found in the collection from the blue-green water along Southern California (Tokioka, 1959, table 27 on p. 390).

Detailed comparisons have been made between *Sagitta friderici* and *S. bipunctata* by Faure (1952) and Furnestin (1957), between *S. friderici* and *S. setosa* by Furnestin (1957, 1958) and between *S. friderici* and *S. hispida* by Furnestin (1957). However, the most serious problem concerns the separation of *S. friderici* from *S. tenuis*. Pierce (1951) considers these two species as ecological forms of *S. tenuis*, and Sund (1959a) seems to agree without giving any clear reasons. On the other hand, Fraser (1952), Furnestin (1957), Bieri

(1959), Colman (1959), and the present writer (Tokioka, 1955, 1959) admit the validity of *S. friderici. S. tenuis* can be separated from *S. friderici* by the smaller size of mature individuals (less than 10.7 mm), the slightly larger number of anterior and posterior teeth (up to eight anterior and up to 19 posterior teeth for individuals less than 8 mm), and the comparatively smaller TC value (55.3 - 84.5, with an average of 64.7, given by Tokioka, 1955; 29.9 - 72.4, usually 40.8 - 61.3 as reported by Colman, 1959). Furthermore, Fraser (1952) mentions the difference in general appearance between *S. tenuis* and *S. friderici.*

However, according to Furnestin's (1959) descriptions of the variability of *S. friderici*, the specimens from the waters along the Senegal coast sometimes look more massive and have longer ovaries than those from the Gulf of Guinea which seem to be weaker in body appearance and attain maturity more rapidly than those of Morocco waters. Colman (1959) records that individuals of *S. tenuis* from Cedar Keys, Florida, differ from those of British Guiana in having a somewhat shorter caudal segment (26%-29% v. 27%-34%), slightly fewer hooks (7-8 v. 7-9), and a higher TC value (53.8%-92.3% v. 29.9%-72.4%). Also, the anterior fin begins more posteriorly and is consequently slightly shorter. The massive body appearance of *S. friderici* from the waters along the Senegal coast somewhat resembles that of *S. tenuis*, and the contrarily higher TC value (53.8%-92.3%) of *S. tenuis* from Cedar Keys, Florida, lies within the range of variation of TC values for *S. friderici.* These two points are noteworthy, although they do not provide sufficient evidence to combine *S. friderici* with *S. tenuis* completely. Usually *S. tenuis* is found in embayments or in areas more or less protected from the open sea (Suárez, 1955; Pierce, 1958; Colman, 1959; and Tokioka, 1959), although its distribution extends more than five miles offshore in the coastal waters of western Florida. On the other hand, the distribution of *S. friderici* is confined to the neritic water mass according to Scaccini and Ghirardelli (1941), Faure (1952), Furnestin (1956, 1957, 1959, 1960), Bieri (1957, 1959), Sund (1959b), Heydorn (1959), and Tokioka (1959). The reported occurrences of *S. friderici* near Trinidad Island in the South Atlantic

(Vannucci and Hosoé, 1952) and in the eastern Central Atlantic (Colman, 1959) indicate that this species is not confined to neritic waters as suggested by Faure. It is probable, however, that the specimens found by these authors are drift forms carried far offshore from neritic waters.

Finally, it may be noted that the individuals of *S. friderici* occurring in the northern part of the range of the species in the Eastern Pacific and those occurring in the southern part differ considerably from each other in tooth number.

SUMMARY

A collection of chaetognaths from the waters off Peru is described; all are referred to *Sagitta friderici* Ritter-Záhony. The range of variation within this species and the distinctness of *S. tenuis* Conant from it are discussed. *S. friderici* is found in neritic water masses, while *S. tenuis* occurs in embayments and areas more or less protected from the open sea.

POSTSCRIPT

After I had sent the manuscript of this paper to the editor, five more papers including descriptions or notes on *Sagitta friderici*, *S. tenuis* or on some forms allied to them were published.

Bainbridge, V. (1960: The plankton of inshore waters off Freetown, Sierra Leone. Colonial Off. Fish. Publ. No. 13,) mentions that *S. friderici* and *S. hispida* were the most important chaetognaths in that area, while the occurrence of *S. tenuis* was sporadic.

Suárez-Caabro, J. A. and Madruga, J. E. (1960: The Chaetognatha of the northeastern coast of Honduras, Central America. Bull. mar. Sci. Gulf Carib., *10*: 421-429.) found a small number of *S. tenuis* near the entrance to Caratasca Lagoon on the northeastern coast of Honduras. These specimens were 4 mm-8 mm in length with the tail segment 26.7%-28.5% as long as the body length, were armed with 6-8 hooks, and had 4-7 anterior and 6-8 (4 mm-5 mm long individuals) to 10-13 (7 mm-8 mm long individuals) posterior teeth. The TC-value measured on Fig. 3A is 86.4. This is unusually large for *S. tenuis* if the figure is made quite accurately.

Fraser, J. H. (1961: Nigerian Chaetognatha-*Sagitta friderici* R. Z. Ann. Mag. nat. Hist. (13) *3*: 289-290.) examined *S. friderici* found in four tubes of plankton taken during half-hour hauls made in August - October 1957 in the estuary of the Bonny River, off Port Harcourt, Nigeria. Only the present species of chaetognath was found in the collections. The maximum length was 9 mm in the August sample, 13 mm in September, and 11.5 mm in October. The annual temperature and salinity ranges are 26 - 30°C and 12 - 23 0/00, but the salinity dropped to 11.5 0/00 in September 1957.

Alvariño A. (1961: Two new chaetognaths from the Pacific. Pacif. Sci. *15:* 67-77.) established a new species, *Sagitta euneritica*, which occurs close to shore from Cape Mendocino to Punta Eugenia in Baja California. She considers this new species as identical with the form which Bieri (1957 and 1959) recorded as *S. friderici* (?) in the same area along the coast of North America and extending south to the waters of Peru and Chile. And very probably many of the *S. friderici* collected and examined by me in the blue-green water along southern California (1959) are to be included in the new species according to her opinion. She compared *S. euneritica* with *S. friderici* and *S. setosa*, but the last species differs distinctly from *S. friderici* and *S. euneritica* in the fully matured state as the seminal vesicle is far from the tail fin. Thus, the most important point is the distinction between *S. euneritica* and *S. friderici*. As far as I am aware, two of the characteristics given by Alvariño for *S. euneritica* seem to be significant. One is the position of the posterior fin which lies more on the trunk than on the tail; the other is the structure of the seminal vesicle. However, the TC-value varied from 76 to 141.7 in 33 specimens of *S. friderici* collected in the blue-green water and vicinity and therefore the former character cannot be a definite one. The latter character may be the only one differentiating *S. euneritica* from *S. friderici*. The author of *S. euneritica* mentions that the seminal vesicle of her species is like that of *S. neglecta* and her Fig. 9 shows that it is devoid of any glandular portion at the anterior end of the vesicle. But I observed seminal vesicles just like those of typical *S. friderici* in some individuals collected in the blue-green water. Moreover, it is noteworthy that the outline of the vesicle shown by Alvariño in Fig. 9 resembles closely some of those shown in Figs. 7-14 of this paper. It is not impossible that *S. euneritica* is nothing but an intraspecific variant of *S. friderici*.

Sund, P. N. (1961: Two new species of Chaetognatha from the waters off Peru. Pacif. Sci. *15:* 105-111.) established two new species, *Sagitta peruviana*, distributed rather widely in the coastal waters of Peru, and *Sagitta popovicii*, found only near the entrance to the Port of Talara, Peru. Evidently *S. peruviana* is identical with the individuals of *S. friderici* treated in this paper, and *S. popovicii* seems to be identical with *S. tenuis*.

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YALE PEABODY MUSEUM

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NOTES ON AMPHISBAENIDS (AMPHISBAENIA; REPTILIA)

2. *Amphisbaena occidentalis* Cope from the Coastal Plain of Northern Peru.

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Amphisbaena occidentalis was described by Cope (1876, p. 176; 1885, pl.) from four specimens collected in the "Valley of Jequetepeque." Elsewhere (p. 159) in the first paper he described the locality as extending "from the Cordillera of Caxamarca to near the coast of Pacasmayo" in western Peru. The description did not include counts of body annuli nor the number of segments at midbody, so that Boulenger (1885, p. 443; also Strauch, 1881, col. 54) omitted the species from his catalog as it was "not sufficiently characterized." Boettger later (1889, p. 311) provided counts for five specimens collected in the immediate vicinity of Pacasmayo.

Boettger's paper appears to have been overlooked by Stejneger (1911, p. 203), who relied on a miscount (179 instead of 279 body annuli) of one of the types and described a single specimen from Piura as the new species *Amphisbaena townsendi*. Parker (1932, p. 178) obtained the body and tail counts

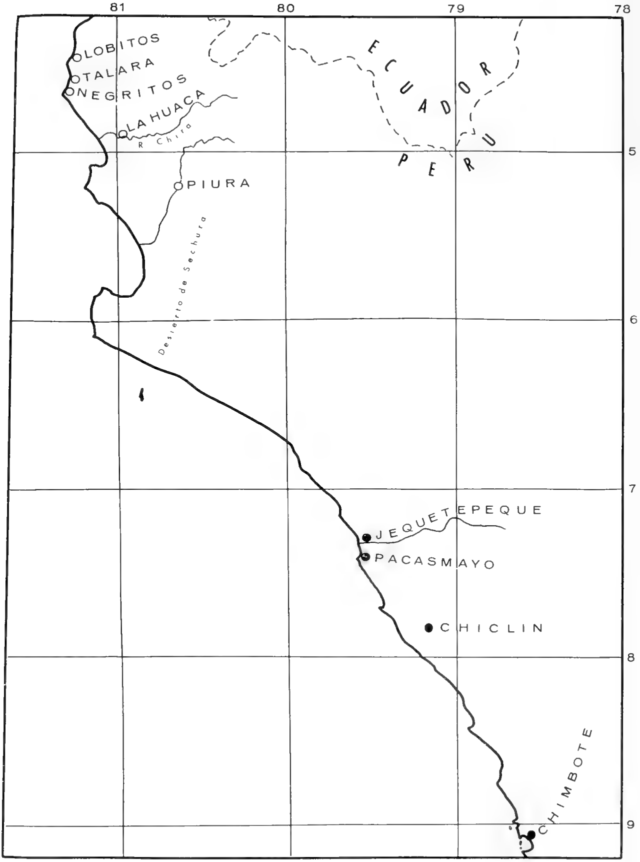

Figure 1. Map of northwestern Peru to show localities mentioned in the text.

of Cope's types and placed *townsendi* into the synonymy of *occidentalis* in a note that also listed data for four specimens from Lobitos, Talara. He remarked that there seemed to be a north-south gradient in the number of caudal annuli within the composite sample.

The present redescription was prompted by the discovery of 14 specimens collected in March 1864 by C. F. Winslow at La Huaca, River Chira, Peru and now in the collection of the

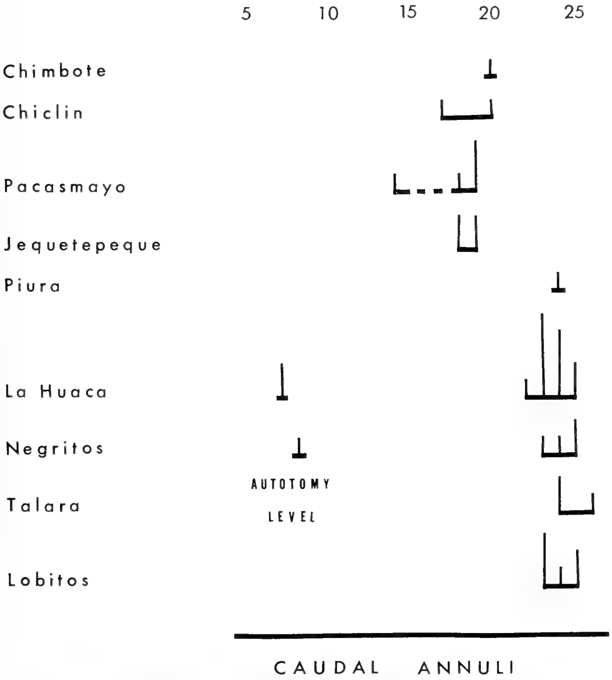

Figure 2. *Amphisbaena occidentalis.* Diagrammatic comparison of the number of caudal annuli for specimens from the several localities. The annulus at which autotomy occurred is indicated. One of the Pacasmayo specimens may have a damaged, but not autotomized, tail.

Peabody Museum at Yale University. These and some others tripled the available number of specimens (all of which have been reexamined) and doubled the known range of the species. The data for all specimens are given in the table.

Analysis of these specimens indicated that Parker was correct, in suggesting that *Amphisbaena occidentalis* was polymorphic, and disclosed a number of other characters in which the populations differed. The species consists of two clearly defined forms, ranging from Lobitos to Piura, and from Jequetepeque to Chimbote respectively (Fig. 1). These populations are differentiated by caudal counts (Fig. 2), body proportions (Fig. 3), chin shield arrangements (Figs. 4 and 5), and nature of caudal autotomy (Figs. 6 and 7).

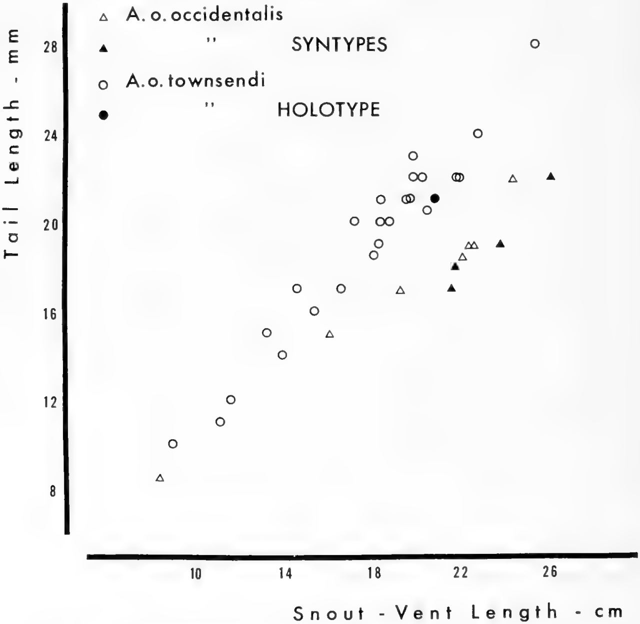

Figure 3. *Amphisbaena occidentalis.* Scatter diagram of tail versus snout-vent length for samples of the two races.

The lack of material from the region between Piura and Jequetepeque does not permit a closer definition of the "break" nor are there intergrade specimens. The decision to call these two forms races rather than full, geographically replacing, species has been taken with considerable reservations. It was based on their general similarity in head shape, head segment arrangement, counts of body annuli, and the remarkable and unique color pattern (Fig. 8). Yet the difference between them is considerably more than that observed in other subspecies situations in amphisbaenids (Vanzolini, 1951; Gans and Alexander, ms.). There is also some parallel to the situation of *A. silvestrii* and *A. neglecta* in Mato Grosso (Gans, ms.), involving two possibly sympatric "sibling" species again distinct from other forms. These two situations seem made to order for the attention of local cytotaxonomists.

It may well be true that the hiatus between the ranges of the two forms of *A. occidentalis* is not presently inhabited. Amphisbaenids seem to be highly dependent upon substrate humidity and all localities from which specimens of *A. occidentalis* have been examined lie along coastal river courses. The Desierto de Sechura between Jequetepeque and Piura is a region without permanent water, in which the water table may be low enough to prevent the survival of amphisbaenids.

It is a pleasure to acknowledge permission of the following curators to examine material stored in their institutions (referred to by the abbreviations in parentheses throughout the text): Mr. Charles M. Bogert, The American Museum of Natural History (AMNH); Dr. James E. Böhlke, The Academy of Natural Sciences of Philadelphia (ANSP); Miss A. G. C. Grandison, British Museum (Natural History) (BM); Dr. Robert F. Inger, Chicago Natural History Museum (CNHM); Dr. Philip S. Humphrey, Peabody Museum of Natural History at Yale University (PMY); Dr. Konrad Klemmer, Senckenbergische Naturforschende Gesellschaft (SMF); Dr. Doris M. Cochran, United States National Museum (USNM); Dr. Heinz Wermuth, Zoologisches Museum der Universität, Berlin (ZMU). I am indebted to Dr. Virginia Cummings for her care in preparing the drawings. Opportunity to visit several European Institutions was afforded by a grant from the estate of

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Amphisbaena occidentalis Cope, 1876.

A small species of *Amphisbaena* with a dark purplish-brown dorsal, and light ventral coloration. The dorsal color is produced by pigmentation of the segments and drops out by segments along the sides (occasionally on the back) producing a characteristic mottled effect. The dorsal surfaces of head and tail are more densely and solidly pigmented than those of the body. The head is flattened and there is considerable dorsoventral compression of the pectoral region. The muscle masses lying over the parietal portion of the skull do not change the outline of the head in large specimens. The rostral is small, scarcely visible from above. Pairs of nasals, prefrontals and frontals form a suture along the head, with the posterior edge of the frontals lying somewhat anterior to the angle of the mouth (for nomenclature see Gans and Alexander, ms.). The occipitals are no larger than the dorsal segments. Four supralabials, the second largest. Three infralabials plus a small fourth scale that also forms the angle of the gape and projects dorsad around the posterior edge of the last supralabial.

261-79 body annuli from the back of last infralabial to and including the pore-bearing precloacals. The first four to six annuli of the neck region shorter than body annuli. Since the posterior edge of the frontals lies anterior to the fourth infralabial the annuli curve forward dorsally. This may be compensated for by an elongation of the dorsal segments of the 7th to 12th annuli (approximately). These annuli thus appear more or less V-shaped in dorsal view. Three to four dorsal half annuli (not included in the counts) are generally present in this region and there is a tendency toward considerable irregular interdigitation and complexity in the ventral portion of this (the pectoral) region. The six precloacal annuli also tend toward irregularities and asymmetries. Segments per midbody annulus generally 16 or 18 dorsals, 24 or 26 ventrals, 42 or 44 total. Ranges are 16 - 19 dorsals, 22 - 27 ventrals, 38 - 47 totals.

Dorsal and ventral folding lines (grooves) are present but not differentiated. The lateral lines may be faintly indicated in approximately 50% of the specimens, on others they are only noticeable as aligned intersegmental sutures.

There are four precloacal pores in all specimens, followed by six to nine precloacal segments, of which the central six are often large and of equal size. The post-cloacal segments are generally subject to splitting, yielding 11 to 16 very irregular radial segments. The pores of males are large and generally pigmented, those of females smaller, faintly indicated and nonpigmented. No other characters show significant sexual dimorphism.

KEY TO SUBSPECIES OF *A. occidentalis*

1. 18 to 21 caudal annuli; no autotomy constriction; no specimens with autotomized tail; tail shorter (fig. 2); 3 post-genials in first row; little if any elongation of dorsal segments of trunk annuli 7 to 12 .... *A. o. occidentalis*
2. 22 to 26 caudal annuli; the seventh and/or eighth caudal annulus narrower, often with pigmented ventral segments, and with tail constricted at this autotomy level; some specimens with autotomized tail; tail longer; 4 to 5 post-genials in first row; marked elongation of dorsal segments of trunk annuli 7 to 12 .... *A. o. townsendi*

Amphisbaena occidentalis occidentalis Cope, 1876

Amphisbaena occidentalis Cope, 1876, p. 176. **Terra typica:** "Valley of Jequetepeque," James Orton, col. **Syntypes:** ANSP 11355-8.

Locality records:—Peru:—ZMU 9631. Departamento Ancash: Chimbote CNHM 5661. Departamento La Libertad: Chiclín CNHM 34290-1. Pacasmayo (Boettger, 1889, 1893; Boulenger, 1890; Parker, 1932); BM 1889.7.19.1; SMF 11815-18. "Valley of Jequetepeque" (Cope, 1876, 1885, 1892; Boulenger, 1885; Stejneger, 1911; Camp, 1923; Parker, 1932; Burt and Burt, 1933); ANSP 11355-58.

Amphisbaena occidentalis townsendi Stejneger, 1911, new combination.

Amphisbaena townsendi Stejneger, 1911, p. 283. **Terra typica:** "Piura, Peru," C. H. T. Townsend, col. **Holotype:** USNM 47987.

Locality records: — Peru: — Departamento Piura: Piura (Stejneger, 1911; Burt and Burt, 1930, 1933; Parker, 1932); USNM 47087. La Huaca, Río Chira PMY 508-1 - 14. Negritos CNHM 5725, 41554. Near Negritos CNHM 38681. Quebrada Pariñas, near Negritos CNHM 8361, 8385. Talara AMNH 66642. Pariñas Valley, northeast of Talara CNHM 8450-51. Lobitos, Talara (Parker, 1932); BM 1929.12.12.2-5. 30 miles from Lobitos BM 1932.9.5.9-10.

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TABLE OF DATA FOR ALL SPECIMENS

Museum Number		Sex	Annuli	Segments	Chin Shield	Length
ZMU	9631	♂	267+3+17S	46	3	213+18
CNHM	5661	♀	262+3+20S	18/24	3	160+15
CNHM	34290	♀	266+3/4+17S	41	3	192+17
CNHM	34291	♀	263+3+20S	16/26	3	243+22
BM	1889.7.19.1	♀	272+4/5+18S	18/26	3	220+18.5
SMF	11815	♂	265+4+19S	43	3	223+19
SMF	11816	juv	268+3+19S	47?	3	83+8.5
SMF	11817	♀	272+5+14+	18/26	3	243+16?
SMF	11818	♀	272+4+20S	20/28	3	226+19
ANSP	11355	♂	275+3+18S	18/26	3	?260+22
ANSP	11356	♀	270+4+19S	44	3	237+19
ANSP	11357	♂	266+4/3+19S	16/24	3	215+17
ANSP	11358	♂	269+4+18S	44	3	217+18
USNM	47087	♂	275+2+(8)24S	18/26	4	208+21
PMY	508-1	♀	267+3/4+(7)23S	16/26	4	187+20
PMY	508-2	♀	271+4+(8)23S	16/26	4	139+14
PMY	508-3	♀	264+4+7 A	19/26	5	211+x
PMY	508-4	♂	263+3+(8)25S	44	4	183+21
PMY	508-5	♀	272+3+7 A	42	4	191+x
PMY	508-6	♂	261+3/2+(8)24S	42	5	145+17
PMY	508-7	♀	267+3+(7)23S	44	4	182+19
PMY	508-8	♂	265+3+(8)22S	16/24	5	165+17
PMY	508-9	♀	266+3+(8)23S	42	4	182+19
PMY	508-10	♂	264+3+(7)23S	16/26	4	197+21
PMY	508-11	♀	263+3+(7)24S	18/26	4	195+21
PMY	508-12	♂	271+3+(8)24S	18/26	4	183+20
PMY	508-13	♀	266+3/4+( )24S	44	4	171+20
PMY	508-14	juv	272+3+(8)25S	42	5	89+10
CNHM	5725	♂	279+3+(8)23S	16/22	5	219+22
CNHM	41554	♂	273+2+8 A	16/26	5	230+x
CNHM	38681	♀	269+3/4+(7)25S	18/26	5	197+23
CNHM	8361	?	271+3+(8)25S	18/26	4	132+15
CNHM	8385	♀	271+4+(7)24S	18/26	4	180+18.5
AMNH	66642	♀	277+3+( )24S	18/25	4	153+16
CNHM	8450	♂	275+3+(8)24S	17/24	4	198+22
CNHM	8451	♂	277+3+(9)26S	47	5	202+22?
BM	1929.12.12.2	♀	271+3+(8)25S	18/26	5	252+28
BM	1929.12.12.3	♀	273+4+(8)24S	16/25	5	227+24
BM	1929.12.12.4	juv	272+5+(8)23S	18/28	5	111+11
BM	1929.12.12.5	juv	278+3+(8)25S	18/26	5	116+12
BM	1932.9.5.9	♂	269+4+(8)23S	16/24	5	218+22
BM	1932.9.5.10	♀	279+4/5+(9)23S	17/26	5	204+20.5

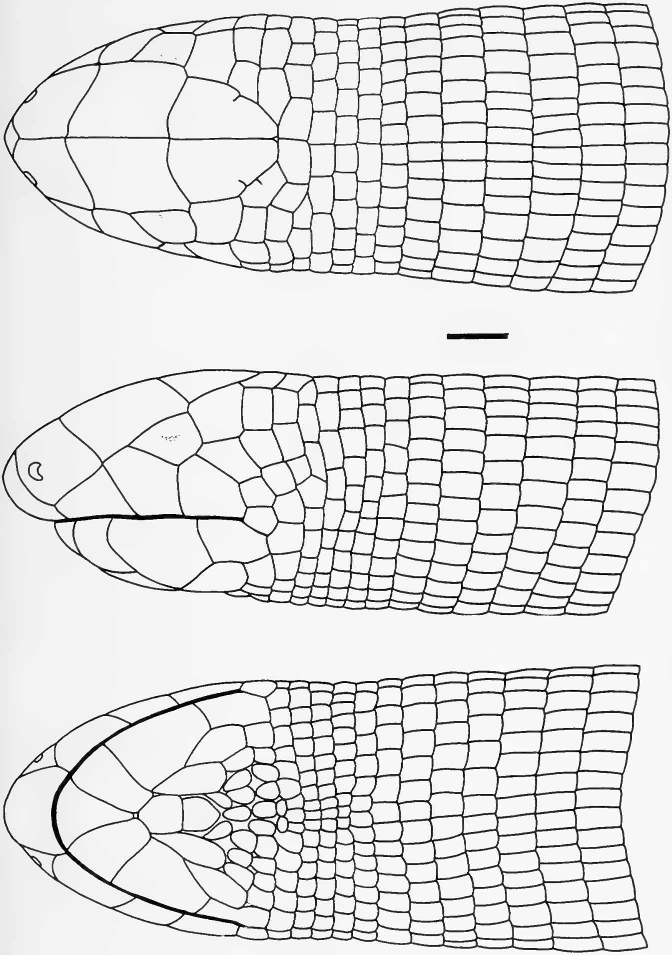
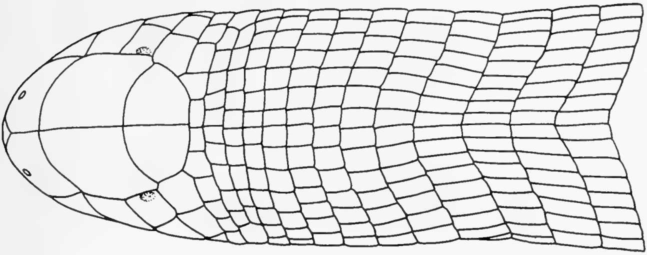
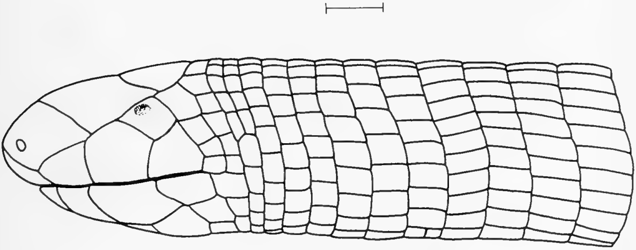


Figure 4. *Amphisbaena o. occidentalis.* Dorsal, lateral and ventral views of the head and neck of CNHM 34290 from Chiclín, Dept. La Libertad. The line equals 1 mm to scale. (V. Cummings, del.)

Figure 5. *Amphisbaena o. townsendi.* Dorsal, lateral and ventral views of the head and neck of PMY 508-9 from La Huaca, Dept. Piura. The line equals 1 mm to scale. (V. Cummings, del.)





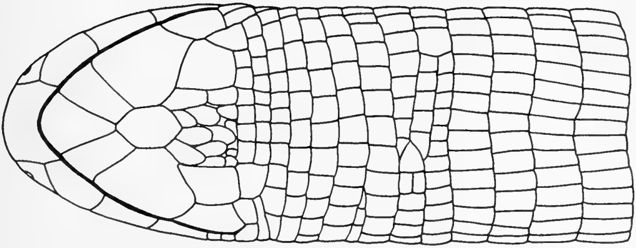
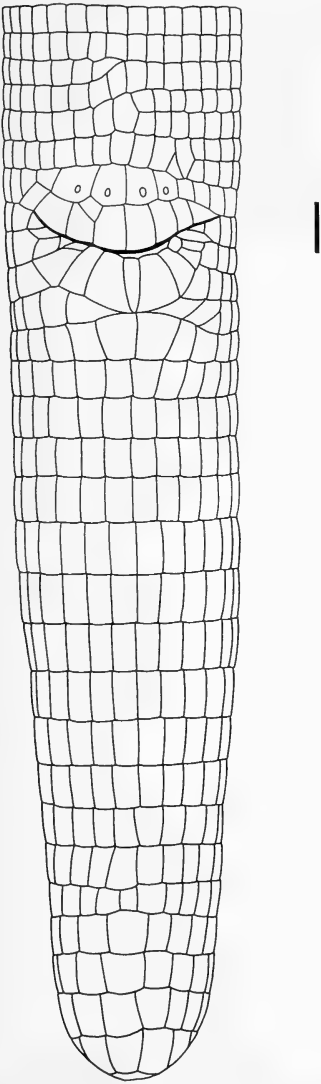
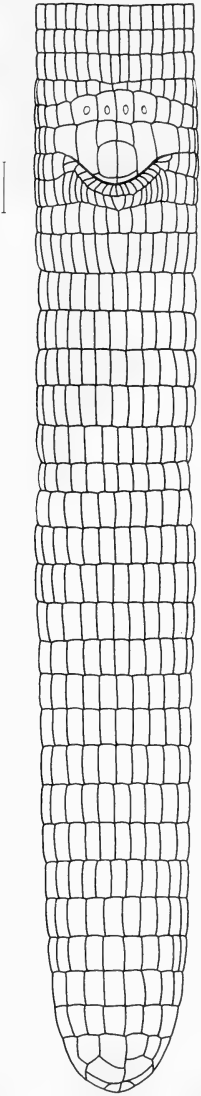


Figure 6. *Amphisbaena o. occidentalis.* Ventral view of cloaca and tail of same specimen as figure 4. Note lack of autotomy level. The line equals 1 mm to scale. (V. Cummings, del.)

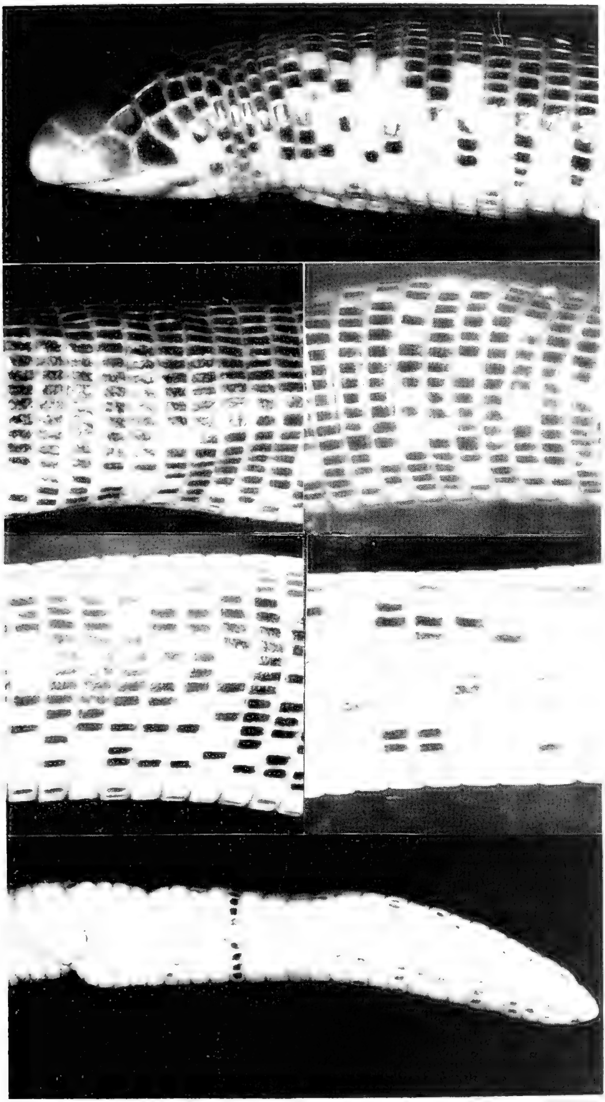
Figure 7. *Amphisbaena o. townsendi.* Ventral view of cloaca and tail of same specimen as figure 5. Note the narrowing of the eighth postcloacal annulus indicating the preferred autotomy level. The line equals 1 mm to scale. (V. Cummings, del.)





Figures 8 - 13. *Amphisbaena occidentalis.* Photographs demonstrating the color patterns. Figs. 8 - 9 show *A. o. occidentalis,* and figs. 10 - 13 show *A. o. townsendi.*

> Figure 8. Lateral view of the head of CNHM 34290 from Chiclin, Dept. La Libertad. Figure 9. Dense dorsal and sharply delimited lighter ventral coloration shown in three-quarter view of the midbody of the same specimen. Figures 10 - 12 show the various stages of lightening on the dorsal color (by the lack of pigment on an increasing number of dorsal segments) within a single series, on midbody dorsal views of PMY 508-4 (Fig. 10), PMY 508-3 (Fig. 11) and PMY 508-9 (Fig. 12) all from La Huaca, Dept. Piura. Figure 13. Ventral view of cloaca and tail of CNHM 8385 from Quebrada Pariñas, Depto. Piura. Note the sharp pigmentation of the reduced postcloacal annulus, which marks the preferred level of autotomy. Also the extremely faint, non-pigmented precloacal pores in this female specimen.



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YALE PEABODY MUSEUM

OF NATURAL HISTORY

Number 57 November 30, 1961 New Haven, Conn.

THE PHYLETIC POSITION OF *RAMAPITHECUS*

Elwyn L. Simons

Recent discoveries of early Pleistocene hominids at Olduvai gorge, Tanganyika, by expeditions under the direction of Dr. L. S. B. Leakey have pushed back certain knowledge of fossil man almost to the beginning of this epoch. To the extent that the K-A date suggested for these early men, 1.75 million years, (Leakey et al. 1961) is accurate, the beginning of the "Villafranchian" provincial age, and thus of the Pleistocene itself, is shown to be considerably earlier than most previous estimates. It therefore seems appropriate that renewed attention be drawn to the only Pliocene fossil primate specimen known to this writer, which can be defended as being within, or near, the population ancestral to Pleistocene and subsequent hominids, the type maxilla of *Ramapithecus brevirostris* at Yale Peabody Museum.

This maxilla, Peabody Museum No. 13799, was collected August 9, 1932 by the Yale North India Paleontological Expedition under Dr. G. E. Lewis (Fig. 1). The geologic occurrence of *R. brevirostris* was first given by Lewis (1934) as "Either latest Middle Siwalik [Dhok Pathan Zone] or basal upper Siwalik [Tatrot Zone]." However, Lewis (1937) later determined the horizon of Y.P.M. 13799 as being within the Nagri zone, which is of Pliocene early Middle Siwalik age.

Gregory et al. (1937) also indicate the level of this specimen as Nagri.

Consequently, Hooijer and Colbert (1951) seem to have erred in listing ***Ramapithecus*** as occurring only in the Tatrot zone fauna which they suggest as being very close to the Plio-Pleistocene boundary. Regardless of these published differences in age determination the provenance of the specimen is known, so that, at least potentially, its temporal position can be verified. Faunal correlations indicate that, even in the unlikely event that ***Ramapithecus*** occurs as late as the Tatrot horizon, this primate is distinctly older than the "Villafranchian" hominids of Olduvai gorge.

In spite of the significance of Y.P.M. 13799, as being possibly the earliest known hominid, it has been largely overlooked, or briefly dealt with in the more recent summaries of hominid evolution, a common conclusion being that the type is too fragmentary to permit taxonomic assignment. Actually, such a conclusion is incorrect and misleading. This right maxilla provides at least some information as to shape, size or positioning of the entire upper dentition except for M^3, in that alveolae of I^{1-2}, C are preserved as well as the series P^3 through M^2. Moreover the base of the nasal aperture can be seen above the incisors, and, contra Hrdlička (1935), the dental arcade can be determined as parabolic and not U-shaped, as was correctly stated by Lewis (1934) in the original description of this form (see Fig. 2). Some may think (as Hrdlička did) that extrapolating from the right maxilla alone, in order to determine that the disposition of the upper cheek teeth is in an arcuate line, instead of being arranged in the parallel series seen in all pongids, is a rather uncertain procedure. However, at one point (see arrow 1, figure 2) the maxilla reaches nearly, if not entirely to the point of the palatal intermaxillary suture. Since we may safely assume that ***Ramapithecus***, like other vertebrates, was bilaterally symmetrical, if the right maxilla and its mirror-image are pivoted around this point the amount of posterior divergence of the cheek tooth rows cannot be further decreased beyond the arrangement shown in figure 2 without assuming an impossibly long basal diameter for the central incisor pair (figure 2, arrow 2). In fact, the space allowed for these teeth in figure 2 (in order to be on the safe side) is intentionally made greater than it is likely to have been. Preservation of the entire length of the alveolar cavity of the right central incisor allows for comparative measurements as to its size. The central incisor root of *Ramapithecus* is only about half as long as it is in a series of chimpanzees examined in this connection and which had cheek teeth of the same absolute size as Y.P.M. 13799. In orangutans the central incisors have, comparatively, still longer roots than does *Pan*. As is well known, possession of large incisors relative to cheek teeth is a general feature distinguishing both fossil and living pongids from known hominids. In this feature of central incisor size, as in others, such as the highly arched palate, *Ramapithecus* agrees more closely with Hominidae than with Pongidae.

It is evident that most of the misapprehensions regarding *Ramapithecus* now current trace back to Hrdlička's discussion of the specimen (1935) in which he insisted that the form could not be a hominid. Even a casual examination of this paper is sufficient to show that it bears every evidence of being a controversial and non-objective contribution. In contrast to this, all of the hominid resemblances cited for Y.P.M. 13799 by Lewis (1934) appear to this writer to have been correctly drawn, and these are reinforced by the additional hominid features called to attention here.

However, another possible source of uncertainty regarding the genus may derive from a mandible, Peabody Museum No. 13807, assigned by Lewis (1934) to *Ramapithecus*, but to a different species *R. hariensis*. This mandible shows heteromorphy in the lower premolars of the sort characteristic of pongids but which is not known in undoubted Hominidae. In view of this heteromorphy, not indicated in P^{3-4} of *R. brevirostris* and inasmuch as the mandible of *R. hariensis* comes from a different locality, and from a horizon that may be considerably lower in the section, I see no convincing reason for associating generically the form it represents with that of the maxilla of *R. brevirostris*.

What then can be stated as fact regarding the type maxilla of *Ramapithecus*? As the species name implies, and as Lewis originally stated, this primate exhibits a reduction in prognathism, upper incisor size, and in length from the alveolar border above the incisors to the base of the nasal opening, when compared to pongids of its general size, whether living or fossil. This length from nasal aperture to I^2 in *Ramapithecus* is approximately 44 per cent of the length of P^3 - M^2 (see arrows, figure 1) while corresponding percentages in a series of specimens of *Pan* range from 70 to 98. Specimens of *Pongo* and *Gorilla* examined fall within the range of *Pan*, in this proportion.

In addition to the foregoing differences, the upper incisors and canine, judging from their alveolae, cannot have been as large as they typically are in even the smallest Great Apes, a fact also pointed out by Lewis (1934), who remarked: "The face is very slightly prognathous, as contrasted with recent Simiidae. There are no diastemata in the dental series. The canine is small, not an antero-posteriorly elongated trenchant tusk but a hominid type with a transverse dimension exceeding the antero-posterior dimension." Lewis (1934: 163-166) fully discussed the dental characters of Y.P.M. 13799, consequently it is unnecessary to repeat this description here. In general, crown patterns resemble both *Dryopithecus* and *Australopithecus* about equally.

Without further extending the polemical atmosphere surrounding this specimen, so unfortunately initiated by Hrdlička, this writer will simply call attention to his final statement regarding *Ramapithecus*, since he appears to be the only person to have studied the actual specimen who has published doubts as to its hominid status. The significance of this remark, in the light of modern understanding of the australopithicines as hominids, seems to have been overlooked. Hrdlička (1935:36) observed: "The genus [*Ramapithecus*], although in the upper denture, in general, nearer to man than are any of the Dryopitheci or the *Australopithecus* cannot . . . be legitimately established as a hominid, that is a form within the direct human ancestry." This curious statement, indicates that Hrdlička would now have to place the genus in the Hominidae since he regarded it as more man-like than *Australopithecus*, a genus universally accepted today by competent students as belonging to this family. Evidently if there are convincing reasons why *Ramapithecus brevirostris* should not be regarded as representing the earliest known hominid they have not been demonstrated to date.

To contend that the specimen is too inadequate for definite taxonomic assignment implies that pongids and hominids cannot be distinguished, even when reasonable information is available regarding the size, emplacement, structure and arrangement (whether arcuate or parabolic) of nearly all of the upper dentition, together with several characters of palate and face as well. Postcranial remains, if found, might make it easier to assign this primate taxonomically, but the six or seven distinct approximations to hominid morphology discussed here for Y.P.M. 13799 provide an adequate basis for associating it with the latter family. It seems illogical to choose the alternative of regarding this form as belonging to an otherwise unknown group of apes, parallelistic toward hominids but not closely related to them, when it occurs in the proper time and place to represent a forerunner of Pleistocene Hominidae.

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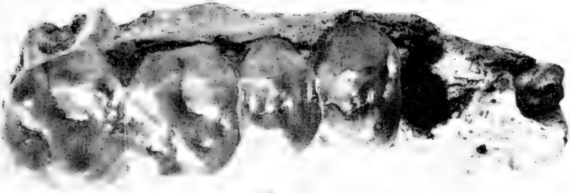
Figure 1

Occlusal view (A) and lateral view (B) of right maxilla of type of *Ramapithecus brevirostris,* Y.P.M. 13799.

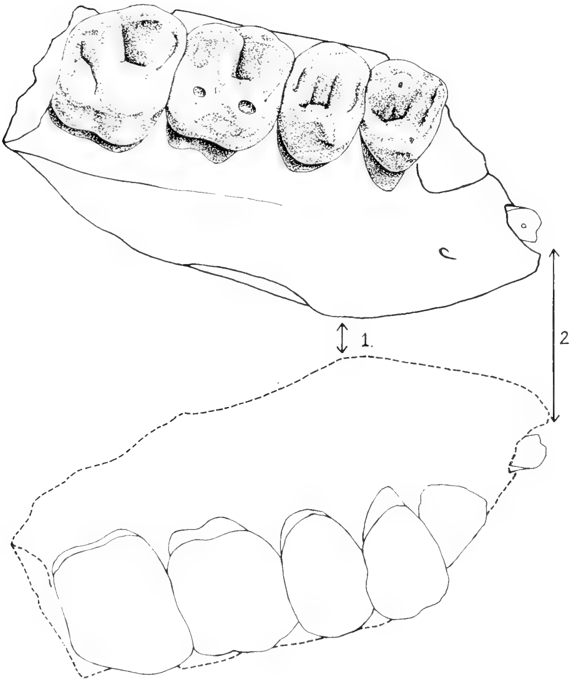


A.

B

Figure 2

Ramapithecus brevirostris, right maxilla, Y.P.M. 13799, and reverse of same, showing arcuate arrangement of teeth.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YALE PEABODY MUSEUM

OF NATURAL HISTORY

Number 58 April 16, 1962 New Haven, Conn.

A NEW DEVONIAN PELECYPOD FROM ALASKA AND ITS BEARING ON PTERIOID PHYLOGENY

A. Lee McAlester

One of the most problematic aspects of a recent revision of some New York Upper Devonian pelecypods (McAlester, 1962a) was the generic status and phylogenetic position of the well-known Chemung stage pterioid species *Cornellites* (formerly *Pterinea*) *chemungensis* (Conrad). This species is known only from the northern Appalachian region where it has long been considered to be an index fossil to the "type" Chemung (Chemung stage of Cooper, 1942; see also Williams, 1907, and Chadwick, 1935). Like most "index fossils," *C. chemungensis* first appears fully-developed in the stratigraphic record and then shows no evolutionary change before it disappears in late Chemung time. It is a common fossil at several localities which expose the middle Chemung stage horizons, but it is rare in the lowest and highest horizons of the stage. Most New York Upper Devonian clams have closely related species in the prolific earlier faunas of the New York Middle Devonian, but no probable ancestral or closely related species have been discovered for *C. chemungensis*. Furthermore, it is a morphologically distinctive species that can only with difficulty be forced into any of the standard genera of Devonian pterioids, and for this reason it was very tentatively assigned to the Lower and Middle Devonian genus *Cornellites* in the revision of the Chemung faunas. This morphologic distinctiveness and apparent temporal and spatial isolation have combined to make the origins and relations of *C. chemungensis* most puzzling.

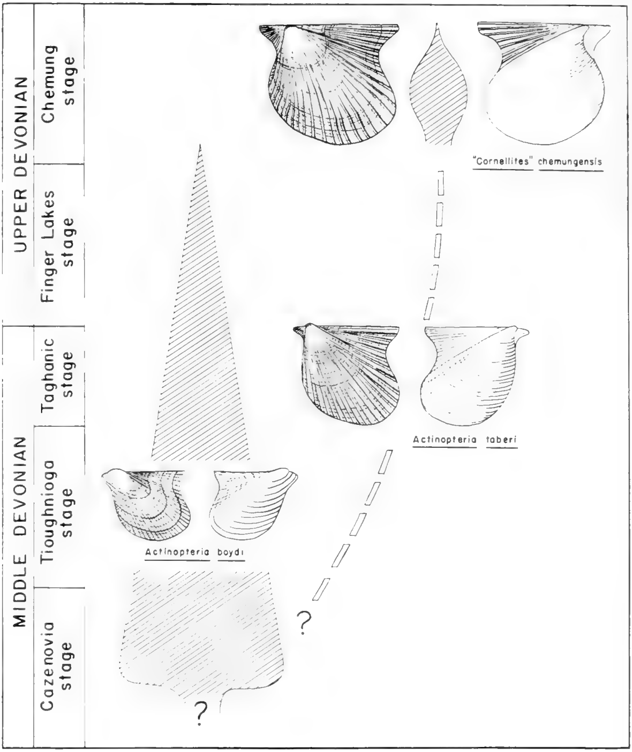

Figure 1. Suggested phylogenetic position of *Actinopteria taberi.* The shaded areas show known ranges and relative abundances of *Actinopteria boydi* and *"Cornellites" chemungensis.* The drawings of the species are schematic and are not intended to represent particular specimens.

Recently some unexpected new light has been thrown on this problem by several collections of poorly-preserved fossils found at Paleozoic outcrops which were exposed during highway construction operations near Livengood, Alaska. These specimens were collected by Bond Taber of the U. S. Geological Survey in the course of stratigraphic investigations in the Livengood region and were kindly sent to me for identification by R. B. Neuman and J. T. Dutro of the Geological Survey.

Pelecypods are the dominant element in the faunas from these outcrops, although some fragmentary gastropods, brachiopods, and crinoid columnals are also found. The pelecypods are of several types including schizodont, grammysioid, mytiloid, and other forms, but by far the most abundant and well-preserved element in these collections is a distinctive pterioid pelecypod which is described below as the new species *Actinopteria taberi.* This form is morphologically intermediate between the enigmatic *C. chemungensis* and the common Appalachian Middle Devonian species *Actinopteria boydi.* It therefore suggests that the Upper Devonian species "*Cornellites*" *chemungensis* may not be related to the Lower and Middle Devonian *Pterinea-Cornellites* stock as has long been assumed, but may instead have had an independent origin from an *Actinopteria* stock. The probable morphologic changes and time relations in this suggested phylogeny are shown schematically in fig. 1.

Mr. Taber anticipates further stratigraphic studies and fossil collecting in these rocks, and we hope that this work will provide additional specimens and data for a full description of the less common pelecypods of this significant fauna.

Actinopteria taberi, n. sp.

Figures 3-18

Description. Shell of medium size (median length of 14 measurable specimens 20 mm), inequivalve, left valve moderately convex, right valve slightly convex in umbonal region, becoming flattened towards margin. Shape variable, height ranging from 73 to 100 per cent of length (mean of 12 measurable specimens 80 per cent). Prominent anterior auricle and posterior wing on both right and left valves, relative length of both auricle and wing variable. Prominent radial surface sculpture on body of left valve, becoming somewhat finer on posterior wing (figs. 3, 4). Well-preserved fragments of left valves show traces of very fine concentric sculpture (fig. 5). Surface sculpture of right valves consisting of strong radial ridges on posterior wing only, rest of valve showing faint radial and concentric sculpture making up fine reticulate network which is most prominent in umbonal region. Dentition and hinge features unknown. Ligament unknown. Musculature and interior features unknown. Shell material unknown.

Types. Holotype: U. S. National Museum No. 140873. Type locality: locality A (see below), near Livengood, Alaska. Stratigraphic position: probably near Middle-Upper Devonian boundary as defined in New York (see below). Additional specimens: U. S. National Museum Nos. 140874-140896 (No. 140897 questionably this species).

Material. The species is based on 18 relatively complete specimens (11 left and 7 right valves) and about 30 fragments. All of the specimens are preserved as predominantly external "composite molds" (see McAlester, 1962b). During diagenetic alteration the composite molds have become colored by a bright orange limonitic stain which clearly distinguishes the outlines of the former shell material against the much darker matrix. All of the specimens are permanently deposited in the U. S. National Museum, Washington, D. C.

Geographic occurrence. The species is known with certainty only from specimens found at the following two localities in the vicinity of Livengood, Alaska. Locality A (U. S. Geological Survey field locality number 60ATb85): medium bedded shale and siltstone from borrow pit on north side of Livengood-Eureka road approximately 7 miles southwest of Livengood, Alaska, Lat. 65° 27′N, Long. 148° 43′W, (N13.9 inches, E8.5 inches from SW corner measured parallel and perpendicular to west margin of Livengood B-4 quadrangle, Alaska, 1953 edition). Twelve relatively complete specimens and about 20 fragments were found at this locality. Locality B (U. S. Geological Survey field locality number 60ATb500): thin-bedded shales and siltstones with minor medium-bedded, medium to coarse-grained sandstone from borrow pit approximately 7.7 miles east of Livengood, Alaska, at approximately mile 61.4 on Elliott Highway (U.S. 97), Lat. 65° 29.1′N, Long. 148° 21.7′W, (N16.2 inches, E3.95 inches from SW corner measured parallel and perpendicular to west margin of Livengood B-3 quadrangle, Alaska, 1954 edition). Six relatively complete specimens and about 10 fragments were found at this locality.

Pterioid fragments also occur less commonly at several other borrow pits along the Livengood-Eureka road west of locality A. Unlike *A. taberi*, some of these specimens show right valves with strong, imbricate, concentric sculpture. Pending discovery of more material which would permit an analysis of variation in pterioids from these localities, only the specimens from localities A and B are included in *A. taberi.*

Stratigraphic occurrence. The following discussion of possible stratigraphic relations is based upon comments generously supplied by Mr. Taber who notes that there is considerable doubt about the age of the exposures from which the pelecypod faunas were collected. Mertie (1937) mapped the outcrop areas of localities A and B as Devonian non-carbonate or intrusive rocks (Dnc, Dbi). The two nearest fossil localities mentioned by Mertie (p. 102 and 120) lie between localities A and B; Mertie's locality 16AMt64a was about 1½ miles southeast of Livengood, and his locality 21AMt128 was about 1½ miles south of Livengood. Both collections were made from limestone beds within essentially clastic sections that Mr. Taber feels are equivalent to each other and also approximately equivalent to the clastic sections in which the pelecypods were found. The fossils from Mertie's two localities (apparently mostly corals and brachiopods) were identified by Edwin Kirk, who regarded collection 16AMt64a to be Middle Devonian (Mertie, p. 103), while 21AMt128 was identified less definitely as "Devonian or Mississippian, more likely the former" (unpublished U. S. Geological Survey memorandum). Since Mertie's localities and the pelecypod bearing clastics may be equivalent, these identifications suggest a Middle Devonian or, perhaps, younger age for *A. taberi.*

The proposed phylogenetic position of *A. taberi* further strengthens this suggested age. The exact first appearance in the Appalachian Middle Devonian of *Actinopteria boydi,* the proposed ancestral form, has not yet been established, but it is extremely abundant in some lower Middle Devonian horizons, particularly the Delphi Station member of the Skaneateles formation (see Cooper, 1930, p. 219; also Cooper, 1942). It remains a locally common form throughout the New York Middle Devonian, but it becomes rare in the Upper Devonian where it is last known from only a few Chemung stage specimens. As mentioned earlier, the probable descendent species, *"Cornellites" chemungensis,* is known only from the Upper Devonian Chemung stage of the New York region. These relations, which are summarized in fig. 1, are fully consistent with a late Middle or early Upper Devonian age for the Alaskan localities which contain the transitional *A. taberi.* It should be noted, however, that the Alaskan specimens could represent a later local survival of the transitional evolutionary stage and hence be contemporaneous with, or even younger than, the *C. chemungensis* bearing rocks of New York. On the other hand, a pre-Middle Devonian age would be most improbable for these localities if the proposed phylogeny is correct.

As noted below, slight morphologic differences in the specimens also vaguely suggest that locality A is the older of the two *A. taberi* occurrences.

Comparisons. *A. taberi* differs in the following ways from its nearest probable relatives:

> *Actinopteria boydi* (Conrad): Left valves of *A. taberi* differ in showing coarser and more prominent radial sculpture and much finer concentric sculpture. Right valves of *A. taberi* show finer and more regular concentric sculpture, somewhat stronger radial sculpture on the posterior wing, and obscure traces of radial sculpture on the body. Both valves differ from *A. boydi* in having smaller but more sharply defined anterior auricles and a generally more upright shape.
>
> *"Cornellites" chemungensis* (Conrad): Left valves of *A. taberi* differ in having faint concentric sculpture and less widely spaced radial sculpture. Right valves of *A. taberi* have more prominent concentric sculpture and finer, less widely spaced radial sculpture on the posterior wing. Both valves have smaller anterior auricles and a less upright shape than *C. chemungensis.*

Discussion. "*Cornellites*" *chemungensis* and *Actinopteria boydi* are dissimilar enough so that the evolution of one from the other would not seem very likely were it not for the transitional Alaskan specimens. The evolution of *A. boydi* into *C. chemungensis* would primarily require an increase in size and erectness as well as a loss of concentric sculpture, a strengthening of radial sculpture, and a slight deepening of the "byssal notch" resulting in a more clearly-defined anterior auricle. An enlargement of the external ligament area and a strengthening of the dentition may have also been necessary, although too little is known of the hinge area in *A. boydi* to evaluate this possibility. As illustrated in fig. 2, the Alaskan specimens are intermediate in erectness. They also show the expected strengthening of radial sculpture and weakening of concentric sculpture, as well as a more clearly-defined anterior auricle. *A. taberi* is not, however, completely ideal as a morphologic intermediate because several of the specimens show anterior auricles that are somewhat smaller than those of either *A. boydi* or *C. chemungensis*. This feature and other more minor differences caution that *A. taberi* may be somewhat removed from the direct evolutionary line between *A. boydi* and *C. chemungensis*.

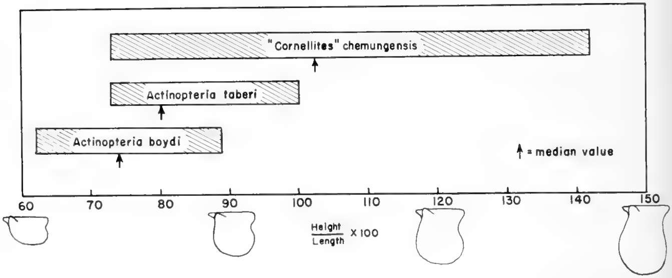

Figure 2. Range of shape variation in *Actinopteria taberi, Actinopteria boydi, and "Cornellites" chemungensis*. The data for *A. boydi* were based on 27 Yale Peabody Museum specimens from Pratts Falls, New York. The *C. chemungensis* measurements were taken from the 41 complete specimens described in McAlester, 1962a.

There also appear to be morphologic differences in the material from each of the Alaskan localities, although too few good specimens are available to fully evaluate the consistency of this variation. Specimens from locality A (figs. 3-6, 8, 11-14, 16-18) are generally smaller, less erect, and show slightly finer sculpture than those from locality B (figs. 7, 9, 10, 15). The specimens from locality A are therefore most like the suggested stem form, *A. boydi*, whereas the locality B specimens are closer to *C. chemungensis*, the proposed descendent form. This tentatively suggests that locality A is the older of the two localities. More material might show these differences, if consistent, to be great enough for two specific names, but it now seems preferable to consider the specimens as one variable species. A single right valve found at locality B (fig. 19) is very erect and has a much larger anterior auricle than any of the other specimens from either locality. This specimen differs from the few known right valves of *C. chemungensis* only in having finer radial sculpture on the posterior wing with traces on the body of the valve. For this reason the specimen is doubtfully identified as *A. taberi* and was not included in the above species description. It may have come from a younger horizon than the other specimens found at locality B.

The dominance of *A. taberi* at these localities suggests similar associations dominated by "*Cornellites*" *chemungensis* in the New York Devonian which have been interpreted as "patch-reef" epifaunal assemblages adapted for life on hard shelly bottoms (McAlester, 1960). On the other hand, the fragmentary preservation of most of the Alaskan specimens also indicates probable strong current or wave action with transportation and perhaps mixing of the pelecypod faunas. Further ecologic interpretation may become possible with the discovery of new material and the description of the several less common pelecypods found at these localities.

No likely descendants of *C. chemungensis* are now known and therefore *A. taberi* and *C. chemungensis* may well form a compact and isolated evolutionary group. Normally it would be appropriate to propose a new generic name for these forms in view of their morphologic distinctiveness and probable evolutionary isolation. Because, however, of the current generic chaos in the Paleozoic pterioid pelecypods, I prefer to avoid adding still another generic name without undertaking a more complete study of at least the Devonian pterioids. In any event, such nomenclatural matters are of minor importance in relation to the more significant evolutionary facts that they are intended to express. The transitional Alaskan specimens, which are clearly specifically distinctive, may of course with equal justification be assigned to the stem genus *Actinopteria* since they are morphological intermediates. This course is followed here pending more complete generic revision. It should be noted, however, that such revision will almost certainty result in a new generic name for "*Cornellites*" *chemungensis.*

Only one other New York Middle Devonian species is at all likely to have been ancestral to *C. chemungensis.* This is the common species *Cornellites* (formerly *Pterinea*) *flabella* (Conrad), which is undoubtedly closely related to the Rhenish Lower Devonian type species of the genus *Cornellites. C. flabella* shows some morphologic similarities with *C. chemungensis* (particularly the upright shape and the distribution of the sculpture on the right valve) but, in general, I regard the differences between these two forms to be even greater than those which separate *C. chemungensis* from *A. boydi.* Among the significant dissimilarities are the very strong reticulate sculpture, the proportionately larger and differently shaped auricles, and the strongly inflated left valve and strongly concave right valve. In particular the strong convex-concave shape appears to be an extreme specialization away from the more typical pterioid pattern of a slightly flattened right valve and a more gently convex left valve which is the pattern of both *A. boydi* and *C. chemungensis.* The evolution of *C. chemungensis* from *C. flabella* therefore now seems to me to be most improbable, based on our admittedly imperfect knowledge of New York Middle Devonian pelecypods.

The species is gratefully dedicated to Mr. Bond Taber of the U. S. Geological Survey to whom I am indebted not only for collecting the specimens, but also for valuable suggestions and enthusiastic cooperation. I also wish to express my appreciation to: R. B. Neuman and J. T. Dutro of the Geological Survey for first sending me the material; to my colleague K.

M. Waage for discussions and advice; and to John Howard and Bruce Unminger who carefully prepared the photographs and line drawings.

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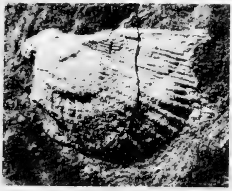
Figures 3 - 11. *Actinopteria taberi,* n. sp. All figures are left valves magnified x 1.5.

Figure 3. Holotype, USNM 140873, loc. A. Figure 4. USNM 140874, loc. A. Figure 5. Latex cast of USNM 140875, loc. A, a fragment of a left valve showing the concentric sculpture. Figure 6. USNM 140876, loc. A. Figure 7. USNM 140877, loc. B. Figure 8. USNM 140878, loc. A. Figure 9. USNM 140879, loc. B. Figure 10. USNM 140880, loc. B; the posterior and ventral regions are preserved only as a fragmentary negative composite mold and are therefore illustrated from a latex cast; the umbonal and anterior regions preserve the original positive composite mold. Figure 11. USNM 140881, loc. A.



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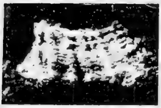

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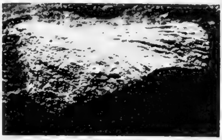

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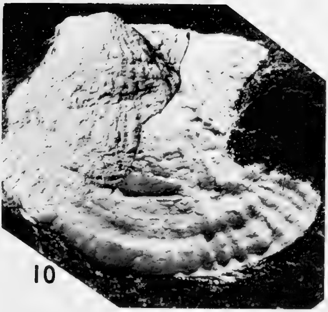

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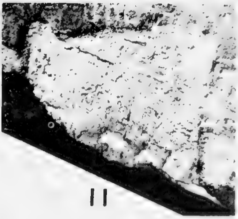

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Figures 12-18. *Actinopteria taberi,* n. sp. All figures are right valves magnified x 1.5.

Figure 12. USNM 140882, loc. A. Figure 13. USNM 140883, loc. A. Figure 14. USNM 140884, loc. A. Figure 15. Latex cast of USNM 140885, loc. B. Figure 16. Latex cast of USNM 140886, loc. A. Figure 17. USNM 140887, loc. A. Figure 18. USNM 140888, loc. A.

Figure 19. ?*Actinopteria taberi,* n. sp. Right valve magnified x 1.5.

Figure 19. USNM 140897, loc. B, a doubtfully identified specimen (see text).

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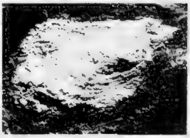

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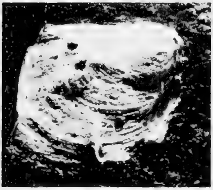

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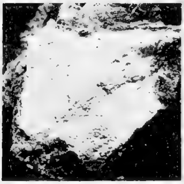

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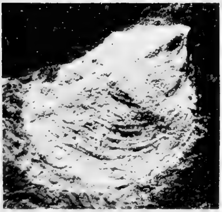

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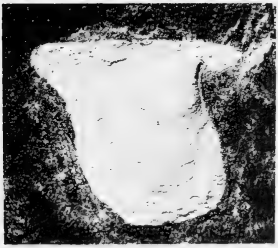

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Postilla

YALE PEABODY MUSEUM

OF NATURAL HISTORY

Number 59 April 18, 1962 New Haven, Conn.

BIRDS OBSERVED IN THE IMHOFF GARDENS OF DHAHRAN, AND AT RAS TANURA, SAUDI ARABIA

1959—1962

MARY G. EDDY*

Dhahran is an oil town with a population of about 3,000 United States citizens, established in 1937 by the Arabian-American Oil Company as headquarters for its overseas staff. About ten miles inland from the Persian Gulf coast and surrounded by desert, its gardens have flourished by reason of the large quantity of natural, slightly brackish water obtained from wells. Gardens, lawns, hedges of mock honeysuckle, and trees, date palms, acacia, tamarisk all now grow freely as well as many ornamental plants such as oleanders and bougainvillea.

Water is used in vast quantities, especially for nearly six months of air conditioning in the settlement. All of the sewage water flows into the desert several miles to the east where it is treated and purified. Here at the Imhoff gardens several small ponds have been created, surrounded partly by cultivation, partly by rank herbage and rushes. This new environment, where only desert existed previously, has naturally altered the

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*Mrs. William Eddy, Beirut, Lebanon.

bird population radically. It was first mentioned by Ripley (1951) in his paper on a visit to Dhahran and Bahrein in the summer of 1950. It was of course totally unknown to Ticehurst and Cheesman (1925) in the only other published short paper on the area.

In winter the Imhoff gardens with their lakes become a stopping place for many migrants. In summer, the tamarisk trees and garden atmosphere provide a welcome shelter from the burning heat of the open desert, though temperatures may reach 120 degrees Fahrenheit in the shade. The gardens are now surrounded by a fence which gives added protection to the bird fauna, although poachers attempt to shoot at the duck during the winter migration.

My first visit to these gardens occurred in July, 1950 accompanied by Mr. and Mrs. S. Dillon Ripley. Since then I have always visited the Imhoff gardens as well as the sand spits along the coast near Ras Tanura, the oil refinery forty miles north along the coast, whenever my husband and I visited eastern Saudi Arabia during the ensuing years. For texts I have used Peterson, Mountfort and Hollom's *Field Guide to the Birds of Europe*, and Meinertzhagen's *Birds of Arabia*, both invaluable aids. The following notes should be of interest when compared with the earlier records of Ripley, as well as Meinertzhagen's book. It is obvious that migrants as well as local resident species are able to exploit rapidly such a newly emerging favorable environment such as that at Imhoff. It is my sincere hope that the following list will encourage further observations by others in this fascinating spot.

Annotated List from the Imhoff Gardens*

Podiceps nigricollis, Black-necked Grebe. January, 1960 and 1961, and April, 1960. Meinertzhagen (op. cit. p. 438) records this species as "scarce."

Podiceps ruficollis, Little Grebe. January, 1960 and 1961; November, 1960. Meinertzhagen (op. cit., p. 439) lists two sight records for the species, from Aden and Bahrein.

*Editorial comments are by S. Dillon Ripley.

Phalacrocorax carbo, Cormorant. March, 1959; January, April, June and November, 1960.

Ardea cinerea, Grey Heron. Seen commonly in January, April, May, June and November, 1960 and 1961. I thought that there were immatures among the four or more birds seen on each visit.

Ardea purpurea, Purple Heron. Seen once in late May-early June, 1961. The neck feathers appeared buffy; perhaps a sub-adult.

Nycticorax nycticorax, Night Heron. Seen only once in January, 1960.

Ixobrychus minutus, Little Bittern. More than two birds were seen from May 27 to June 3, 1961 in heavy reeds. Breeding?

Milvus migrans, Black Kite. January, 1961.

Falco tinnunculus, Kestrel. Seen at all seasons.

Falco naumanni, Lesser Kestrel. Seen migrating in March.

Falco peregrinus, Peregrine. April, 1960, and in late May, 1951, a very late date unless the bird was an escape.

Phoenicopterus ruber, Flamingo. Seen once, a single bird in late May, 1961.

Anas platyrhynchos, Mallard. January and November, 1960.

Anas crecca, Teal. January, 1960 and 1961.

Anas clypeata, Shoveler. January, April and November.

Anas acuta, Pintail. January and November.

Aythya nyroca, White-eye or Ferruginous Pochard. January, November and June. The June record was repeated in 1960 and again in 1961 when a pair was seen every day for a week. This is not only the southernmost record for the species in Arabia, but also seems exceptionally late in the year.

Aythya ferina, Pochard. Numerous in January and November.

Fulica atra, Coot. Common in January, April and November.

Charadrius squatarola, Grey Plover. January and November.

Charadrius apricarius, Golden Plover. April, 1960. (A valuable record, as sight records or specimens from Arabia are almost nonexistent, Ed.)

Charadrius alexandrinus, Kentish Plover. Resident, seen displaying in late May-early June in the Gardens.

Charadrius dubius, Little Ringed Plover. Seen in January, April, May-June and November.

Charadrius hiaticula, Ringed Plover. January, April, June and November.

Calidris alpina, Dunlin. January, April and November.

Calidris testacea, Curlew Sandpiper. Six seen in the Gardens in late May-June, 1961.

Calidris minuta, Little Stint. Very common in January and November. A few seen in April, and one or two still lingering as late as late May-June, 1961.

Tringa totanus, Redshank. January, April and May, (May 3, 1957).

Tringa nebularia, Greenshank. January, April and November.

Tringa stagnatilis, Marsh Sandpiper. January, November.

Tringa ochropus, Green Sandpiper. January, March, April, and late May-June, 1961. Not recorded so late in Arabia before.

Tringa glareola, Wood Sandpiper. January, late May-June, 1961 (a new late record for Arabia, Ed.) and November.

Tringa hypoleucos, Common Sandpiper. January, April, late May-June, 1961 (a new late record for Arabia), and November.

Tringa erythropus, Spotted Redshank. January, 1960, and May 3, 1957. (A first winter record for Arabia, Ed.)

Calidris canutus, Knot. April, 1960. A first record for Saudi Arabia, although the species has been recorded from Muscat.

Limosa limosa, Black-tailed Godwit. January, April and September in various years from 1956 to 1960. Records are scarce for Arabia.

Himantopus himantopus, Stilt. April, 1960. Called a "rare straggler" by Meinertzhagen (op. cit., p. 508).

Capella gallinago, Snipe. January, April and November.

Cursorius cursor, Cream-colored Courser. January.

Glareola pratincola, Pratincole. A single bird, late May, 1961.

Larus argentatus (expanded L. *fuscus* of Meinertzhagen, Ed.) Herring Gull. January, March, April, and June.

Larus fuscus, Lesser Black-backed Gull. March, April and November, 1959-60.

Larus ridibundus, Black-headed Gull. January and April.

Chlidonias leucoptera, White-winged Black Tern. Up to eight individuals in late May-June, 1961; also a single bird in June, 1960. Third record for Arabia *vide* Meinertzhagen (op. cit., p. 517).

Pterocles alchata, Pin-tailed Sandgrouse. Several seen in November, 1960. Rarely recorded in Arabia, but probably straggles erratically in the area.

Streptopelia turtur, Turtle Dove. A single dove seen in the Gardens in late May-June, 1961, Dhahran, April, 1957.

Psittacula krameri, Rose-ringed Parakeet. Now established at Dhahran and a new record for Saudi Arabia. (Known previously only from Oman and Muscat, see de Schauensee and Ripley, 1953, Ed.)

Apus apus, Swift. Several seen in late May-June. (An attempt should be made to find the Swift as a breeding species in Arabia, Ed.)

Merops apiaster, Bee-eater. Seen in January and May.

Merops superciliosus, Blue-cheeked Bee-eater. March and April.

Hirundo rustica, Swallow. March, April, June.

Hirundo d. daurica, Red-rumped Swallow. A migrating flock of twenty birds seen in February, 1962.

Riparia riparia, Sand Martin. Commonly seen in May-June, far later than recorded by Meinertzhagen, (op. cit., p. 279-80).

Delichon urbica, House Martin. January, April.

Upupa epops, Hoopoe. Seen in March and April, as well as July (Ripley, 1951, p. 5).

Lanius excubitor, Great Grey Shrike. Seen throughout the year. (Subspecies? Ed.)

Lanius minor, Lesser Grey Shrike. May, 1957, a new spring record for Arabia.

Lanius senator, Woodchat Shrike. January, March, May.

Lanius collurio, Red-backed Shrike. Dates in late May-June are later than recorded by Meinertzhagen (op. cit., p. 171-2).

Lanius isabellinus, Isabelline or Pale Brown Shrike. Seen in January, 1960 and 1961.

Galerida cristata, Crested Lark. Seen at every month of the year; (probably *magna*, Ed.)

Certhilauda alaudipes, Bifasciated Lark. Seen at various seasons.

Alauda arvensis, Skylark. (Not unexpected in January, Ed.)

Eremopteryx nigriceps, Black-crowned Finch-lark. Lives on the desert fringes of the Gardens and Dhahran town.

Sturnus vulgaris, Starling. Seen in January and March at Dhahran.

Oriolus oriolus, Oriole. Three to four birds seen singing in late May-June form a most unusual record for this species which is not known to breed south of southern Iran.

Corvus corax, Brown-necked Raven. March, April, July.

Pycnonotus leucotis, Bulbul. Common in the Gardens, but now far less common in Dhahran town since heavy doses of DDT were given to the lawns to control worms. Thus even in Arabia pesticides have had an effect on the birds which are attracted by human habitation. (In spite of Meinertzhagen's doubts about this population, op. cit., p. 180, I find Dhahran birds still paler and larger than *mesopotamiae* from Iraq, Ed.)

Muscicapa striata, Spotted Flycatcher. Seen in late May-June and at the normal spring and fall migration dates. Are some individuals resident?

Musicapa albicollis, Collared Flycatcher. Seen in March, 1957.

Sylvia curruca, Lesser Whitethroat. April, 1960 (probably *minula* which has been taken in Oman and the Hadramaut in March, Ed.)

Sylvia atricapilla, Black Cap Warbler. April and May, 1957, seen both at Imhoff and in Dhahran.

Sylvia borin, Garden Warbler. January, April.

Sylvia nana, Desert Warbler. Seen in the desert in late May-June.

Hippolais languida, Upcher's Warbler. Seen in late May-June. Breeding?

Hippolais pallida, Olivaceous Warbler. Seen in late May-June. This warbler may breed in Arabia, but it is not at present known to do so.

Hippolais icterina, Icterine Warbler. Seen once in late May-June. A second record for Arabia.

Phylloscopus trochilus, Willow Warbler. January, March, April, June and November.

Phylloscopus collybita, Chiffchaff. January, March, April, June and November.

Phylloscopus sibilatrix, Wood Warbler. Seen once in April, 1960.

Acrocephalus schoenobaenus, Sedge Warbler. Very secretive, but the churring insect-like call reveals its whereabouts in the cut-over tamarisk trees near the lake. Seen in late May-June, a very late record for the species.

Lusciniola melanopogon, Moustached Warbler. More than one specimen seen on several occasions walking over the rocks near the lake edge close to bushes and trees. The eye-stripe was very clear indicating that this was not the Sedge Warbler. Seen in late May-June.

Prinia gracilis, Graceful Warbler. Resident and seen at all seasons.

Erithacus megarhynchos, Nightingale. Observed once in late May-June.

Erithacus svecicus, Bluethroat. Several seen in January and April.

Phoenicurus phoenicurus, Redstart. January, April, late May-June, and November. (Not previously recorded from eastern Arabia, Ed.)

Phoenicurus ochruros, Black Redstart. January and April.

Saxicola rubetra, Whinchat. January, March.

Saxicola torquata, Stonechat. January, March and November.

Oenanthe oenanthe, Wheatear. Seen in January and April.

Oenanthe hispanica, Black-eared Wheatear. April, 1960.

Oenanthe leucomela, Pleschanka's or Pied Wheatear. March April records are useful as they are the first from eastern Arabia.

Oenanthe isabellina, Isabelline Wheatear. January, March, April, May and November.

Oenanthe finschii, Finsch's Chat. March, April.

Oenanthe xanthoprymna, Red-tailed Chat or Wheatear. Seen in November, 1960.

Monticola saxatilis, Rock Thrush. January, March and May.

Turdus ericetorum, Song Thrush. Seen in January, 1960 and 1961.

Turdus ruficollis atrogularis, Black-throated thrush. Two birds seen in gardens of Dhahran, February, 1962.

Anthus pratensis, Meadow Pipit. Seen in January, 1960, 1961, March, 1959 and April, 1960. A first sight record for Arabia.

Anthus spinoletta, Water Pipit. January, 1960.

Anthus campestris, Tawny Pipit. January and April.

Anthus cervinus, Red-throated Pipit. January, March, April and May.

Anthus trivialis, Tree Pipit. January, April and November.

Motacilla alba, White Wagtail. January, March, April and November.

Motacilla flava, Blue-headed Wagtail. March and April.

Motacilla flava, Yellow form or Yellow Wagtail (*lutea?* Ed.) March and April.

Motacilla flava feldegg, Black-headed Wagtail. Seen in April, 1960 and again a pair in late May-June. One was panting in the heat. (A late date for these migrants, Ed.)

Motacilla cinerea, Grey Wagtail. A single record in March, 1959.

Passer domesticus, House Sparrow. Extremely common especially near the horse corrals.

Carduelis spinus, Siskin. November 13, 1959, a flock of Siskin in the thickets of Imhoff. I am very familiar with the Siskin on migration in Lebanon and I remember that I looked up

Meinertzhagen to see what he had to say and found the Siskin not mentioned in his *Birds of Arabia*. The Bannermans in *Birds of Cyprus* (1958) call the Siskin a winter visitor and passage migrant. (New record for Arabia, Ed.)

Emberiza calandra, Corn Bunting. Seen in January, 1960 and 1961. (A new winter record for Arabia, Ed.)

Emberiza hortulana, Ortolan Bunting. April, 1960.

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Postilla

YALE PEABODY MUSEUM
OF NATURAL HISTORY

Number 60 May 7, 1962 New Haven, Conn.

NOTES ON A COLLECTION OF BIRDS FROM SURINAM

PHILIP S. HUMPHREY AND RUDOLF FREUND

During the period November 18 to December 17, 1961, Mr. and Mrs. Rudolf Freund traveled in Surinam and made small collections of vertebrates and insects for the Yale Peabody Museum of Natural History. They collected birds at three localities in southern Surinam. One of these localities (Kaysergebergte Airstrip) had been visited in October of the same year by Mr. Harry A. Beatty who collected birds there for the Chicago Museum of Natural History (Blake, 1961). To our knowledge no previous collections of birds have been made at the two other localities visited by the Freunds (Sipaliwini Airstrip and Paru Savannah).

The Freunds collected a total of 117 birds which they preserved in 10 per cent buffered Formalin. When the specimens arrived at the Peabody Museum they were washed in water and then stored in 70 per cent alcohol. All specimens were dried with a jet of compressed air and then identified; 32 specimens were prepared as study skins by Mr. David H. Parsons.

ACKNOWLEDGMENTS

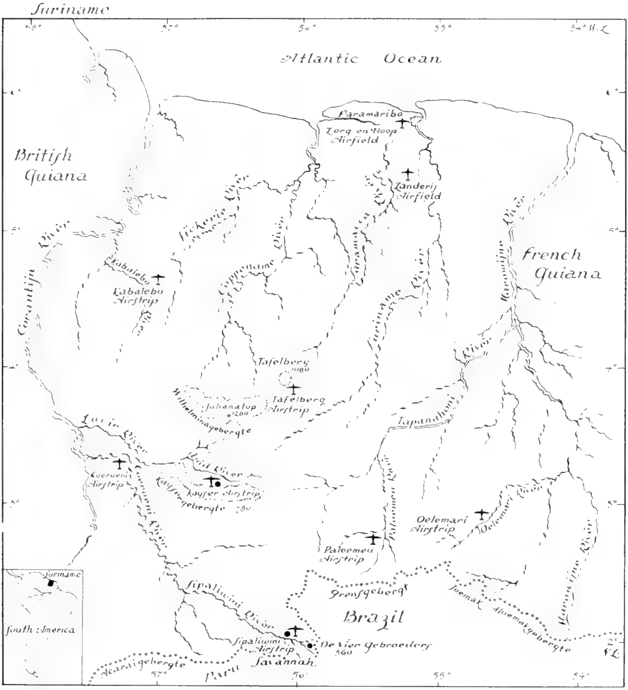
The Freunds' trip to the interior of Surinam would have been impossible without the generous assistance of the government of Surinam. Mr. and Mrs. Freund and the Peabody Museum of Natural History are especially grateful to the following people and institutions: Mr. Harold Nassy, Director of the Government Information Service; LARECO, the Land Reclamation Corporation; Mr. Fritz Barends, Mayor of Paramaribo; Dr. D. C. Geijskes, Director of the Surinam Museum; Corporal H. P. Pijpers of the Surinam Army; Mrs. Dorothy Badger, Surinam Tourist Bureau, New York; Surinamse Luftvaartmaatschappij (Surinam Airways); and Pan American Airways.

We are also grateful to Mr. Emmet R. Blake, Chicago Museum of Natural History; Mr. James Bond, Philadelphia Academy of Natural Sciences; Dr. Kenneth C. Parkes, Carnegie Museum; and Dr. Dean Amadon, American Museum of Natural History, for use of specimens in their care. We are especially indebted to Mr. F. Haverschmidt for calling to our attention a species misidentified in the manuscript of this note and for bringing up to date our comments on three species. Dr. Wesley E. Lanyon and Mr. George E. Watson kindly examined specimens for us at the American Museum of Natural History. Dr. S. Dillon Ripley, Mr. Peter Ames, and others have given us advice or assistance.

COLLECTING LOCALITIES

Kaysergebergte Airstrip. The Freunds collected 58 birds at Kaysergebergte Airstrip (see map) from November 23 through December 6, 1961. This airstrip is one of seven recently built during "Operation Grasshopper," a program which is opening the previously almost inaccessible forested interior of Surinam to travel. Kaysergebergte Airstrip is a clearing of approximately 200 by 2000 yards in the tropical forest. Most of the specimens were collected near or at the forest edge bordering the airstrip; some were collected along trails from the airstrip to nearby Oranje Creek.

Sipaliwini Airstrip and Paru Savannah. The Freunds collected 58 birds at Sipaliwini Airstrip and Paru Savannah December 7 through 11, 1961. Sipaliwini is the southernmost of seven airstrips constructed during "Operation Grasshopper" (see map). It is close to the vast Paru Savannah which extends from British Guiana through southernmost Surinam and French Guiana down into northern Brazil where it forms the drainage basin of the northern tributaries of the Amazon.



Map of Surinam showing locations of airstrips and airfields. Black dots mark localities visited by Mr. and Mrs. Freund.

From Sipaliwini the Freunds traveled by dugout southeast up the Sipaliwini River to its junction with Vier Gebroeders Creek; from there they went on foot to a camp established in March, 1961, by Dr. Geijskes and Corporal Pijpers. The camp is located on Vier Gebroeders Creek which at this point forms the meeting place of the tropical forest and the Paru Savannah. In December the Paru Savannah is criss-crossed with dry creek beds lined with Mauritius Palms, shrubs and luxuriant growth of grasses and sedges three feet in height. All birds were collected in vegetation bordering the dry creek beds.

LIST OF SPECIES

Harpagus bidentatus bidentatus (Latham). ♀ skin (J 927), Sipaliwini River, December 11, 1961. Skin around eye light gray; cere green; beak black; feet yellow. Bird seen when it flew across trail in forest and landed forty feet up in tree at edge of trail; this individual was quite tame.

Buteo magnirostris magnirostris (Gmelin). Specimen in Formalin (J 776), collected along the roadside of "Garnizoen Pad," twenty-five kilometers from Paramaribo, going west to the Saramacca River, November 19, 1961.

Colinus cristatus sonnini (Temminck). ♂ ♀ skins (J 883, J 884), Sipaliwini Airstrip, December 8, 1961. These specimens were collected at edge of airstrip in an area of dry, sandy clay soil with patches of grass and sedges varying in height from six to eighteen inches. Freund first saw these birds in a flock of six to eight which did not flush until after his second shot.

Actitis macularia (Linnaeus). Specimen in Formalin (J 837), Kaysergebergte Airstrip, December 1, 1961, collected 10:30 p.m. in a mist net set over a drainage ditch at the edge of the airstrip.

Columbigallina passerina griseola (Spix). Four specimens in Formalin (J 804, J 809, J 810, J 813), Kaysergebergte Airstrip, November 23 and 24, 1961. Freund found a nest on November 23 containing two eggs which hatched December 5. The nest was on the ground in a patch of grass in an area of dry, sandy soil at edge of airstrip.

Columbigallina minuta minuta (Linnaeus). Two specimens in Formalin (J 900, J 901), Paru Savannah, December 10, 1961.

Leptotila rufaxilla rufaxilla (Richard and Bernard). Three specimens in Formalin (J 917, J 925, J 926), Sipaliwini Airstrip, December 10 and 11, 1961.

Ara manilata (Boddaert). ♂ skin (J 835), palm tree at edge of Kaysergebergte Airstrip, December 1, 1961; specimen in Formalin (J 899), Paru Savannah, December 10, 1961.

Pyrrhura picta picta (P.L.S. Müller). Specimen in Formalin (J 866), trail to Oranje Creek, Kaysergebergte Airstrip, December 5, 1961.

Piaya melanogaster melanogaster (Vieillot). Specimen in Formalin (J 898), junction of Sipaliwini River and Vier Gebroeders Creek, December 9, 1961. Bill brilliant red; patch of skin around eye yellow and blue. Haverschmidt (*in litt.*) notes that he has collected several of these cuckoos since 1955 and that the species is "not common."

Caprimulgus nigrescens nigrescens Cabanis. ♂ skin (J 824), Kaysergebergte Airstrip, November 25, 1961. This nightjar was first seen in the beam of Freund's headlamp at 9:00 p.m.; its eyes glowed red. The bird was perched on a low branch of shrub at the beginning of a forest trail. ♀ skin (J 941), Sipaliwini, December 11, 1961. This bird was collected at 4:00 p.m. at the forest edge. Haverschmidt (1955:70)lists this species as rather rare on savannahs.

Polytmus theresiae theresiae (Da Silva Maia). Sex? skin (J 868), Kaysergebergte Airstrip, December 6, 1961.

Heliothryx aurita aurita (Gmelin). Specimen in Formalin (J 943), Sipaliwini, December 11, 1961. Considered rare by Haverschmidt (1955:76) who lists Neger Kreek as the only recent locality.

Trogon viridis viridis Linnaeus. Specimen in Formalin (J 935), Sipaliwini, December 11, 1961. Flesh around eye pale blue: bill gray-black.

Brachygalba lugubris lugubris (Swainson). Specimen in Formalin (J 920), Sipaliwini Airstrip, December 10, 1961.

Galbula leucogastra leucogastra Vieillot. Specimen in Formalin (J 888), Sipaliwini, December 8, 1961; ♀ skin (J 933), Sipaliwini, December 11, 1961. J 888 was collected in a bamboo thicket.

Bucco tamiata tamiata Gmelin. Sex? skin (J 942), Sipaliwini, December 11, 1961. Considered by Haverschmidt (1955: 80) to be "rather rare in the savanna belt."

Monasa atra (Boddaert). Specimen in Formalin (J 873), Oranje Creek, Kaysergebergte Airstrip, December 6, 1961.

Chelidoptera tenebrosa tenebrosa (Pallas). Four specimens in Formalin (J 806, J 828, J 829, J 830), Kaysergebergte Airstrip, November 23 and 28, 1961. Specimen in Formalin (J 860), trail to Oranje Creek, Kaysergebergte, December 5, 1961. Two specimens in Formalin (J 893, J 939), Sipaliwini, December 8 and 11, 1961, (J 893, Surinam Museum).

Picumnus exilis buffoni Lafresnaye. Specimen in Formalin (J 885), Sipaliwini, December 8, 1961.

Celeus elegans subsp.? ♀ skin (J 819), Kaysergebergte Airstrip, November 25, 1961; eye reddish brown; bill bluish ivory.

Dryocopus lineatus lineatus (Linnaeus). Specimen in Formalin (J 807), Kaysergebergte Airstrip, November 24, 1961. Specimen in Formalin (J 906), Sipaliwini Airstrip, December 10, 1961.

Campephilus rubricollis rubricollis (Boddaert). Three specimens in Formalin (J 826, J 827, J 867), Kaysergebergte Airstrip, November 26 and December 5, 1961.

Glyphorynchus spirurus spirurus (Vieillot). ♂ skin (J 825), Kaysergebergte Airstrip, November 26, 1961.

Xiphorhynchus guttatus polystictus (Salvin and Godman). Specimen in Formalin (J 872), trail to Oranje Creek, Kaysergebergte Airstrip, December 6, 1961.

Lepidocolaptes albo-lineatus albo-lineatus (Lafresnaye). ♀ skin (J 842), specimen in Formalin (J 871), Kaysergebergte Airstrip, December 3 and 6, 1961. Specimen in Formalin (J 907), Sipaliwini Airstrip, December 10, 1961.

Formicivora rufa subsp. Sex? skin (J 904), Paru Savannah, December 10, 1961. To our knowledge this species has not been reported previously for Surinam. Collected along a dry creek bed lined with Mauritius Palms and heavy shrubs. This specimen is in streaked female plumage; it is darker ventrally than most specimens of *F. r. chapmani* but is matched by extreme specimens in series at the American Museum of Natural History, and a series before us from Carnegie Museum, Chicago Museum of Natural History, Philadelphia Academy, and Yale Peabody Museum of Natural History.

Thamnophilus punctatus punctatus (Shaw). Specimen in Formalin (J 913), Sipaliwini Airstrip, December 10, 1961.

Tityra cayana cayana (Linnaeus). Two specimens in Formalin (J 846, J 847), Kaysergebergte Airstrip, December 3, 1961.

Tyrannus melancholicus despotes (Lichtenstein). Five specimens in Formalin (J 817, J 823, J 831, J 832, J 858), Kaysergebergte Airstrip, November 25, 28, 29, and December 5, 1961. Specimen in Formalin (J 886), Sipaliwini Airstrip, December 8, 1961.

Tyrannus albogularis Burmeister. ♀ ♀ skins (J 805, J 833). Kaysergebergte Airstrip, November 23 and 29, 1961. Not previously reported for Surinam. Both specimens were collected at forest edge bordering the airstrip.

Megarhynchus pitangua pitangua (Linnaeus).Two specimens in Formalin (J 928, J 929), Sipaliwini, December 11, 1961.

Myiozetetes cayanensis cayanensis (Linnaeus). Specimen in Formalin (J 874), Kaysergebergte Airstrip, December 6, 1961. Specimen in Formalin (J 896), Paru Savannah, December 9, 1961.

Myiarchus ferox ferox (Gmelin). Specimen in Formalin (J 910), Sipaliwini Airstrip, December 10, 1961.

Myiarchus sp? Sex? skin (J 934), Sipaliwini, December 11, 1961. Dr. Wesley E. Lanyon very kindly examined this specimen; he says (*in litt.*) that it is an immature bird and belongs to the *ferox-swainsoni* complex.

Todirostrum cinereum cinereum (Linnaeus). Specimen in Formalin (J 889), Sipaliwini, December 8, 1961.

Colopteryx galeatus (Boddaert). ♀ skin (J 921), Sipaliwini Airstrip, December 10, 1961.

Myiopagis gaimardii guianensis (Berlepsch). Specimen in Formalin (J 940), Sipaliwini, December 11, 1961.

Hirundo rustica erythrogaster Boddaert. Two specimens in Formalin (J 811, J 816), Kaysergebergte Airstrip, November 24 and 25, 1961. Listed by Haverschmidt (1955: 118) as a "numerous migrant . . . in open country in the coastal area."

Turdus leucomelas albiventer Spix. ♀ skin (J 897), Paru Savannah, December 9, 1961.

Polioptila plumbea plumbea (Gmelin). Four specimens in Formalin (J 864, J 865, J 869, J 870), trail to Oranje Creek, Kaysergebergte Airstrip, December 5 and 6, 1961. Three specimens in Formalin (J 908, J 909, J 937), Sipaliwini Airstrip, December 10 and 11, 1961.

Cyanerpes cyaneus cyaneus (Linnaeus). Three ♂ and one ♀ skins (J 845, J 848, J 849, J 850) and one specimen in Formalin (J 851), Kaysergebergte Airstrip, December 3 (J 845) and 4, 1961. Specimen in Formalin (J 892), Sipaliwini, December 8, 1961 (Surinam Museum).

Dacnis cayana cayana (Linnaeus). Specimen in Formalin (J 863), Kaysergebergte Airstrip, December 5, 1961. Specimen in Formalin (J 931), Sipaliwini, December 11, 1961.

Cacicus cela cela (Linnaeus). Specimen in Formalin (J 818), Kaysergebergte Airstrip, November 25, 1961; bill greenish ivory, eye light turquoise blue.

Scaphidura oryzivora oryzivora (Gmelin). Specimen in Formalin (J 859), Kaysergebergte Airstrip, December 5, 1961. For use of *Scaphidura* see Parkes (1954:229).

Icterus cayanensis cayanensis (Linnaeus). Specimen in Formalin (J 932), Sipaliwini, December 11, 1961. Haverschmidt (*in litt.*) notes that he has collected several since 1955 and that the species is "not common" in Surinam.

Tersina viridis occidentalis (Sclater). ♂ skin (J 890), savannah at Sipaliwini, December 8, 1961. Third specimen reported for Surinam (cf. Blake, 1961:182).

Tanagra violacea violacea (Linnaeus). Four specimens in Formalin (J 852, J 853, J 861, J 862), Kaysergebergte Airstrip, December 4 and 5, 1961.

Thraupis palmarum melanoptera (Sclater). Three specimens in Formalin (J 854, J 855, J 856), Kaysergebergte Airstrip, December 4, 1961. Two specimens in Formalin (J 930, J 938), Sipaliwini Airstrip, December 11, 1961.

Tachyphonus surinamus surinamus (Linnaeus). Two specimens in Formalin (J 911, J 918), Sipaliwini Airstrip, December 10, 1961.

Tachyphonus phoenicius Swainson. ♂ ♀ skins (J 919, J 936), Sipaliwini Airstrip, December 10 and 11, 1961; specimen in Formalin (J 944), Sipaliwini Airstrip, December 11, 1961. Upper bill black, lower bill pale gray, feet black in male and female.

Hemithraupis guira nigrigula (Boddaert). Specimen in Formalin (J 844), path to Oranje Creek, Kaysergebergte Airstrip, December 3, 1961.

Hemithraupis flavicollis flavicollis (Vieillot). ♂ skin (J 843), path to Oranje Creek, Kaysergebergte Airstrip, December 3, 1961. Third record reported for Surinam (cf. Blake, 1961:182).

Schistochlamys melanopis melanopis (Latham). ♂ skin (J 914), Sipaliwini Airstrip, December 10, 1961.

Zonotrichia capensis tocantinsi Chapman. ♂ skin (J 903), Paru Savannah, December 10, 1961. The occurrence of this form in southernmost Surinam confirms Chapman's (1940:400) suspicion that the species occurs from lower Amazonia to the range of nominate *capensis*.

Sporophila lineola (Linnaeus). ♂ skin (J 808), Kaysergebergte Airstrip, November 24, 1961. Listed by Haverschmidt (1955:136) as "not common in open places in the coastal area."

Sporophila minuta minuta (Linnaeus). ♀ skin (J 902), Paru Savannah, December 10, 1961.

Myiospiza humeralis humeralis (Bosc). Specimen in Formalin (J 905), Paru Savannah, December 10, 1961; specimen in Formalin (J 912), Sipaliwini Airstrip, December 10, 1961.

Emberizoides herbicola sphenurus (Vieillot). Two ♀ skins (J 887, J 916), Sipaliwini Airstrip, December 8 and 10, 1961; two specimens in Formalin (J 891, J 915), Sipaliwini Airstrip, December 8 and 10, 1961.

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THE AFFINITIES OF THE PINK-HEADED DUCK

(*RHODONESSA CARYOPHYLLACEA*)

PHILIP S. HUMPHREY AND S. DILLON RIPLEY

The rare or extinct Pink-headed Duck of India has had a checkered taxonomic history, having been placed at one time or another with the perching ducks (Cairinini), the dabbling ducks (Anatini), and the pochards (Aythyini). Delacour and Mayr (1945:23-24) in their brilliant revision of the family Anatidae considered *Rhodonessa* as belonging to the tribe Anatini because of similarities in display and posture. Later, Delacour (1956:197) stated that it "is probably related to *Anas* more nearly than to any others, but it may also have some connection with the pochards, as it somewhat approximates in proportions the species of *Netta*, and it has a similar trachea. It certainly shows no close relationship to the Wood Ducks (Cairinini)." Verheyen (1955:22) places *Rhodonessa* with the pochards, an alliance which had been suggested earlier by Garrod (1875:153-154) on the basis of the trachea. Peters (1931:170) put *Rhodonessa* between *Malacorhynchus* (Pink-eared Duck) and *Aix* (Wood Duck) in his subfamily Anatinae, which also included the dabbling ducks and a variety of other forms. Phillips (1922:90-93) and Salvadori (1895:61-63) placed the genus in a subfamily Plectropterinae among genera which are now considered to be perching ducks (Cairinini).

Most recently Johnsgard (1961:78,80) has recognized the aythyine affinities of *Rhodonessa;* he considers *Rhodonessa* a connecting link (along with *Marmaronetta*) between the Aythyini and the Anatini. Woolfenden (1961:114), using several osteological features as evidence, has placed *Rhodonessa* in the tribe Aythyini.

Rhodonessa has had an uncertain status because it combines some of the characters of two very different groups of waterfowl: the pochards on the one hand, and on the other, ducks which are better adapted for a more terrestrial existence, namely the dabbling ducks and perching ducks. This combination of characters has led some workers to suggest that the Pink-headed Duck might be a "link" relating in a phylogenetic sense the pochards and the dabbling ducks.

Humphrey's interest in this problem was aroused when it was noted that the trachea of the male Pink-headed Duck is very similar to tracheae of males of species in the tribe Aythyini, differing from these only in small details. This striking morphological similarity and Ripley's interest in the curious distribution of *Rhodonessa* and other Indian birds have prompted us to investigate further the affinities of this puzzling genus.

ACKNOWLEDGMENTS

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Anatomical specimens examined during the course of this study were obtained through the generosity of M. C. Downes (Department of Fisheries and Game, Australia), H. J. Frith (Wildlife Survey Section, C.S.I.R.O., Australia), R. P. Grossenheider, G. S. Hunt, G. V. T. Matthews (The Severn Wildfowl Trust), K. C. Parkes, W. H. Partridge, Peter Stettenheim, the Departments of Conservation of the states of Michigan and Washington, the Department of Animal Pathology (Cambridge, England), and the University of Washington Marine Biological Station at Friday Harbor; this study would not have been possible without the invaluable help of these people and institutions. We are indebted to the British Museum of Natural History, the American Museum of Natural History,

the United States National Museum and the University of Michigan Museum of Zoology for the use of specimens in their care. Many of the specimens examined during the course of this study were first obtained while Humphrey was at the University of Michigan Museum of Zoology; we are especially grateful to R. W. Storer and the late Josselyn Van Tyne for allowing this material to be incorporated in the collections of the Yale Peabody Museum of Natural History.

Our thanks must also go to Mrs. Shirley Hartman for preparing the illustrations and to Mr. George E. Watson for many helpful suggestions.

STRUCTURAL FEATURES

Little is known of the anatomy of the Pink-headed Duck. Garrod (1875:153-154) described and figured the trachea and syrinx of both sexes; Verheyen (1955:22) and more recently Woolfenden (1961:14, 41, 52, 54, 114) have commented on the osteology of the species.

Plumage pattern and general appearance. The Pink-headed Duck was a long-necked, rather awkward looking bird and at first sight, little like a pochard in bodily proportions. The posture of the species and its display habits (discussed below) have led some authors, notably Delacour and Mayr (1945), to ally it with the dabbling ducks.

A general comparison of the plumage patterns of the Pink-headed Duck and all other waterfowl leaves us with the impression that the species has in this character more in common with the pochards than with any other group. The coloration of the Pink-headed Duck (apart from the pink head and neck, which are in color unique among waterfowl) is very much like that of the pochards. The similarity is especially noteworthy in the pattern of coloration of the wing (Ripley, 1950:903-904). *Rhodonessa* lacks an iridescent speculum, and in fact has secondaries which are practically identical in markings with those of many pochards.

Trachea. The trachea of the male Pink-headed Duck is in its general features indistinguishable from the tracheae of males of the tribe Aythyini. However, it differs in the aggregate of several details of structure from the tracheae of males of any of the pochards.

We have examined specimens or figures of tracheae of males of all species in the tribe Aythyini except *Netta erythrophthalma*, *Aythya nyroca*, and *Aythya novae-seelandiae*.

Through the courtesy of Dr. James D. McDonald of the British Museum of Natural History we have been able to study a specimen of the caudal part of the trachea of a male Pink-headed Duck. Males of *Rhodonessa* and the various species of Aythyini are alike in general conformation of the syringeal region. The similarity is most striking in 1) the form of the partly bony, partly membranous swelling or dilatation to the left, and 2) the conformation of the laterally expanded, partly fused rings anterior to the tracheo-bronchial junction (Figure 1).

In form of the dilatation to the left, male *Rhodonessa* differs from males of the tribe Aythyini as follows:

1) the membrane-covered fenestrae are poorly developed.

2) the dilatation is not as strongly laterally compressed as in the Aythyini.

3) the dilatation does not extend as far anteriorly (cephalad) as in the Aythyini.

4) the lateral plane of orientation of the dilatation is dorsal to ventral not dorso-medial to ventro-lateral as in the Aythyini.

5) the dilatation is more expanded or swollen caudally than in the Aythyini.

In every respect save the last, the dilatation of the caudal end of the trachea of *Rhodonessa* is less well developed than in the Aythyini. In *Rhodonessa* this dilatation is clearly a somewhat less elaborate version of the same structure in the Aythyini. *Rhodonessa* resembles no other group of ducks in this respect.

According to Garrod (1875:154), the trachea of the male Pink-headed Duck has "a slight fusiform dilatation" anterior to the syringeal region. Mid-tracheal swellings of one kind or another occur commonly in only two of the major groups of waterfowl, the Mergini (*Bucephala*, *Mergus*, *Histrionicus*, *Melanitta*) and the Aythyini (several species of *Aythya*,

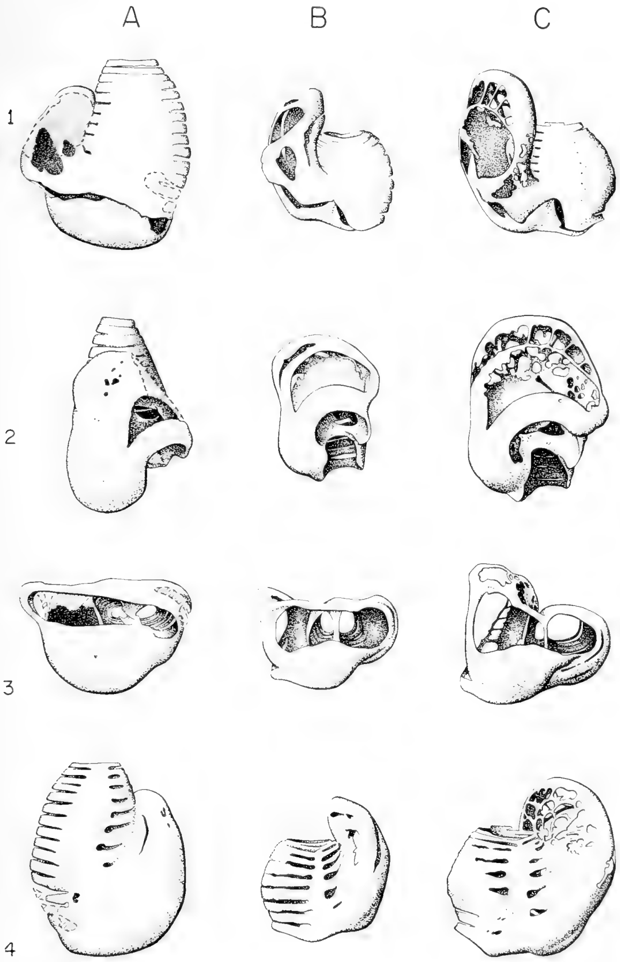

Figure 1. Caudal ends of tracheae of males of A) *Rhodonessa caryophyllacea,* B) *Metopiana peposaca,* and C) *Aythya affinis;* each specimen drawn in the following views: 1) dorsal, 2) left lateral, 3) caudal, and 4) ventral. Magnification x 1.18.

Netta). One, and possibly more, species of *Anas* (*Anas versicolor*, but not all species are known anatomically) have a midtracheal swelling.

Garrod (1875:154) describes the caudal end of the trachea just anterior to the syringeal region of the male Pink-headed Duck as follows: "the lower end of the trachea is hardly contracted at all. There is, however, a slight thinning of the anterior portions of some of the inferior tracheal rings, . . . a small, transverse, anterior fenestra being the result." Garrod's figure of the trachea of the male of this species illustrates 13 such fenestrae. A similar modification of the ventral parts of some of the more caudal tracheal rings occurs in male *Clangula* (tribe Mergini), but there are in that species only seven fenestrae. Males and females of *Sarkidiornis* (Cairinini) have fenestrae of this kind in the caudal part of the trachea; these fenestrae are fewer and less well developed in the females.

The structure of the syringeal region of the tracheae of males of the genera *Aythya*, *Netta*, and *Metopiana* is peculiar to the group. From the standpoint of the structure of the male syrinx, *Rhodonessa* clearly belongs in the tribe Aythyini. The syringes of males of the tribes Anatini and Cairinini have much in common structurally and differ significantly from those of *Rhodonessa*, *Aythya*, *Netta*, and *Metopiana*.

Humerus. Woolfenden (1959:184) has described a method of distinguishing "the humeri of the Anatinae from those of the Aythyinae [classification of Peters, 1931], based on certain characters of the pneumatic fossa . . . . In the Anatinae the fossa is deeper and partially excavates the medial bar. The construction is such that the palmar surface of the bar is not completely visible. Furthermore, the fossa usually possesses many bony struts. In the Aythyinae the pneumatic fossa is shallower, and the medial bar is essentially continuous with the shaft, exposing its palmar surface. Struts within the fossa are rare; in most cases the wall is solid."

Woolfenden found that the pneumatic fossa of *Metopiana peposaca* agrees "in all respects with those of the Anatinae." He says further that "this deviation from what seems a reliable method of distinguishing the two subfamilies may be of phylogenetic significance, for Delacour and Mayr (1945:25-26) consider *Metopiana*, along with *Netta rufina* and *Aythya erythrophthalma*, to 'constitute a bridge between the river ducks and the more specialized pochards of the genus *Aythya* . . . .' "

We have examined the pneumatic fossa of the humerus of *Anas platyrhynchos*, *A. fulvigula*, *A. falcata*, *A. poecilorhyncha*, *Aythya marila*, *A. fuligula*, *A. ferina*, *Metopiana peposaca*,

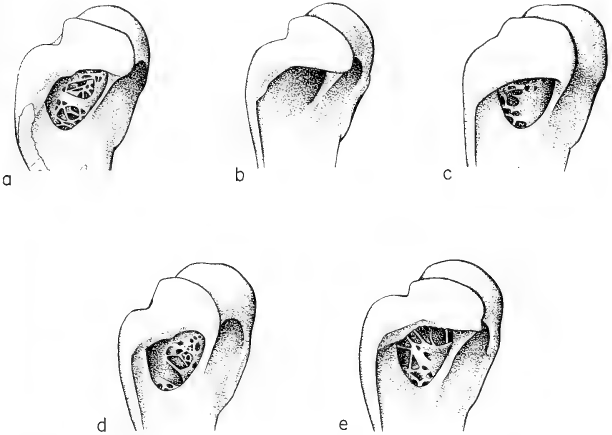

Figure 2. Head of left humerus, anconal view; a) *Rhodonessa caryophyllacea*, b) *Aythya marila*, c) *Metopiana peposaca*, d) *Mergus serrator*, and e) *Anas platyrhynchos*. Magnification x 1.75.

Rhodonessa caryophyllacea, *Histrionicus histrionicus*, *Melanitta fusca*, *M. nigra*, *Somateria mollissima*, *Bucephala albeola*, *Mergus serrator*, *M. merganser*, and *Aix sponsa*. Using Woolfenden's criterion for classifying pneumatic fossae into "aythyine" or "anatine" types, we find the following:

"Anatine" pneumatic fossa: *Anas*, *Metopiana*, *Rhodonessa*, *Mergus*, *Aix*. (Figure 2.)

"Aythyine" pneumatic fossa: *Aythya*, *Bucephala*, *Histrionicus*, *Melanitta*, *Somateria*.

The fact that *Mergus* has an "anatine" pneumatic fossa suggests to us that this character has undoubtedly arisen independently in three or more different groups (Mergini, Aythyini, Anatini). Delacour and Mayr (1945) have pointed out the close relationship between *Bucephala* and *Mergus;* Humphrey (1955) has shown that *Mergus* probably evolved from a *Bucephala*-like ancestor. We feel that the "aythyine" pneumatic fossa of *Bucephala* is evidence that the "anatine" pneumatic fossa of *Mergus* is a derived condition which in no way indicates relationships with the tribe Anatini. Therefore, the *Anas*-like condition of the pneumatic fossa of *Metopiana* does not necessarily indicate that this genus has any close affinity to the Anatini. In view of the foregoing, the "anatine" condition of the pneumatic fossa of *Rhodonessa* cannot be used as evidence to clarify the relationships of this genus.

Feet. The feet of the Pink-headed Duck have a number of characters in common with those of *Anas*, e.g., lack of a lobe on the hallux, digits III and IV approximately equal in length or digit III slightly longer, digits relatively short compared to length of humerus. However, there are some features of the foot of *Rhodonessa* which suggest that its resemblance to the feet of dabbling ducks is secondarily derived.

The fact that the Pink-headed Duck, by its tracheal anatomy obviously a pochard, has feet like a dabbling duck prompted us to compare the feet of dabbling ducks and pochards. To this end we measured skeletal elements of the feet of the following species:

Anas discors ♂
" *acuta* ♂
" *querquedula* ♀
" *gibberifrons* ♂
" *cyanoptera* ♂
" *rubripes* 10 ♂
Aythya marila ♂
" *fuligula* ♂
" *nyroca* ♀

Aythya collaris ♂
" *americana* ♂
" *ferina* ♀
" *valisineria* ♂
" *affinis* 8 ♂
Metopiana peposaca ♂
Netta rufina
Rhodonessa caryophyllacea ♀

Measurements of these specimens are presented in Table 1 which also includes means, standard deviations, minima and maxima of the measurements of samples of *Anas rubripes* and *Aythya affinis.*

As is apparent from examination of specimens of dabbling ducks (*Anas*) and pochards (*Aythya*), these two groups of waterfowl differ in size of foot, the pochards having relatively much larger feet than the dabbling ducks. Using greatest length of humerus as an index of general body size, the greatest length of the tarsometatarsus and of each digit (minus ungual phalanx) was expressed as a per cent of humerus length. These ratios are presented in Table 2 where it can be seen that in every case except length of tarsometatarsus the ratios of the elements of the foot of *Rhodonessa* are much smaller than those of *Aythya* and fall among those of the *Anas* group. The tarsometatarsus of *Rhodonessa* is relatively somewhat shorter than that of any dabbling duck but rather long for a pochard, although those of some pochards (*Aythya nyroca, A. valisineria, Metopiana*) are about the same relative length or slightly longer. In common with the dabbling ducks and *Rhodonessa, Metopiana* has relatively short digits; except for the hallux, the digits of *Netta rufina* are also very short. The relative length of the tarsometatarsus of *Netta* is short like that of the more typical pochards.

Possibly there is a difference in the relative lengths of the humeri of dabbling ducks and pochards correlated with differences in the flying abilities of the two groups. Although we know of no way of testing for this possibility, we doubt that there is enough of an adaptive difference in relative length of the humerus in the two groups to invalidate using length of this element as a measure of body size and as a means of comparing the relative lengths of the elements of the foot.

There is a clear cut difference between the species of *Anas* and those of *Aythya* in the relative lengths of digits III and IV. In *Aythya* (and *Netta rufina*) digit IV is longer than digit III (see Table 3). In *Anas* digit III is usually longer but may be equal to or slightly shorter than digit IV. In *Anas rubripes* (sample of ten males) digit IV is usually slightly shorter (up to 3.6 per cent shorter) than digit III; in five out of ten speci-

TABLE 1

Measurements in (millimeters) of skeletal elements of feet of *Netta rufina*, *Metopiana peposaca*, *Rhodonessa carophyllacea*, and various species of *Anas* and *Aythya*. One specimen of each species measured except as indicated below.

1. Mean and standard deviation of samples of 10 males.
2. Maximum.
3. Minimum.
4. Mean and standard deviation of samples of 8 males.

	Digit II		*Digit III*			*Digit IV*	
	IIp	*IId*	*IIIp*	*III2*	*IIId*	*IVp*	*IV2*
Anas							
discors ♂	14.4	10.6	14.8	10.8	8.8	12.1	8.2
acuta ♂	20.7	16.1	21.7	15.0	13.1	16.9	12.0
querquedula ♀	14.3	11.3	14.7	10.2	8.8	12.0	7.8
gibberifrons ♂	17.4	13.4	17.9	12.1	11.4	14.4	9.7
cyanoptera ♂	16.2	12.7	16.5	12.3	10.2	13.5	9.3
rubripes[1]	22.4 ± 0.2	16.7 ± 0.6	22.8 ± 0.7	15.5 ± 0.4	13.1 ± 0.4	18.2 ± 0.5	12.4 ± 0.5
rubripes[2]	23.7	17.7	24.0	16.2	13.7	19.0	13.3
rubripes[3]	21.2	15.9	21.9	14.9	12.5	17.2	11.7
Aythya							
marila ♂	26.2	18.6	25.7	18.8	15.7	20.7	15.7
fuligula ♂	22.8	17.0	22.2	16.1	14.0	18.5	13.3
nyroca ♀	20.7	15.8	21.1	15.5	13.2	17.5	12.5
collaris ♂	23.2	17.3	23.0	16.8	14.5	19.1	14.2
americana ♂	26.2	19.2	25.0	18.1	15.7	20.4	15.5
ferina ♀	25.2	18.6	25.0	18.1	15.0	20.0	14.3
valisineria ♂	29.6	22.2	28.6	20.8	17.3	23.9	16.9
affinis[4]	23.4 ± 1.1	17.3 ± 1.1	22.7 ± 1.2	16.2 ± 1.0	13.9 ± 1.0	18.9 ± 0.9	13.7 ± 0.8
affinis[2]	24.6	18.6	23.8	17.1	15.0	20.0	14.3
affinis[3]	20.9	14.9	20.0	13.8	11.7	16.8	11.8
Netta							
rufina ♀	25.2	19.2	24.5	17.9	16.0	19.9	14.3
Metopiana							
peposaca ♂	24.7	18.0	24.0	17.5	14.6	19.5	13.9
Rhodonessa							
caryophyllacea ♀	23.0	16.6	23.1	15.7	12.9	18.5	12.3

TABLE 1 (Continued)

Measurements in (millimeters) of skeletal elements of feet of *Netta rufina, Metopiana peposaca, Rhodonessa carophyllacea,* and various species of *Anas* and *Aythya.* One specimen of each species measured except as indicated below.

1. Mean and standard deviation of samples of 10 males.
2. Maximum.
3. Minimum.
4. Mean and standard deviation of samples of 8 males.

	Digit IV						
	IV3	*IVd*	*Digit I*	*Digit II*	*Digit III*	*Digit IV*	*Tarsometatarsus*
Anas							
discors ♂	6.4	6.7	6.4	25.0	34.4	33.4	31.2
acuta ♂	9.0	11.3	10.5	36.8	49.8	49.2	45.5
querquedula ♀	5.9	7.0	6.9	25.6	33.7	32.7	31.0
gibberifrons ♂	7.5	9.1	8.3	30.8	41.4	40.7	36.5
cyanoptera ♂	7.5	8.5	7.5	28.9	39.0	38.8	34.6
rubripes[1]	9.6 ± 0.4	10.6 ± 0.4	10.3 ± 0.5	39.1 ± 1.3	51.3 ± 1.3	50.7 ± 1.6	46.9 ± 1.2
rubripes[2]	10.4	11.5	11.0	41.0	53.9	53.8	49.0
rubripes[3]	9.0	9.9	9.7	37.1	49.6	48.2	44.8
Aythya							
marila ♂	13.0	13.5	14.4	44.8	60.2	62.9	38.9
fuligula ♂	11.4	12.4	11.6	39.8	52.3	55.6	33.3
nyroca ♀	10.7	11.4	10.2	36.5	49.8	52.1	33.5
collaris ♂	12.1	12.5	11.1	40.5	54.3	57.9	34.7
americana ♂	12.9	13.2	12.8	45.4	58.8	62.0	39.3
ferina ♀	12.2	12.7	13.5	43.8	58.1	59.2	37.7
valisineria ♂	15.2	15.2	14.3	51.8	66.7	71.2	45.0
affinis[4]	11.3 ± 0.7	12.5 ± 1.0	12.6 ± 1.0	40.7 ± 2.2	52.7 ± 3.2	56.3 ± 3.3	35.4 ± 0.9
affinis[2]	11.8	13.8	13.6	43.2	55.9	59.3	36.7
affinis[3]	9.6	10.5	11.2	35.8	45.5	48.7	20.9
Netta							
rufina ♀	12.0	13.3	14.6	44.4	58.4	59.5	43.7
Metopiana							
peposaca ♂	11.1	12.1	12.1	42.7	56.1	56.6	45.6
Rhodonessa							
caryophyllacea ♀	9.7	11.0	11.5	39.6	51.7	51.5	45.7

mens, digit IV was about the same length as or slightly longer (up to 1.4 per cent longer) than digit III.

Rhodonessa is *Anas*-like in this character; digit IV is 0.9 to 2.1 per cent (three specimens) shorter than digit III.

We have compared the relative lengths of the phalanges of the feet of *Rhodonessa*, *Netta*, *Metopiana*, and the various species of *Anas* and *Aythya* using the proximal phalanx of digit III as the basis for the intramembral proportions. The relative lengths of the phalanges of *Rhodonessa* as compared with those of the pochards and the dabbling ducks lead us to believe that the dabbling-duck-like foot of *Rhodonessa* has evolved from a typical pochard foot. Unfortunately, lack of material makes it impossible to analyze the variability of the relative lengths of the phalanges of *Rhodonessa*. We suspect, however, that the variability is of the same order of magnitude as found in a sample of eight *Aythya affinis*. If this is true, we see no other explanation for the peculiar phalangeal proportions of the foot of *Rhodonessa* than that they are the result of modification of an ancestral pochard-like foot.

The relative length of the proximal phalanx of digit II of *Rhodonessa* is greater than the maximum found for *Anas* and well within the minimum range for *Aythya*. Allowing for variability, one could safely say that this element is on the large side for *Anas* or on the small side for *Aythya*. The distal phalanx of digit II of *Rhodonessa* is relatively rather short for either *Anas* or *Aythya*. In digit III of *Rhodonessa* the second phalanx is relatively shorter than in any of the eight pochards studied and is slightly below the average of the six dabbling ducks. The distal phalanx is relatively smaller than the smallest of *Anas* and much smaller than in *Aythya*. The hallux (digit I) of *Rhodonessa* is relatively longer than in *Anas* and among the shorter of *Aythya*. (See Table 4.)

In summary, the foot of *Rhodonessa* is *Anas*-like in 1) the relative shortness of digits II, III and IV, 2) the absence of a lobe on the hallux and 3) the relative lengths of digits III and IV; it is more pochard-like (but perhaps intermediate) in 1) length of tarsometatarsus and 2) length of hallux. The intramembral proportions of the foot of *Rhodonessa* suggest that the phalanges have undergone in evolution a differential

TABLE 2

Lengths of digits and tarsometatarsus expressed as per cent of length of humerus.

1. Mean and standard deviation of ratios from sample of 10 males.
2. Maximum.
3. Minimum.
4. Mean and standard deviation of ratios from sample of 8 males.

	Digit I	*Digit II*	*Digit III*	*Digit IV*	*Tarsometatarsus*
Anas					
discors ♂	10.1	39.4	54.3	49.2	49.3
acuta ♂	11.4	39.8	54.0	49.3	49.3
querquedula ♀	10.5	39.0	51.3	49.8	47.2
gibberifrons ♂	11.8	43.9	58.9	58.0	52.0
cyanoptera ♂	11.4	44.0	59.5	59.1	52.7
rubripes[1]	10.8 ± 0.5	41.0 ± 1.1	53.9 ± 1.3	53.0 ± 1.6	49.3 ± 0.7
rubripes[2]	11.6	43.0	56.6	56.5	50.2
rubripes[3]	9.9	39.4	52.2	51.1	48.0
Aythya					
marila ♂	16.4	51.0	68.6	71.5	44.4
fuligula ♂	14.8	51.0	67.9	71.2	42.5
nyroca ♀	14.1	50.5	69.0	72.2	46.4
collaris ♂	14.6	53.1	71.2	75.9	45.5
americana ♂	14.1	50.0	64.8	68.3	43.3
ferina ♀	15.9	51.7	68.6	70.0	44.5
valisineria ♂	15.2	55.0	70.9	75.5	47.8
affinis[4]	15.7 ± 1.2	50.9 ± 2.6	65.9 ± 3.6	70.3 ± 3.8	44.3 ± 0.9
affinis[2]	17.1	53.0	68.5	72.6	45.2
affinis[3]	14.2	45.2	57.5	61.5	42.7
Netta					
rufina ♀	14.2	43.1	56.8	57.9	42.5
Metopiana					
peposaca ♂	12.5	44.1	58.0	58.6	47.2
Rhodonessa					
caryophyllacea ♀	11.7	40.3	52.6	52.4	46.5

TABLE 3

Comparison of lengths of digts III and IV. The differences in the lengths of digits III and IV are listed; in the adjacent columns these differences are expressed as per cent of the length of digit III. *Aythya affinis:* of 8 specimens (males) digit IV was always longer by 5.6 per cent to 8.2 per cent. *Anas rubripes:* of 10 specimens (males) digit III was longer than digit IV in 7 individuals and shorter than digit IV in 3 individuals.

1. Mean of sample of 7 males.
2. Minimum.
3. Maximum.
4. Mean of sample of 8 males.
5. Mean of sample of 3 males.

	Digit III longer than Digit IV	
	III-IV	$\frac{(III\text{-}IV) \times 100}{III}$
Anas		*per cent*
discors	1.0	2.9
acuta	0.6	1.2
querquedula	1.0	3.0
gibberifrons	0.7	1.7
cyanoptera	0.2	0.5
rubripes[1]	1.0	1.9
rubripes[2]	0.1	0.2
rubripes[3]	1.9	3.6
Rhodonessa		
caryophyllacea	0.2	0.9

	Digit III longer than Digit IV	
	IV-III	$\frac{(IV\text{-}III) \times 100}{III}$
Aythya		*per cent*
marila	2.7	4.5
fuligula	3.3	6.3
nyroca	2.3	4.6
collaris	3.6	6.6
americana	3.2	5.5
ferina	1.1	1.9
valisineria	4.5	6.8
affinis[4]	3.6	6.8
affinis[2]	3.0	5.6
affinis[3]	4.3	8.2
Netta		
rufina	1.1	1.9
Metopiana		
peposaca	0.5	0.9
Anas		
rubripes[5]	0.4	0.8
rubripes[2]	0.2	0.4
rubripes[3]	0.7	1.4

TABLE 4

Lengths of phalanges expressed as per cent of the length of the proximal phalanx of digit III.

1. Mean and standard deviation of ratios from sample of 10 males.
2. Maximum.
3. Minimum.
4. Mean and standard deviation of ratios from samples of 8 males.

	Digit II		*Digit III*		*Digit IV*			
	IIp	*IId*	*III2*	*IIId*	*IVp*	*IV2*	*IV3*	*IVd*
Anas								
discors ♂	97.4	71.6	73.0	59.5	81.8	55.4	43.2	45.3
acuta ♂	95.5	74.2	69.2	60.4	78.0	55.4	41.5	52.1
querquedula ♀	97.3	76.9	69.4	59.8	81.6	53.1	40.1	47.6
gibberifrons ♂	97.2	74.9	67.6	63.7	80.5	54.1	41.9	50.8
cyanoptera ♂	98.3	77.0	74.5	61.9	81.8	56.4	45.5	51.5
rubripes[1]	98.5 ± 1.6	73.4 ± 2.0	67.9 ± 0.9	57.4 ± 1.8	79.8 ± 1.2	54.5 ± 1.3	42.2 ± 1.7	46.4 ± 1.6
rubripes[2]	101.3	76.6	69.6	60.0	81.4	56.8	44.7	49.1
rubripes[3]	96.5	70.9	66.5	54.4	78.0	52.8	39.6	44.5
Aythya								
marila ♂	104.0	72.4	73.1	61.1	80.5	61.1	50.6	52.5
fuligula ♂	102.8	76.5	72.5	63.1	83.3	59.9	51.4	55.9
nyroca ♀	98.2	74.9	73.5	62.6	83.0	59.3	50.7	54.0
collaris ♂	100.9	75.2	73.0	63.0	83.0	61.8	52.6	54.4
americana ♂	104.8	76.8	72.4	62.8	81.6	62.0	51.6	52.8
ferina ♀	100.8	74.4	72.4	60.0	80.0	57.2	48.8	50.8
valisineria ♂	103.5	77.6	72.7	60.5	83.6	59.1	53.2	53.2
affinis[4]	103.1 ± 1.5	76.1 ± 1.4	71.1 ± 1.1	61.0 ± 1.6	83.1 ± 1.1	60.2 ± 0.7	49.7 ± 1.2	55.0 ± 2.0
affinis[2]	104.9	78.2	72.6	63.0	84.4	61.4	51.5	58.0
affinis[3]	100.5	74.5	69.0	58.5	81.5	59.0	48.0	52.5
Netta								
rufina ♀	102.9	78.4	73.1	65.4	81.3	58.4	49.0	54.3
Metopiana								
peposaca ♂	103.0	75.0	73.0	60.8	81.3	57.9	46.2	50.4
Rhodonessa								
caryophyllacea ♀	99.6	71.9	68.0	55.9	80.1	53.3	42.0	47.6

reduction, the more proximal phalanges being least affected and the distal phalanges most affected. This is most apparent in digit III but is suggested in digit II. Digit IV must have undergone the greatest reduction of all from the presumed ancestral pochard condition of having been longer than digit III. Miller (1937:45) found in his studies of the feet of geese that "increase or decrease in toe length takes place to a greater degree in digits two and four than in three, and increase or decrease in phalangeal length takes place to a greater degree in distal (exclusive of ungual) than in proximal phalanges."

BEHAVIOR AND ECOLOGY

There has been little recorded about *Rhodonessa* beyond the fact that it has always been observed uncommonly. The Pink-headed Duck appears to have been a solitary species, occurring as pairs in the breeding season or small groups in winter (Hume and Marshall, 1881, 3:176) on isolated marshy ponds or swampy lakes and not joining the large wintering concentrations of migrant waterfowl. Delacour (1956:198) notes that its behavior was much like that of dabbling ducks. The species nested in April in long grass (*Andropogon*) or grass tufts sometimes away from the water. The eggs were white and uniquely spherical (Finn, 1909:25) and the nests well-formed with no special lining.

The male had a whizzy whistle like a Mallard but lower and weaker. The female had a low quack. Finn (1909:86), however, speaks of the male's call as quite unlike that of any other duck, resembling the syllables "wugh-ah."

Males when together (in captivity) were noted to display like Mallards but more simply. The head was drawn in between the shoulders while the head feathers were puffed out. Following this the neck was stretched upwards and the call uttered. However, as Delacour (1956:198) has observed and described the display, it was so simple that it lacks any real relationship to the display of a dabbling duck. It resembled equally well the simplest forms of aythyine display such as that of *Metopiana* for example, lacking only the angular position of the bill pointed upwards at the climax of the neck-stretch. These observations, in captivity, may have been of birds insufficiently stimulated to have produced a diagnostic display.

Flight of *Rhodonessa* is said to have been light and easy and the habits like those of a true surface-feeder (Finn, 1909: 86). Finn (1915:25) observed an individual dive "as neatly and long as a pochard." Perching was never observed.

The Pink-headed Duck was a solitary, non-migratory species which was local in distribution: the center of its restricted distribution was the Gangetic area of the "terai" of northern Bihar. The last record of its occurrence in nature was in 1935 (C. M. Inglis). Jerdon (in Hume and Marshall, 1881, 3:176) reports that the birds remained out in the center of the pond during the day and so presumably fed at night. Shillingford (in Hume and Marshall) reports that a gizzard contained water weeds and small shells. The duck was said not to have been a palatable species, indicating an animal diet.

It is unfortunate that so little is known of the habits and behavior of the Pink-headed Duck. The lack of information is particularly aggravating considering that this now extinct or nearly extinct species was at one time not uncommon in collections of European aviculturists where it displayed but never nested. All that can now be said is that the anatomy and proportions of the foot of *Rhodonessa* indicate feeding and locomotor adaptations very much like those of dabbling ducks. The sparse behavioral information available provides some if not overwhelming support for this notion.

DISCUSSION

What sort of history of ecological changes can have produced the Pink-headed Duck, a pochard with strikingly anatine modifications of the foot? The most likely sorts of environmental changes would have involved a shift from the more typical pochard habitat, that is, a marine or inland sea littoral environment, to the present one of marshy, fresh water ponds. It appears that just such a change took place in India during Tertiary times.

The Neogene period, characterized by a general regression in the middle Miocene, brought an isolation of the eastern

Mediterranean into an inland sea. This eastern Mediterranean province is described by Gignoux (1955:554-5, 587-8, fig. 144). Characteristically beginning with the upper Vindobonian or upper Sarmatian, the inland sea thus formed began to show isolated genera of invertebrates responsive to decreased salinity with the outpourings of large fresh water rivers. The easternmost of these lacustrine basins is the Aral-Caspian which stretched north to Samara and east far beyond the Aral Sea. This eastern basin escaped the reinvasion of the Mediterranean which occurred in the Quaternary with the opening of the Dardanelles and the extinguishing of the Levantine and western Caspian faunas.

The southern parts of this area of trapped inland sea in the southern Caspian and south of the newly risen Caucasus represent part of the old Mesogean or Tethys Sea basin, continuous through to the Indian Ocean and cut at the beginning of the Miocene.

Similarly in India, the Miocene system (Wadia, 1944:256-275) shows a series of clays and sandstones whose characters suggest deposition in an estuary or the broad mouth of a river (Gaj Series in Sind). This shows a regression of the sea border and its replacement by the wide basin of an estuary. A good example of this sequence is the Potwar trough which shows deposits of nummulitic form over Mesozoic rocks, overlain by brackish-water sediments of Aquitanian and Burdigalian age (=lower Oligocene and upper Miocene) followed by the fluviatile and sub-aerial Siwalik strata.

How far southward the Siwalik system lies is unclear; much of it is probably buried under the recent alluvium of the Ganges. Siwalik birds are interesting in that *Phalacrocorax*, *Pelecanus*, and *Mergus* are represented, genera found in India today, and characteristic of very large lakes or large river systems.

The Pleistocene system in India reveals evidences of glaciation in the form of moraines and polished and grooved rock at low altitudes in the Himalayas, and also the desiccation of the Tibetan lakes consequent on the disappearance comparatively recently of the glaciers of the ice age.

The plains of India north of the peninsula reveal another aspect of the Pleistocene in the Indo-Gangetic depression filled with thousands of feet of alluvium (Wadia, 1944, fig. 33). The present river systems bear little relation to their past history even during historic times. This is a vast area of wandering rivers and repeated alterations of clays, sand and marls with recurring layers of peat, lignite and some forest beds. Huge deltaic areas as in Bengal cover parts of the former Bay of Bengal, or in the west, as in the Rann of Kutch, remains of bays of the Arabian Sea.

All of this intervening plain except for occasional projections of older rocks must represent the remains of an inland sea, perhaps formerly continuous with the Aral-Caspian basin of Miocene times. The whole recent history of this area would appear to be one of shift from marine to brackish to lacustrine to riverine conditions. Following this has been the sustained recent desiccation of central India in historic times (Sálim Ali, 1927:833-861). Seventeenth century records show the range of the great Indian rhinoceros for example as occurring up to Peshawar and the foothills of the northwest in what is now a semi-desert area.

In view of the above it seems very likely that certain animals adapted for life in or about large bodies of water if capable of the necessary evolutionary modifications, would have been able to adjust to this radical change in environment and continue to persist. Of the four endemic species of Indian birds discussed by Ripley (1961: xxiii) two are endemic Indian genera whose normal habitat is aquatic or semi-aquatic. One is the bristled grass warbler, *Chaetornis*, a bird of the Gangetic drainage system, local in habitat, found in moist grassy places. The other is the Pink-headed Duck, which has been found only in lakes or ponds in the arc from Bihar to eastern Assam, although there are scattered records of nearly a hundred years ago indicating a wider distribution throughout the Indian plains and spottily into the Peninsula. If this species indeed shows affinities with the estuarine diving ducks as we believe the anatomical evidence suggests, then it would appear to be descended from a form which was plastic enough to respond adaptively to long-term changes in the ecology of southern Asia. It evolved gradually into a fresh water surface feeding type of duck as the total water area diminished. Again, with the disintegration of the Aral-Caspian, it became isolated in the furthest reaches of the increasingly dessicated Gangetic system. The Pink-headed Duck ultimately became trapped, so to speak, in the evironment to which it had become adapted and as a sedentary relict species appears at present to have vanished almost, if not completely, from the scene.

The evolution of the Pink-headed Duck appears to have been related to the major environmental changes which took place in India during Tertiary times. The principal occurrence in the history of this peculiar genus was the development of dabbling-duck-like locomotor adaptations, at least so we infer from the curious modifications of the foot. The trachea, plumage pattern and certain characteristics of the foot leave no doubt about the aythyine relationships of ***Rhodonessa.***

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THE CRANIAL CRESTS OF HADROSAURIAN DINOSAURS

John H. Ostrom

INTRODUCTION

Ever since 1914 when Lawrence Lambe described and figured the first of the hooded dinosaurs, there has been considerable speculation and debate about the function of the hadrosaurian cranial crest. Although the debate has subsided somewhat in recent years, it has not been because general agreement has been reached. Dozens of crested hadrosaurs have been collected and described since that first discovery and one cannot help but be impressed by the variety of crestal shapes and sizes represented. There are the relatively small, almost incipient crests of *Procheneosaurus* and *Cheneosaurus*, the large "Corinthian helmets" of *Corythosaurus* and *Hypacrosaurus*, the "top hats" of *Lambeosaurus*, and the curved, tubular crests of *Parasaurolophus*. But in spite of the number and diversity of available specimens, the crestal function has remained quite elusive.

In 1920, Lambe discovered that the hadrosaurian crest was not a solid bony structure, but was instead constructed as a thin and delicate bony sheath which enclosed folded and sometimes complicated passages and chambers. Prior to this discovery, most paleontologists had viewed these cranial prominences simply as interesting decorative features. Lambe's revelation, however, made such an interpretation quite untenable and a rash of hypotheses attempting to explain these structures ensued. The aquatic adaptations of the hadrosaurs had already been noted by this time and consequently many of these theories related the complex crestal cavities to the probable semi-aquatic habits of these ornithischian dinosaurs.

In spite of some popular appeal, and what may appear to be a certain degree of adaptive significance, most of the crestal hypotheses that are correlated with an aquatic mode of life involve serious weaknesses that have generally been overlooked. This situation, together with certain recently acquired information, warrants a careful reconsideration of the hadrosaurian crest problem.

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ABBREVIATIONS

Reference is made to specimens in the collections of several institutions, and in such references the institutional names are abbreviated as follows:

A.M.N.H. — American Museum of Natural History
C.N.H.M. — Chicago Natural History Museum
N.M.C. — National Museum of Canada, Ottawa
R.O.M. — Royal Ontario Museum, Toronto
Y.P.M. — Peabody Museum of Natural History, Yale University.

Abbreviations used in the text figures are as follows:

AC. — Anterior chamber of nasal capsule
AS. — Anterior space of olfactory chamber
AT. — Anterior nasal tube of nasal capsule
CO. — Concha
CT. — Choanal tube
EN. — External naris
IN. — Internal naris
LC. — Lateral crest cavity
MC. — Medial crest cavity
OB. — Olfactory bulbs
OC. — Olfactory chamber of nasal capsule
OS. — Antorbital space of olfactory chamber

PREVIOUS THEORIES

William Parks was the first to succumb to the temptation of theorizing about the functional significance of hadrosaurian crests. In his description of *Parasaurolophus walkeri* (1922) he argued rather persuasively that the crest of this species had been joined to the neural spines of the anterior dorsal vertebrae by means of a strong muscular or ligamentous connection. By inference, at least, this would have facilitated movement of the rather large and unwieldy head. Parks' hypothesis, however, was based almost entirely upon what appears to the present writer to be a pathologic aberration of the sixth and seventh dorsal spines.

In opposition to Parks' interpretation, it must be noted that no identifiable muscle or ligament scars can be seen on the crest of *P. walkeri*, or on that of any other crested hadrosaur. It might also be pointed out that other hadrosaurs, such as *Edmontosaurus* and *Kritosaurus*, possessed far larger heads, but failed to develop such supporting or leverage structures. Furthermore, the crest of *P. walkeri* itself is largely responsible for the unwieldy nature of the head and therefore it cannot be seriously considered as an adaptation to counteract its own disadvantageous effects. And finally, Parks' hypothesis, published two years after Lambe's discovery, in no way accounts for the passages within the crest.

In 1924 Othenio Abel published the more fanciful suggestion that hadrosaurian crests were defensive structures, perhaps used in mating combat. In the same paper Abel very briefly considered the possibility that the crest cavities were also related to olfaction and he compared the crested hadrosaurs with crocodiles and their somewhat intensified olfactory powers. This paper was followed in 1929 by Nopcsa's sex character hypothesis wherein he presumed the crests to be secondary sex characters, the crested forms being the "males" and the non-crested varieties the "females." Again, with the exception of olfaction, neither Abel's nor Nopcsa's suggestion accounts for the presence of crestal passages, and Nopcsa's hypothesis proves somewhat inadequate on other grounds as well. (With the exception of *Parasaurolophus tubicen*, only non-crested "females" have been recovered from the Lance and equivalent stratigraphic units.)

Carl Wiman's resonating chamber theory (1931) was the first to give serious consideration to the most striking feature of hadrosaurian crests—the crestal cavities. That these cavities may have served as resonating chambers similar to those found in certain modern birds, appears entirely plausible, especially in view of the notoriously noisy habits of modern crocodiles. In fact, this suggestion is perhaps the best of any theory proposed so far, but it does seem somewhat improbable that this activity alone could have been responsible for such extensive cranial modifications.

A. S. Romer (1933) initiated the aquatic adaptation school with his comment that there may have been external narial openings near the top of the crest through which the animal could have breathed while almost completely submerged. An elevated or dorsal position for the external nares is a well known adaptation in certain living and extinct, air breathing, aquatic animals, but to date no such condition has been verified in the hadrosaurian crests, in spite of some comments to the contrary.

A series of papers by Martin Wilfarth (1938, 1939, 1940, and 1947) expanded the suggestion of Romer's relating the crests to an aquatic mode of life. In the first of these papers, Wilfarth suggested that the flat-headed hadrosaurs were proboscis-bearing reptiles in which there existed a large muscular, "telescoping air tube" that rose from the preorbital fossae of the snout. This device enabled the animal to "reach" up to the surface for air without interrupting its underwater feeding. The deep excavation of the snout is interpreted by Wilfarth as the origin scar of the large proboscis muscles. In the crested hadrosaurs, a similar muscular "snorkel" was pictured as attached to the crest, but strangely enough, in the same paper, Wilfarth accepts Parks' ligamentous connection between the dorsal vertebrae and the crest in *Parasaurolophus.* In later papers, the "snorkel" interpretation is greatly elaborated by Wilfarth. The crested hadrosaurs are represented with unique "upper" external nares located high on the crests. The usual narial openings situated rostrally on the snout are considered as nonfunctional relicts closed in life by skin and other tissues. The large surface area of the crest presumably provided large areas for the origins of proboscis muscles and inspired air was conducted down the flexible "breathing tube," through dorsal "nares" into the crest cavities and then to the mouth cavity and trachea. It is further suggested that this remarkable breathing tube may also have been prehensile and therefore useful in feeding.

Wilfarth's imaginative solution to the hadrosaurian crest problem, appealing and exotic as it may be, is not supported by any evidence. In the first place, not all of the hollow hadrosaurian crests are characterized by the required external openings which Wilfarth has interpreted as external nares. The crest of *Cheneosaurus tolmanensis,* for example, is not penetrated by any lateral or dorsal openings. The same is also true of *Corythosaurus frontalis, Corythosaurus brevicristatus,* and *Hypacrosaurus altispinus.* And in spite of Wilfarth's implications to the contrary (1947), there are no terminal openings in the crest of either *Parasaurolophus walkeri* or *P. tubicen* and they appear to have been absent in *P. cyrtocristatus* as well. Furthermore, the highly varied and irregularly shaped crestal openings that do occur in some specimens, (*Corythosaurus casuarius, Lambeosaurus lambei,* and *Procheneosaurus praeceps*) appear to be due to incomplete ossification at bone margins, and the areas involved were probably closed by cartilage or membrane. Still more doubt is cast on Wilfarth's hypothesis by the lack of any discernible muscle scars on any of the hadrosaurian crests. Although the preorbital fossae of the non-crested hadrosaurs might be considered as excellent scars left by proboscis muscles, it seems much more likely that these excavations contained narial sphincter muscles together with relatively large nasal organs.

Although perhaps not comparable, proboscis-bearing mammals are generally characterized by a marked reduction in the size of the nasal bones rather than an enlargement as is the case in many of the crested hadrosaurs. Furthermore, the nearest thing to a homologous structure, the elephant trunk, is not used as a "snorkel," but is a prehensile feeding mechanism and it apparently has always been such a device. If the hadrosaurian snorkel-like proboscis were also prehensile, as suggested, it would hardly seem to be functionally advantageous together with an expanded beak, as C. M. Sternberg (1939) has already pointed out.

Two additional explanations that have received a much greater degree of acceptance are similarly correlated with the semi-aquatic habits of the hadrosaurs. C. M. Sternberg (1935, 1939, 1942, and 1953) and L. S. Russell (1946) considered the crest as a trapping device which prevented the entrance of water into the narial passages and lungs while the animal was submerged. According to this thesis, the S-shaped narial loop is considered analogous to an inverted U-tube, and the greatly elongated crest of *Parasaurolophus* is represented as the functional peak of this adaptation. In contrast to the trap theory is the air storage hyothesis put forward by E. H. Colbert (1945 and 1955) and Romer (1933 and 1945). Here, the crestal cavities are interpreted as chambers for retaining a reserve supply of air which would have enabled the animal to remain submerged for longer periods. Both of these capabilities would seem to be highly advantageous adaptations for air breathing, aquatic animals. However, neither of these functions seems possible for the structure involved.

The U-tube trap explanation is unsatisfactory for several reasons. First, the mere presence of an inverted loop in the narial passage could not in itself have prevented the entrance of water into the narial passages, or even into the lungs. Water does not rise in the inverted U-tube for the simple reason that pressures at both ends of the tube are equal. In the case of the hadrosaurian loop, equal pressures on opposite sides of the loop could only occur in the emerged state. Even at shallow depths, hydrostatic pressure would have exceeded the air pressure within the crestal cavities and lungs. Such excessive hydrostatic pressure would have resulted in compression of crestal air and the entrance of water into the narial passages — even in an upward path against the force of gravity. Only excessive lung pressure (over hydrostatic pressure) could have prevented water from rising within the narial loop with the consequent admission of water into the nasal chambers and possibly into the lungs as well. No modern air breathing vertebrates, aquatic or semi-aquatic, rely solely on lung pressure to prevent drowning. Moreover, when one considers that the far simpler and more effective sphincter valves or vascularized narial tissues have been developed repeatedly for this very same function in such diverse aquatic animals as cetaceans, sirenians, pinnepeds, rodents, crocodiles, lizards, snakes and amphibians, the proposed water trapping function of the hadrosaurian crests loses much of its appeal.

Storage of a reserve air supply, for the purpose of prolonging the period of submergence, at first glance seems to be a very plausible and practical adaptation for semi-aquatic, air breathing animals. However, two quite unrelated factors make such a thesis highly improbable—if not impossible. First, the available volume of the crestal chambers appears totally inadequate in comparison with the probable lung capacity. A very conservative estimate of the lung capacity of *Corythosaurus casuarius*, (A.M.N.H. No. 5338) for example, is approximately 65,000 cc., or less than one fifth of the total volume of the rib cage. If it be assumed that the entire crest volume of this species could have been utilized as storage space, the total available volume of the uncrushed crest probably did not exceed 2500 cc. Thus in this particular species, the crest volume at best represented only about four per cent of the total lung capacity, and it is more than likely that it actually represented a much smaller fraction. Species with much smaller crests, such as *Procheneosaurus* and *Cheneosaurus*, would have had an even less significant volume of reserve air. It therefore seems unlikely that such extreme structural modifications were related to air storage. Furthermore, it seems somewhat anomalous that a semi-aquatic vertebrate should have undergone such extreme modifications for this purpose when purely aquatic air breathers have been so conservative with regard to such adaptations.

Finally, if we consider the manner in which the proposed storage cavities would have been utilized, it is immediately apparent that highly undesirable or totally impossible conditions would have resulted. For example, in order to withdraw this "reserve air supply" from the crest cavities and into the lungs, something (either air or water) must have displaced it. Water seems a most unlikely agent in view of its adverse effects and the numerous effective precautions against just such circumstances that have been repeatedly developed in other aquatic tetrapods. Air as a displacing substance, obviously was available only in an emerged state—in which case the "reserve air supply" was unnecessary. If narial sphincter muscles or vascularized narial valves prevented the entrance of water into these narial passages, as seems probable, these very same valves must have prevented air withdrawal from the crest during submergence. Thus, in spite of the attractiveness of the air storage theory, it seems quite improbable on the basis of current evidence.

NASAL APPARATUS IN MODERN REPTILES

Partial or complete dissection of several hadrosaurian crests has shown that the crestal cavities are continuous with the rostrally situated external nares and demonstrates most clearly that this structure was largely, if not entirely, related to the nasal apparatus and to some phase of respiratory activity. It is necessary therefore to examine the nasal anatomy of modern reptiles and to consider the various functions of the tetrapod nasal system.

The primary function of the nasal apparatus quite obviously is the conduction of air from the exterior to the lungs. In addition, this principal activity requires other preparatory functions such as cleansing, warming (or cooling), and humidifying of the inspired air. (The trapping hypothesis relates to the first of these.) It should not be necessory to consider each of these functions in detail in order to arrive at the respective merits of each as an explanation of the structures under consideration. It is true that temperature regulation or humidification of inspired air may be the proper explanation, but all of these seem improbable in view of the humid, temperate to subtropical conditions indicated for the hadrosaurian environment.

A second major function involving the nasal apparatus is that of olfaction. It is surprising that this activity, which is associated with respiratory activities in all tetrapods, has not been considered more seriously before this. Perhaps the reason for this may lie in the general impression that modern reptiles do not possess a highly developed sense of smell. This is certainly true, if one compares them with mammals—particularly with macrosmatic mammals, but the fact that reptiles do have olfactory powers cannot be disputed.

Mammals which are characterized by a highly developed sense of smell show a corresponding expansion of the olfactory sensory epithelium. This is reflected in the expanded and complex turbinal and ethmoid systems. There is of course no comparable "ethmoid-turbinal complex" in the hadrosaurs, but the crestal cavities could well have contained analogous structures. The question to be answered here is—what was the purpose of the greatly elongated and complex path of the narial passages? Might not this expanded passage have been a means of increasing the surface area of sensory epithelium? The form, pattern and size of the cavities are quite variable, but in every crested hadrosaur there has been some increase in the length of the narial passages through which the inspired air traveled. This is the only common denominator for all lambeosaurine crests.

Examination of the nasal capsule in modern reptiles reveals some interesting morphologic evidence pertinent to this subject. The reptilian nasal capsule (see fig. 1), which is largely cartilaginous, encloses the membranous nasal sac. The sac itself consists of four major parts: the anterior nasal tube, the anterior chamber, the olfactory chamber, and the choanal tube (Beecker, 1903; Pratt, 1948; Bellairs and Boyd, 1950; and Oelrich, 1956). Each of these regions may vary from one form to another, but they are at least partly distinct from each other functionally as well as morphologically. The anterior chamber is principally a preparatory mechanism (filtering, humidifying, and temperature regulating), while the olfactory

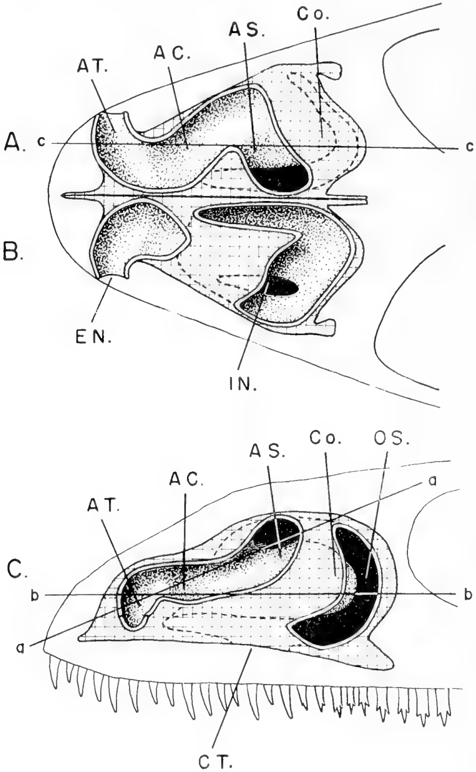

Fig. 1. Cartilaginous nasal capsule of *Ctenosaura pectinata.* A. Dorsal view of capsule as seen in rostrally inclined section (see line a - a in diagram C.) showing the anterior part of the nasal canal. B. Dorsal view as seen in horizontal section through the center of the capsule (see line b - b in diagram C.) showing the posterior and ventral parts of the nasal canal. C. Lateral view of the capsule as seen in parasagittal section (see line c - c in diagram A.) For abbreviations see text.

chamber is in large part sensory in function. The olfactory chamber is further divisible into three regions relating to an epithelial swelling or protuberance of its lateral wall—the concha. These are: the anterior space (anterior to the conchal swelling), the conchal zone, and the antorbital space (posterior to the concha) (Oelrich, 1956). Ventrally the olfactory chamber (usually in the conchal zone) opens into the choanal tube and thereby communicates with the oral cavity.

In *Sphenodon* (see fig. 2) a short anterior nasal tube passes posteromedially from the laterally situated external naris to a short but slightly expanded anterior chamber adjacent to the nasal septum. The anterior chamber is continuous with a larger olfactory chamber behind. (Although the olfactory chamber of *Sphenodon* is larger than the anterior chamber, it is relatively smaller than the olfactory chamber in most lizards [Pratt, 1948].) Within the olfactory chamber, the anterior space is restricted and the concha occurs as a very weakly developed swelling of the lateral wall. The antorbital space is also restricted. Sensory epithelium is limited to relatively small

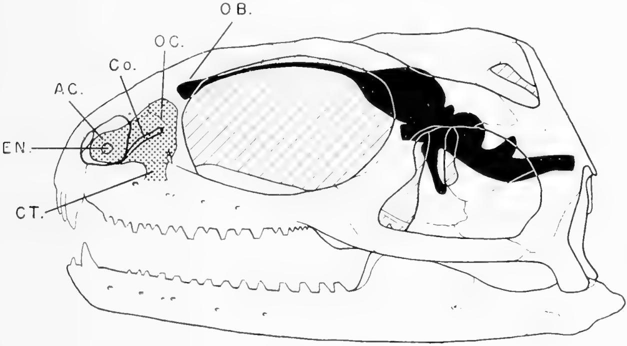

Fig. 2. Lateral view of the skull of *Sphenodon punctatum* illustrating the locations and relative sizes of the cartilaginous nasal capsule (stippled pattern) and the olfactory structures of the brain. Notice the long olfactory stalks and the olfactory bulbs situated just behind the relatively small nasal capsule.

areas on the medial and dorsal surfaces of the restricted concha, a relatively much smaller proportion of the available area as contrasted with certain lizards (Pratt, 1948). Olfactory nerve fibers arise from these small areas of olfactory epithelium and pass posteriorly along the lateral wall of the antorbital space and through the posterior wall of the nasal capsule (planum antorbitale) where they join the olfactory bulb just behind. It is important to note here that in spite of the relatively weak development of the olfactory chamber, the small olfactory bulbs are situated immediately behind the short nasal capsule anterior to the orbits.

The relatively short preorbital length, together with the large eyes of *Sphenodon*, limits the available space for the nasal capsule and undoubtedly is related to the restricted development of the olfactory chamber and concha. The latter apparently is not related, however, to the limited olfactory sensitivity of *Sphenodon*, because even the available surface area of the olfactory chamber is not fully utilized for sensory functions. The limited olfactory powers (Pratt, 1948) would appear to be in contradiction to the nocturnal, predatory nature of the animal where an acute sense of smell would seem to be advantageous, but on the other hand it is consistent with the burrow-living (but possibly not fossorial) habits of *Sphenodon*.

Stebbins (1943 and 1948) and Pratt (1948) have demonstrated that there is considerable variation in the respective parts of the lizard nasal sac depending upon the mode of life. For example, in deserticolous lizards the trapping and humidifying functions are more critical and there is a corresponding enlargement of the anterior chamber. In arboreal lizards, vision is of greater importance than olfaction and the visual apparatus seemingly has expanded and limited the development of the olfactory chamber. In cursorial forms, particularly in the nonburrowing varieties, vision and olfaction are both important. Thus there commonly exists a relatively large eye which limits the expansion of the olfactory chamber in front. However, in such cases, the concha is usually greatly expanded and it appears that conchal expansion is an alternative method of maintaining or increasing the available area for olfactory epithelium when other factors (orbital expansion or short snout length) restrict expansion of the olfactory chamber itself (Pratt, 1948).

In *Ctenosaura* (see figs. 1 and 3), the anterior nasal tube extends for a short distance anteromedially from the anterolaterally placed external naris. Adjacent to the nasal septum it turns abruptly backward and upward, extending to a long and expanded anterior chamber. This is continuous dorsomedially with a narrow anterior space and inflated conchal zone. Posteriorly, a large antorbital space extends ventrally and then forward to the choanal tube. Within the olfactory chamber, olfactory epithelium lines the medial and dorsal walls, the medial and posterior surfaces of the concha, and the posterior wall of the antorbital space (Oelrich, 1956). Olfactory nerve fibers pass posteriorly from these areas, penetrate the planum antorbitale and unite with the olfactory bulb situated anterior and dorsomedial to the orbits.

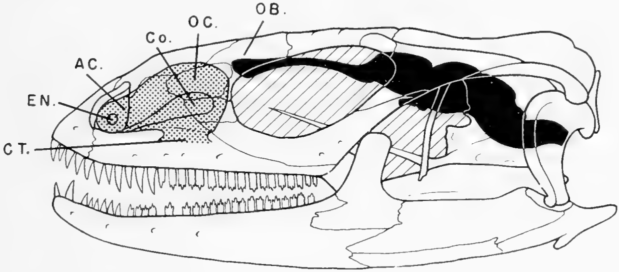

Fig. 3. Lateral view of the skull of *Ctenosaura pectinata* showing the locations and relative sizes of the nasal capsule (stippled pattern) and the olfactory centers of the brain.

Relative to *Sphenodon*, *Ctenosaura* possesses enlarged olfactory chambers and considerably more extensive olfactory epithelium. As in *Sphenodon*, the olfactory bulbs are situated far forward, immediately behind the planum antorbitale of the nasal capsule and in front of the orbits.

In *Alligator* (see fig. 4), an extremely short anterior nasal tube descends from the dorsally situated external naris. At its ventral limit it turns abruptly backward and opens into a very long and slightly inflated anterior chamber that reaches caudally to the anterior extremity of the palatine. Although compressed dorsoventrally, the anterior chamber expands laterally reaching its maximum width at about mid-length Posteriorly, the anterior chamber is continuous with a rather large olfactory chamber. A very prominent concha occupies most of the olfactory chamber with the result that both the anterior space and the antorbital space are restricted in volume, although both are of moderate size. The total length of the nasal capsule is approximately equal to the total preorbital skull length, the planum antorbitale being situated just beneath the anterior rim of the orbit.

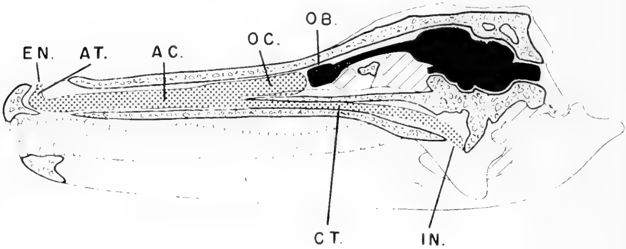

Fig. 4. Skull of *Alligator mississipiensis* as seen in near-sagittal section, showing the relationships between the olfactory centers of the brain and the enlarged nasal capsule (stippled pattern). Notice the enlarged anterior chamber and olfactory chamber as well as the elongated choanal tube.

Olfactory epithelium lines portions of the medial, dorsal, and ventral walls of the olfactory chamber, the dorsal, medial, and ventral surfaces of the concha, and the posterior wall of the antorbital space. From these rather extensive sensory areas, olfactory nerve fibers extend dorsoposteriorly to the moderately sized olfactory bulbs that are placed dorsomedially at the level of the anterior margins of the orbits. As in *Sphenodon* and in lizards, the olfactory bulbs lie immediately behind the rear wall of the nasal capsule.

Generally speaking, there is a marked reduction in the olfactory sensitivities of aquatic animals, but this does not seem to be true of the Crocodilia. The long snout has provided space for a relatively long nasal capsule that extends over the entire preorbital length. Extensive development of sensory epithelium, an expanded concha, and moderately sized olfactory bulbs all indicate a significant (if not acute) level of olfactory sensitivity.

NASAL APPARATUS OF THE HADROSAURIDAE

Turning our attention back to the group in question, the Hadrosauridae are subdivided into three subfamilies (four by Lull and Wright [1942] and certain other workers) chiefly on the basis of cranial anatomy. The three subfamilies recognized here are the Hadrosaurinae, characterized by flat, non-crested skulls; the Lambeosaurinae, possessing hollow bony crests composed of the premaxillaries and nasals extending over the top of the cranium; and the Saurolophinae, which bear less prominent, solid, bony crests composed exclusively of the nasals. The lambeosaurine crests have been referred to as "true narial" crests because they are all hollow and enclose parts of the elongated and sometimes complicated narial passages. The various species of *Procheneosaurus*, *Cheneosaurus*, *Corythosaurus*, *Lambeosaurus*, *Hypacrosaurus*, and *Parasaurolophus* all display variations of the true narial crest. Crests of the Saurolophinae (*Saurolophus*, *Prosaurolophus*, and *Brachylophosaurus*) have been labeled "pseudo-narial" crests, because of their solid construction and the fact that they do not enclose any part of the nasal apparatus (Ostrom, 1961b).

Correlated with these cranial conditions is the construction of the hadrosaurian snout. Those hadrosaurs which bear true narial crests have greatly reduced snouts, while all other hadrosaurs are characterized by a long and inflated snout. As a result, all members of the Hadrosaurinae and the Saurolophinae have conspicuous preorbital fossae, while the Lambeosaurinae have virtually no preorbital space available in the snout. It is quite reasonable to assume that the prominent preorbital excavation of the hadrosaurine and saurolophine premaxillaries and nasals housed (at least in part) rather large nasal organs as suggested by Versluys in 1936. In the Lambeosaurinae, on the other hand, the snout is greatly compressed dorsoventrally and there is no large excavation of these bones. Instead, the premaxillaries and nasals have been prolonged dorsocaudally and inflated at a more dorsal and posterior level forming the true narial crest.

In *Procheneosaurus* the inflated region occurs dorsal to the maxillaries immediately in front of the orbits. In *Cheneosaurus* it occupies a similar position, but has expanded dorsocaudally and lies over the orbits as well. The inflated zone of *Corythosaurus*, *Hypacrosaurus*, and *Lambeosaurus* has expanded still further dorsocaudally so that in nearly every instance it lies well above and behind the orbital level in a supracranial position. And in *Parasaurolophus*, an extreme expansion has carried the inflated region well behind the cranium, as well as above it, to a postcranial position. These hadrosaurs would seem to form a sequence of structural stages through which the

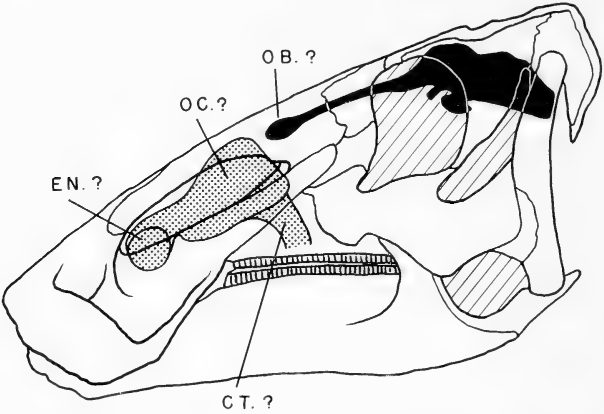

Fig. 5. Outline sketch of the skull of *Edmontosaurus regalis* (N.M.C. No. 2288) illustrating the probable position of the cartilaginous nasal capsule (stippled pattern) in the preorbital fossa. The preorbital position of the olfactory bulbs suggested here is based upon the close proximity of nasal capsule and olfactory bulbs found in all modern reptiles. Notice that the expanded snout of the Hadrosaurinae provides ample space for a nasal capsule and narial sphincter muscles.

nasal apparatus has expanded and shifted from a rostral position on the snout to a preorbital, to a supraorbital, to a supracranial, and finally to a partially postcranial position. (See figs. 6-9.)

Considering the true narial crests in more detail, they all involve a dorsal and caudal expansion of both the premaxillaries and the nasals, the degree of expansion and the relative participation of each varying considerably between different species. Most conservative are those of the three species of *Procheneosaurus* (*P. praeceps*, *P. erectofrons*, and *P. cranibrevis*) and the only known species of *Cheneosaurus* (*C. tolmanensis*). In these species the premaxillaries are split into

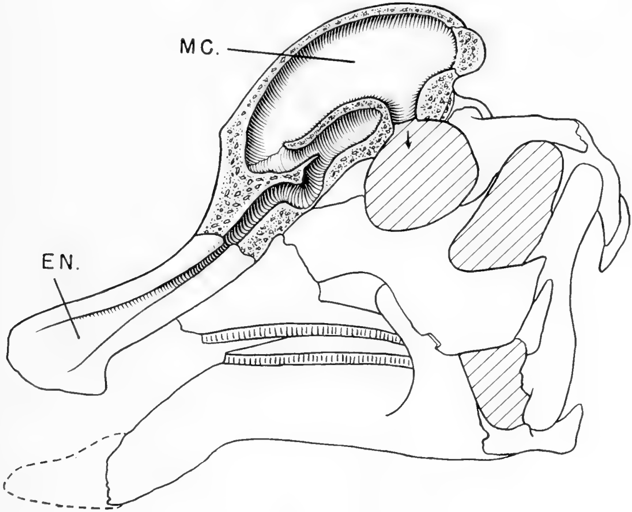

Fig. 6. Outline sketch of the skull of *Procheneosaurus cranibrevis* (N.M.C. No. 8633) showing a reconstruction of the narial passages of the crest. The left premaxillary and nasal have been partially removed to show the paired lower canals and the "undivided" medial cavity and "choanal" tube. The arrow indicates the passage of the "choanal" canal from the crest. (From Ostrom, 1961b.)

superior and inferior rami or lobes lying above and below the nares. Both lobes ascend caudally, almost completely enclosing the anterior portion of the narial passage. The nasal bone occupies a dorsal position between the upper extremities of the premaxillary lobes and encloses the upper part of the narial canal.

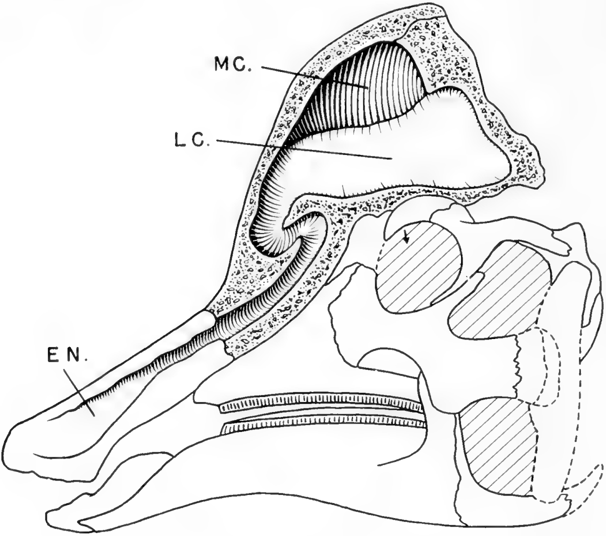

Fig. 7. Outline sketch of the skull of *Corythosaurus excavatus* (N.M.C. No. 8676) showing a reconstruction of the narial passages of the crest. The left premaxillary and nasal have been partially removed to show the paired lower canals and lateral cavities and the "undivided" medial cavity. The arrow indicates the approximate passage of the "choanal" canal from the crest. (From Ostrom, 1961b.)

Within the crest of *Procheneosaurus* (as may be seen in *P. cranibrevis*, N.M.C. No. 8633) the narial passages ascend as separate canals from the rostrally situated external nares. (See fig. 6.) This portion of the canal, although quite long, may be analogous to the anterior nasal tube of modern reptiles. Dorsally, at the anterior limit of the nasal bone, the narial canals loop forward and then upward in an S-shaped curve and finally enter a common medial crest cavity anterior to and at the level of the orbits. (This medial cavity quite probably was divided by cartilage or membranous tissues in life, consistent with the paired conditions of modern reptilian nasal structures.) Ventroposteriorly, a single (also probably paired in life) "choanal" canal descends from this medial crest cavity into the interorbital region. The latter feature is certainly comparable to the choanal tube of the modern reptilian nasal capsule and the undivided cavity above it would appear to represent the location of paired olfactory chambers. The S-shaped curve of the nasal passage then seems to represent the anterior chamber.

The crest of *Corythosaurus excavatus* (N.M.C. No. 8676), although differing in details, displays a very similar pattern (see fig. 7). In this and most other species of *Corythosaurus*, the nasal is a very prominent bone forming a major part of the crest. Again, separate narial passages (anterior nasal tubes?) ascend posteriorly from the external nares, enclosed for most of their length by the two lobes of the premaxillaries. In front of and slightly above the level of the orbits, the two passages turn forward and then upward and back again, forming separate S-shaped curves (anterior chambers?) similar to those of *Procheneosaurus cranibrevis*. Unlike the condition in that species, however, the paired narial canals lead into paired lateral cavities above and posterior to the S-shaped loops. These lateral cavities (olfactory chambers?) occupy the lower half of the crest, but dorsally they open into a common medial cavity that extends well up into the crest. Although this latter cavity could not be fully explored, it apparently extends ventrally as a single "choanal" tube between the lateral cavities to the interorbital region just anterior to the olfactory canal of the brain case. These relationships indicate a great expansion of the lateral (olfactory) chambers back around the more medially placed "choanal" tube.

Two specimens of *Lambeosaurus* (*L. lambei*, N.M.C. No. 2869, and *L. clavinitialis*, Y.P.M. No. 3222) display similar narial patterns characterized by the independently ascending passages (anterior nasal tubes?) and the S-shaped loops (anterior chambers?) (see fig. 8). In both of these specimens, however, the canals remain separated for some distance behind these loops before entering the large undivided medial cavity in the posterior half of the crest. As in other forms, this medial crest cavity (site of the olfactory chambers?) is continuous ventrally with an unpaired "choanal" tube leading to the interorbital region just anterior to the brain case.

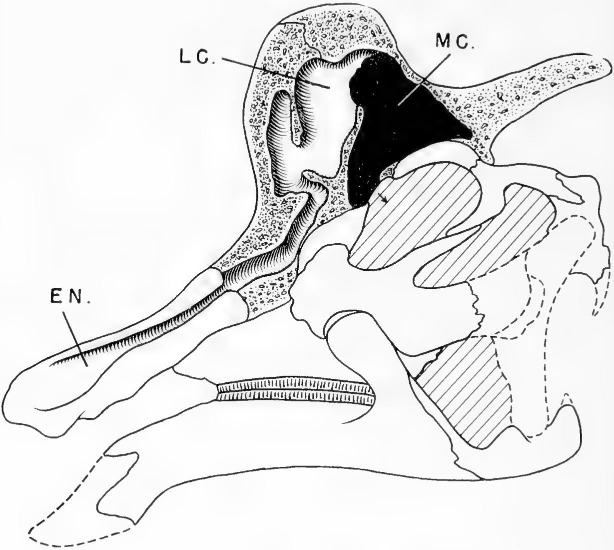

Fig. 8. Outline sketch of the skull of *Lambeosaurus clavinitialis* (Y.P.M. No. 3222) showing a reconstruction of the narial passages of the crest. The lateral elements of the crest have been partially removed to show the paired condition of the lower canals and the "undivided" dorsal (posterior) cavity and "choanal" tube. Organic material, perhaps representing cartilaginous tissues, found in the posterior cavity indicates this cavity may have been divided by a median septum in life. The arrow indicates the passage of the "choanal" canal from the crest. (From Ostrom, 1961b.)

The crest of *Parasaurolophus cyrtocristatus* (C.N.H.M. No. P27393) provides the most detailed information yet available about hadrosaurian crestal cavities (Ostrom, Ms.) (see fig. 9). Dissection of one side of the crest illustrates that the narial canals extend as separate passages along the full length of the crest. From the rostrally situated external nares, the paired passages (anterior nasal tubes?) ascend in the upper half of the tubular crest. At the caudal extremity, they loop down to the lower half of the crest and pass forward to the roof of the skull. Only at the base of the crest, just above and behind the orbits do these paired passages join in a common cavity. (These inferior passages and the undivided basal cavity may represent the location of the olfactory chambers.) Thin medial lamellae of the premaxillaries form a continuous wall between the canals over their entire length, and similar transverse bony walls separate the upper and lower canals as well. The undivided medial cavity at the base of the crest communicates with the interorbital region by way of a "choanal" tube as in other crested hadrosaurs. The only subsidiary chambers discovered

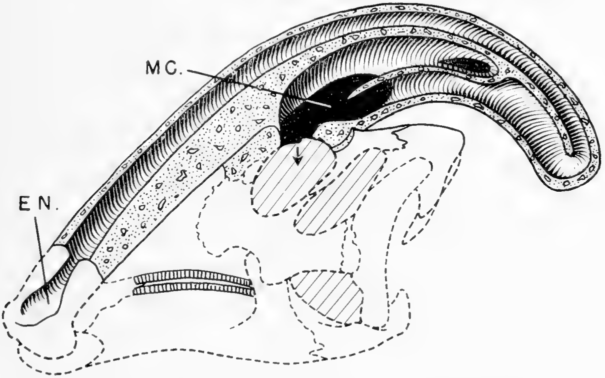

Fig. 9. Outline sketch of the crest of *Parasaurolophus cyrtocristatus* (C.N.H.M. No. P27393) with the lateral elements removed to show the pattern of the crestal cavities. The only "unpaired" portion of the passages occurs at the base of the crest just above the orbits. The "choanal" tube extends ventrally (arrow) from the medial cavity into the interorbital region. (From Ostrom, 1961b.)

in this relatively simple crest plan were a pair of elongated cavities situated between the upper and lower passages. These extend caudally from the common cavity for about half of the total crest length.

In each of these specimens, at least a part of the crest is occupied by a large undivided or unpaired chamber—that part of the narial cavities adjacent to the "choanal" canal. It is quite probable that this common cavity, as well as the "choanal" canal, was actually divided by cartilage or membranous tissue. In support of this are numerous patches of organic material dispersed throughout the matrix of these crestal cavities of both *Parasaurolophus cyrtocristatus* and *Lambeosaurus clavinitialis.* These appear to represent remnants of thin sheets of organic material—probably cartilage—which were originally situated within the crestal cavities. In view of the cartilaginous nature of the modern reptilian nasal capsule, it is quite possible that the hadrosaurian capsule was of similar construction and that these bits if organic material are remnants of this structure. No similar material could be discovered in the matrix outside of the crestal cavities, but most of the matrix had already been removed prior to the present study. None of the other crests which were examined showed any comparable material within the accessible parts of the crest.

OLFACTION IN THE HADROSAURS

That the hadrosaurian dinosaurs were like all other tetrapods in the possession of a nasal capsule, is not likely to be disputed. And that this capsule was concerned with the same fundamental activities as those of modern tetrapods is likewise beyond doubt. It even seems safe to assume that the hadrosaurian nasal capsule was probably of the same basic design as that of modern reptiles. But as to the precise capsule form and the relative importance of the several nasal functions there is considerable uncertainty.

The restricted construction of the lambeosaurine snout indicates that the nasal apparatus could not have been located rostrally. The crest, on the other hand, not only provides a likely site—it constitutes the only possible site for the lambeosaurine nasal capsule. Moreover, the construction of the crest cavities seems to parallel in a very general way the basic pattern of the capsule in modern reptiles, consisting of a long narrow "anterior nasal tube," a more inflated and sinuous "anterior chamber," a large, inflated "olfactory chamber," and a "choanal tube."

The origin of this expanded nasal "capsule" cannot be explained by the primary nasal function—air conduction. Nor does it seem probable that air preparation was a significant causal factor. Olfaction, on the other hand, appears very likely as a principal factor in the development of the lambeosaurine crest. As we have seen in the several modern reptiles

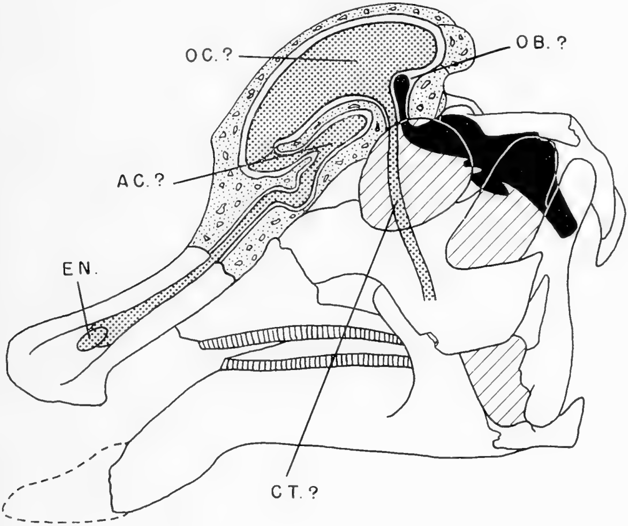

Fig. 10. Outline sketch of the skull of *Procheneosaurus cranibrevis* (N.M.C. No. 8633) illustrating the dorso-ventrally compressed snout of the Lambeosaurinae and the inflated narial crest. The stippled pattern indicates the proposed disposition of the nasal capsule within the crestal cavities and its probable relationship to the olfactory bulbs.

considered here, appreciable variation occurs in the total amount of olfactory epithelium, and the available surface area may be expanded in certain forms by an invagination (concha) of the olfactory chamber wall. In mammals, still more complex folding of the epithelium has resulted in an increase in sensory epithelial surface area and more acute olfactory powers. Within the lambeosaurine crest, the nasal passage has been elongated and in some sections greatly inflated. But not only has it been lengthened and inflated, the total surface area has also been increased, perhaps as a parallel means of increasing the total area available for olfactory epithelium. In support of this interpretation, it should be noted that the largest of the crestal cavities is always situated immediately adjacent to the "choanal" canal and it is this segment of the modern reptilian capsule that is usually involved with sensory activities.

If the large chamber of the lambeosaurine crest did in fact house the olfactory chambers of the nasal capsule, how were the contained areas of olfactory epithelium innervated? Several specimens suggest an answer. *Corythosaurus casuarius* (R.O.M. No. 1933), *Corythosaurus excavatus* (N.M.C. No. 8676), *Lambeosaurus lambei* (N.M.C. No. 2869), and *Lambeosaurus clavinitialis* (Y.P.M. No. 3222) display a uniform relationship between the "choanal" passage from the crest and the olfactory foramen at the anterior limit of the brain case. In each of these specimens, the "choanal" passage opens into the interorbital region immediately in front of the olfactory nerve canal. The distance between the olfactory foramen of the brain case and the "choanal" opening of the crest never exceeds 40 mm. A fifth specimen, *Parasaurolophus cyrtocristatus* (C.N.H.M. No. P27393) displays the "choanal" opening located in a similar position that must have been immediately anterior to the brain case. Unfortunately, however, the brain case is not preserved so the relationship cannot be verified in this particular case.

The proximity of these two openings, together with their respective dimensions, indicate that the olfactory bulbs were probably located up in the crest cavities and the olfactory tracts passed downward out of the crestal cavities through the "choanal" canal and then turned backward into the endocranial cavity (see figs. 10 and 11). In fact, no other suitable site for the olfactory bulbs seems to exist. Additional support for this interpretation was recently found in *Lambeosaurus clavinitialis* (Y.P.M. No. 3222) where remains of what appears to have been a cartilaginous extension of the walls of the olfactory nerve canal passes from the brain case up into the crestal cavities through the "choanal" canal. Strange as such a position may appear, it conforms only with a crestal position of the olfactory chambers and is entirely consistent with the modern reptilian condition where the olfactory bulbs are located immediately adjacent to the nasal or olfactory sac.

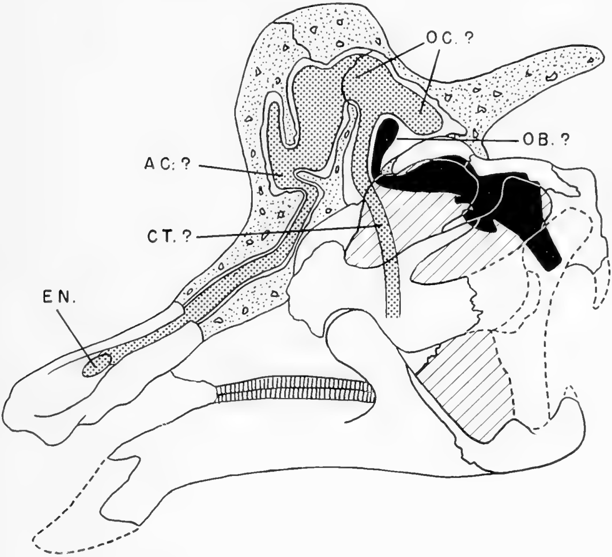

Fig. 11. Outline sketch of the skull of *Lambeosaurus clavinitialis* (Y.P.M. No. 3222) showing the dorso-ventrally compressed snout and the greatly inflated narial crest. The stippled pattern indicates the generalized arrangement of the nasal capsule proposed here together with the probable location of the olfactory bulbs.

CONCLUSION

From all available evidence, it appears quite likely that the lambeosaurine crest was an adaptation for increasing olfactory sensitivity by providing an increase in the total surface area available for olfactory epithelium. (It also seems probable, in view of the very large and unique preorbital fossae, that the non-crested hadrosaurs had also developed enlarged or modified nasal apparatus situated in a more normal position in the inflated snout. See fig. 5.) But the inevitable question arises, why should the hadrosaurs, rather than any other dinosaur, have required superior olfactory powers? Of course this question cannot be answered to the complete satisfaction of everyone concerned, but some interesting possibilities are suggested by reconsidering hadrosaurian ecology.

It is quite probable that hadrosaurs lived a rather passive, perhaps even retiring existence as relatively slow moving, terrestrial or amphibious herbivores. That they were able to move about over the land is verified by their skeletal construction and that they may have been terrestrial browzers, at least in part, is suggested by Kräusel's (1922) analysis of the "stomach contents" of *Anatosaurus* (*Trachodon*) *annectens*. Other evidence (the large laterally compressed tail and the webbed manus) points to a certain dependency upon an aquatic environment—perhaps for food in the form of soft aquatic plants or perhaps as a place of refuge from terrestrial predators.

In comparing the hadrosaurs with other dinosaurian herbivores, it is striking that they alone lack any obvious defensive or protective adaptations. They possessed no horns, no claws, no sharp teeth, they carried no clubbed or spiked tail, and they had no bony armor. They certainly were not constructed for rapid flight and they cannot be considered giants for their time. In short, the hadrosaurs appear to have been quite defenseless—a most improbable plight. As an alternative it seems increasingly probable that they depended upon the relative security of lakes, swamps, or rivers and thereby escaped from their enemies.

However, such inland waters represented only *potential* safety as long as the individual was out on the land—potential safety contingent upon adequate advance detection of the im-pending danger by one or more of the sensory systems. Here is where acute olfactory sensitivity may have had significant survival value for the hadrosaurs, just as it does for many modern mammalian herbivores.

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Postilla

YALE PEABODY MUSEUM

OF NATURAL HISTORY

Number 63 July 9, 1962 New Haven, Conn.

BRIEF COMMENTS ON THE THRUSHES

S. Dillon Ripley

In Postilla no. 13, 1952, pp. 1-48 *et seq.*, 1952, 1954, I published a fairly extensive review of this large and sprawling subfamily of the Old World Muscicapidae. More recently I have been gathering data on this assemblage for Peters' *Check-list*, and so it appears worthwhile to list here a few of the changes and revisions which have been made subsequent to my earlier publication.

Certain large general works have been of the greatest use such as Chapin's (1953) section on thrushes in his monograph on birds of the Congo, Vaurie's (1959) monograph on Palearctic birds and Mackworth-Praed and Grant's (1955) volumes on birds of eastern Africa. In addition shorter papers have been of value such as that of White (1961) on African thrush genera. I have been very grateful for comments and help received from Messrs. Clancey, Deignan, Dilger, Charles Hartshorne, Ivanov, Johansen, Mmes. B. P. Hall and E. Koslova, Messrs. Lees-Smith, Meinertzhagen, Terence Oatley, George Watson, White, and Winterbottom.

After correspondence and discussion with these various authors, as well as with the editors of the *Check-list*, Messrs. Greenway, Mayr, and Paynter, it appeared wise to retain the Prunellidae as a monotypic family close to the thrushes. I believe my preliminary revisional work of 1952 has served a good purpose, however, in raising comments and criticism. Without such preliminary work and the subsequent eddies and fluctuations of opinion aroused, little long-range revisional work would be possible.

Erythropygia, *Cercotrichas*, and *Pinarornis.*

Following the suggestion of White (1961), I have grouped *Cercotrichas* and *Pinarornis* next to *Erythropygia.* I do not agree to merging *Cercotrichas* with *Erythropygia.* This is a rather distinct species and such field workers as Meinertzhagen (1954) would keep them decidedly separate.

Pogonocichla and *Erithacus.*

Moreau's interesting paper (1951) offers evidence that *Pogonocichla* with two included species has characters which set it sufficiently apart to be kept as a separate genus. Little published work has convinced me that the genus *Erithacus* cannot be kept as an expanded genus. Japanese workers, among them Morioka (in litt.), point out the close resemblance of the Japanese robin, *akahige* to the European *rubecula,* contra Lack (1954). More recently Hall (1961) has suggested adding the species *gabela,* described from Angola in 1957, to the genus *Erithacus.*

Cossypha and *Xenocopsychus.*

The reasons advanced by White (1961) for transferring *Xenocopsychus* to *Cossypha* seem provocative, and I accordingly have followed this suggestion, having already included *Dessonornis* (*Bessonornis* auct.) earlier.

Pseudocossyphus.

I have removed the species *sharpei* and *imerina* from *Cossypha* and placed them in *Pseudocossyphus* following Goodwin (1956) whose suggestions and evidence I have found most helpful.

Rhyacornis and *Chaimarrornis.*

I also follow Goodwin (1957) in keeping *Rhyacornis* as a separate genus for the small tropical redstarts with such distinctive alternate plumages, and placing *Chaimarrornis* close to *Monticola* following *Oenanthe.*

Grandala and *Sialia.*

It is not obvious to anyone apparently where *Grandala* should be listed. I leave it near *Sialia* for lack of a better linear arrangement suggestion, not out of any conviction on the basis of anatomy or phenotypic characters.

Phaeornis.

From personal observation in the field and listening to songs I have decided that my earlier feeling that *Phaeornis* was close to *Myadestes* following Stejneger (1887) was wrong. *Phaeornis* has two species on Kauai Island which overlap ecologically. The larger, a subspecies of *obscurus,* has a broad bill which resembles a solitaire. I believe it is a secondary adaptation to coexistence in an overlapping niche, the separate first invader being small and possessing a much smaller bill. In powerful song and apparently in habits these birds seem far closer to *Catharus* especially the central American nightingale-thrush group.

Stizorhina.

Stizorhina may well prove to be a flycatcher. Unpublished work in this laboratory (Ames ms.) shows un-turdine-like indications in the syrinx of S. *fraseri* although the evidence is by no means compelling, as *Myadestes* also has a very similar syrinx.

Myrmecocichla, Pentholaea and *Thamnolaea.*

I follow White (1961) in combining *Pentholaea* with *Myrmecocichla,* although I keep *Thamnolaea* distinct, both on account of slight plumage differences as well as partially of habits, as Cave and Macdonald (1955) emphasize for *T. coronata.* I have moved the Buff-streaked Chat, *bifasciata,* to *Oenanthe* on further examination, convinced that in plumage and behavior it fits better with the wheatears.

Catharus and *Platycichla.*

A few species changes have been made in the arrangement of *Catharus* on the advice of various tropical American specialists such as Messrs. Blake, Paynter, Skutch, and Wetmore. I have placed *Platycichla* as a separate genus on the advice of several authors including Messrs. Bond and Phelps (personal communication).

Turdus.

For advice on the large genus *Turdus* I have been much indebted to Dr. Chapin and Mrs. Hall on African species and specimens in the British Museum. This huge genus with more than sixty-five species is a difficult one to arrange and I have felt constrained to list the species regionally beginning with Africa and ending with the New World. I have valued Dr. Wetmore's comments on *ignobilis* and *plebejus* which I have separated as two species. I have also moved *swalesi* near to our North American robin, feeling that this species is merely a relict robin.

Several problematical genera have been removed from the arrangements of thrushes of earlier authors just as others have been added to it. Some of these former are *Turnagra,* the New Zealand "thrush," obviously not a thrush at all, *vide* Oliver (1955), who places the genus in a separate family based on the presence of mouth bristles, union of maxillo-palatines, long first primary and lack of spotted young. *Namibornis* (or *Bradornis*) *herero,* the south West African flycatcher, *Achaëtops,* another South West African genus, inadvertently assigned to the thrushes by the South African Ornithological Society List Committee (1958), and "*Cercomela*" *buryi* which may or may not be a *Parisoma*, but certainly with its wing structure appears to be a warbler rather than a chat, are all problematical species which I would include in the Muscicapinae, Timaliinae and Sylviinae respectively.

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Postilla

YALE PEABODY MUSEUM

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TWO NEW PRIMATE SPECIES FROM THE AFRICAN OLIGOCENE

ELWYN L. SIMONS

One of the major objectives of the Yale 1961-1962 Paleontological Expedition to the Fayum region of Egypt was to recover a larger sample than previously known of the earliest mammalian microfauna from the continent of Africa, that of the Fluviomarine formation of the Fayum early Oligocene. During the course of our investigations the expedition staff succeeded in locating specimens assignable to two new species of Primates. In view of the considerable interest in, and rarity of, Old World Primates dating from this epoch it seems advisable to publish a preliminary description of these two forms without delay, so that they will be available for consideration by other authors. It is intended that a fuller analysis of their morphology and relationships will be included in a study of the Fayum mammalian microfauna now being prepared by the writer.

ACKNOWLEDGMENT

I wish to express my sincere thanks to Dr. Osman Moharam, Director of the Department of Geological and Mineralogical Research, Ministry of Industry, United Arab Republic; Dr.

Riad Higasy, former Minister of Industry, and Dr. Y. Shawki Moustafa, Curator of Fossil Vertebrates, Cairo Museum of Geology, for generously supplying facilities and assistance which contributed greatly to the success of our expedition to the Fayum badlands. The field research of which this report is an outgrowth was made possible by a grant in Geology of the National Science Foundation. Illustrations were prepared by Margaret E. Freeman of New Haven and their execution was partly financed by a grant from the Wenner-Gren Foundation of New York. The photograph (figure 3) was prepared by John Howard of the museum staff.

ABBREVIATIONS

A.M.N.H.	American Museum of Natural History, New York.
Y.C.P.E.	Yale-Cairo, Paleontological Expedition (field numbers).
Y.P.M.	Yale Peabody Museum, New Haven.

SYSTEMATICS

Class MAMMALIA

Order **PRIMATES**

Suborder ANTHROPOIDEA

Infraorder CATARRHINI

OLIGOPITHECUS,[1] new genus

Type: *Oligopithecus savagei,* new species

Generic characters: Lower dental formula 2?. 1. 2. 3., size of mandible approximately that of the living ceboid primate *Leontocebus rosalius,* slightly smaller than its contemporary *Propliopithecus haeckeli.* Differs from the latter in having a slightly shallower mandibular ramus, more

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[1] Named with reference to the Oligocene occurrence of this catarrhine.

anteroposteriorly elongated P$_3$, distinct paraconid on P$_4$-M$_1$, lower molar external cingula less distinct and hypoconulid shifted much more lingually than in *Propliopithecus* and not distinctly separated from entoconid. Differs from *Parapithecus fraasi* in its larger size and in possession of undoubted, large canine anterior to P$_3$, in absence of metaconid cusp on P$_3$,—present in *Parapithecus,* in possession of anteroposteriorly elongated P$_3$ not seen in the latter genus, and in having a much more lingually extended paraconid ridge on M$_{1-2}$.

Figure 1. External view of left mandible, *Oligopithecus savagei,* Type, Y.C.P.E. 207. x 3 approx.

Discussion: In depth of jaw and canine morphology *Oligopithecus* much more nearly resembles *Propliopithecus* than it does *Parapithecus* or *Apidium,* three other primates from the Fayum early Oligocene. On the other hand, the anteroposteriorly elongate P$_3$, a feature which typically characterizes post-Oligocene cercopithecoids and pongids, is not to be seen in any specimens of these three Fayum genera. Such a lower P$_4$ does occur in a damaged mandible, A.M.N.H. 13389 from the Fayum, lacking tooth crowns other than on P$_3$, described by Simons (1961), but in spite of this resemblance P$_3$ of A.M.N.H. 13389 is three rooted, a feature of great rarity among Primates, while that of *Oligopithecus* is more normal in being two rooted. Moreover, A.M.N.H. 13389 is, in comparable measurements, over twice larger than the type of *Oligopithecus.* Presumably the former specimen belongs to yet another Egyptian Oligocene primate species, diagnosis of which will have to await recovery of more satisfactory material; see Simons (1961: 3).

The relationship of *Oligopithecus* to *Moeripithecus markgrafi*, also from the Egyptian early Oligocene, is more obscure, since comparison of M_{1-2} crown patterns in the two forms fails to reveal any significant similarity. The overall morphology of the tooth series preserved in *Oligopithecus* appears to be more like that of certain Eocene prosimians than are these patterns in other Fayum Primates, except that the P_{1-2} are lost, the horizontal ramus is deep compared to tooth crown height, and P_3 is anteroposteriorly elongate—all similarities to Old World Anthropoidea. Among Eocene Primates perhaps the greatest resemblances of *Oligopithecus* are to Omomyidae, Anaptomorphidae and Necrolemurinae, which fact agrees well with the supposition that Anthropoidea are more closely allied to the so-called tarsioids of Eocene times than they are to other known Eocene, and earlier, families of the order. The lingual position of the M_{1-2} hypoconulid in *Oligopithecus* creates a partial posterior loph parallel to the anterior loph, between metaconid and protoconid, which might represent an early stage in the transition to the bilophodont lower molar pattern of Cercopithecoidea. This possibility will require further confirmation before definite assignment of this primate to the latter superfamily would be advisable. Placement of *Oligopithecus* among the Hominoidea is also conceivable but M_{1-2} crown patterns are so primitive that such an association is equally dubious. Clearly, however, the creature is not a ceboid or a prosimian.

OLIGOPITHECUS SAVAGEI[2]

Figures 1 and 4.

Type: Left mandibular ramus, with $\overline{C}$-M_2 inclusive, Y.C.P.E. 207.[3]

Horizon and locality: Yale Expedition quarry E, Fossil Wood Zone, Fluviomarine Formation, early Oligocene age, Fayum Province, Egypt, about 2.3 miles northeast of American Museum Quarry A (1907) and about

[2] Named for Dr. D. E. Savage of Berkeley University who discovered the type and only specimen.

[3] By agreement with the Egyptian authorities concerned, types collected on the Yale 1961-62 expedition will eventually be deposited in the paleontological collections of the Cairo Museum of Geology. Pending such assignment they are here identified by their field numbers.

eight miles west-northwest of Quasr el Sagha Temple, thirty feet below the top of the Fossil Wood Zone, see Beadnell (1905).

Specific characters: Not distinguished from generic.

Discussion: The species, *O. savagei*, is at present known only from the type individual so that little can be said of variability in this primate. Although M$_3$ is missing in Y.C.P.E. 207 the fact that it had fully erupted is indicated by the preservation of the anterior root of this tooth in the type. A large wear facet on the anterior crest descending from P$_3$ protoconid indicates that this species must have possessed a sizeable upper canine which sheared against this facet.

Measurements in millimeters of *Oligopithecus savagei* are listed below in comparison with similar measurements on contemporary Fayum Primates taken from Kälin (1961).

Mandibular dimensions *(O. savagei).*

Anteroposterior

Length of $\overline{C}$ through M$_2$	19.4
Depth of mandible beneath M$_2$	9.5
Depth of mandible beneath P$_3$	10.2

MEASUREMENTS OF TEETH

	Oligopithecus savagei left side	*Parapithecus fraasi* left side	*Propliopithecus haeckeli* left side	*Moeripithecus markgrafi* right side
Canine				
length	3.7	3.2 ($\overline{C}$ or P$_2$)	4.0 (right)	
width	3.3	2.5 ($\overline{C}$ or P$_2$)	4.3 (right)	
P$_3$				
length	4.2	3.3	3.5	
width	3.1	2.5	3.8	
P$_4$				
length	3.3	3.3	3.5	
width	3.0	2.5	4.0	
M$_1$				
length	4.2	4.2	4.8	5.0
width	3.4	3.2	4.5	4.8
M$_2$				
length	4.2	4.3	4.8	5.4
width	3.5	3.4	4.5	5.4

Genus *APIDIUM* Osborn, 1908

Type: *Apidium phiomense* Osborn, 1908.

Discussion: Although Osborn (1908) was reluctant to state the ordinal position of this species, it subsequenlty came to be regarded as a primate, and Gregory (1922) held that it might be related to the basic cercopithecoid stock or to *Oreopithecus;* see Simons (1959: 14). More recently a few authors have again questioned the primate status of *A. phiomense* but its resemblance to *Oreopithecus* seems more than convergent, as was discussed by the writer (1960). Moreover, the discovery of several isolated upper teeth of a species of this genus, (described below) in association in one quarry with several lower jaws of this form, shows us that similarities to *Oreopithecus* in the upper dentition are about equal to those seen in the lower teeth. Nevertheless, *Apidium* species are rather unlike other known Oligocene Anthropoidea in that the cheek-teeth are more polycuspidate, the mandibular ramus is shallow, and the canine may have been small, or alternatively there may have been three premolars—inadequate preservation of the new materials rendering this point equivocal. Clearly the stock of *Apidium* had differentiated from that of other Fayum Primates at a considerable remove in time from their common ocurrence in the Early Oligocene of Egypt, but it is in many ways closest to *Parapithecus* insofar as the two forms can be compared. The question, therefore, as to the relation of species of these two genera to the earliest undoubted Old World Anthropoidea is interrelated. Provisionally the study of *Apidium* suggests that it, together with *Parapithecus,* may eventually be ranked with some certainty among the Anthropoidea.

APIDIUM MOUSTAFAI,[4] new species
Figures 2, 3.

Type: Left mandibular ramus with P_3-M_1, Y.C.P.E. No. 260.

Hypodigm: Type and Y.P.M. numbers 18007, left mandibular rumus with damaged P_3-M_3; 18008, unassociated right P^4-M^3; 18009 right mandibular ramus with P_3-M_3; 18018 left mandibular ramus with $\overline{C}$?-M_3; 18042

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[4] Named in honor of Dr. Y. Shawki Moustafa, whose earnest assistance and advice were most helpful to our Egyptian expedition.

left mandibular fragment with P_4-M_1; 18081, unassociated left P^4?, left M^2, left M_2, left M_3, all from Quarry G.

Horizon and locality: Yale Expedition Quarry G, below upper fossiliferous zone, Fluviomarine Formation, early Oligocene age, Fayum Province, Egypt. One mile due north of American Museum Quarry A and approximately 100 feet above top of lower Fossil Wood Zone.

Specific diagnosis: About one-eighth smaller than *A. phiomense,* with slighter development of lateral basal cingula and fewer accessory cuspules on P_4 heel and on M_{1-3}, and as a whole, comparatively smaller and more primitive than in *A. phiomense,* with posterointernal angle of M_1 produced more lingually.

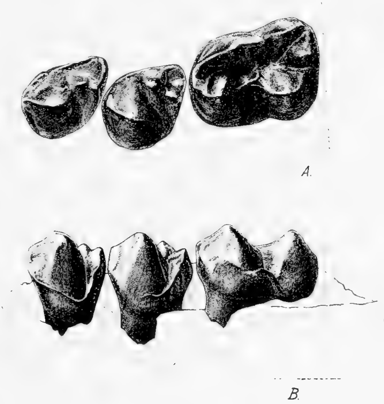

Figure 2. A. Crown view and B. External view, *Apidium moustafai* Type, Y.C.P.E. 260. x 5 approx.

Discussion: This species is both smaller and earlier occurring than the type of *A. phiomense.* That a significant lapse of time exists between the populations from which the two species are derived seems probable in view of studies of other faunal elements from the upper part of the Egyptian Fluviomarine Formation now in progress. Although the exact locality of the type of *A. phiomense* is not known, it was reported by Osborn (1908) as having been discovered upon the upper fossiliferous level, which begins about 100 feet stratigraphically above the horizon of Quarry G. If the practice of some past students of fossil Primates were followed here, a case for generic separation of these two species could probably be made, but this type of splitting should not be attempted until these forms are much better known.

MEASUREMENTS IN MILLIMETERS OF *Apidium moustafai*

	Y.P.M. 18018	Y.P.M. 18009	TYPE: Y.C.P.E. 260
$\overline{C}$, D $\overline{C}$., or P_2			
length	2.5	. .	. . . .
width	2.0	. . . .	. . . .
P_3			
length	2.7	2.7	2.8
width	2.0	1.9	2.0
P_4			
length	2.7	2.7	2.8
width	2.3	2.2	2.3
M_1			
length	3.5	3.6	3.7
width	2.8	2.7	3.0
M_2			
length	3.6	3.6	. . . .
width	3.2	3.1	. . . .
M_3			
length	3.6	4.0	. . . .
width	3.0	2.9	. . . .
Depth of mandible beneath M_1	6.0	7.1	6.8
Anteroposterior length P -M_3	15.3	16.8	. . . .
A-P length P_3-M_1	8.6	9.0	8.8

CONCLUSIONS

Recent collections of Primates from the Fayum early Oligocene deposits of Africa indicate the existence of at least two new forms of Primates. Study of the first of these, *Oligopithecus savagei,* suggests that it is assignable to the Anthropoidea and that it may represent an early stage in the differentiation of Cercopithecoidea. Near agreement in expected size, and approximation in horizon and locality suggests that a catarrhine frontal bone described by Simons (1959) may provisionally be referred to this species. Placement of this frontal with *Apidium* or *Parapithecus,* which are also of suitable size, seems less appropriate in view of non-anthropoidean features such as are to be seen in their anterior dentitions. Known *Propliopithecus* and *Moeripithecus* are probably too large to have had a frontal this size, but of course this skull fragment could well belong to a species otherwise unkown. A second species, *Apidium moustafai,* here described, appears to represent an earlier and ancestral population to *Apidium phiomense* which was recovered from the upper part of the Fluviomarine Formation. Newly discovered upper teeth of *Apidium* strengthen the view that species of this genus, together with *Oreopithecus bambolii,* represent a fourth major group of Old World Higher Primates distinct from cercopithecoids, pongids and hominids.

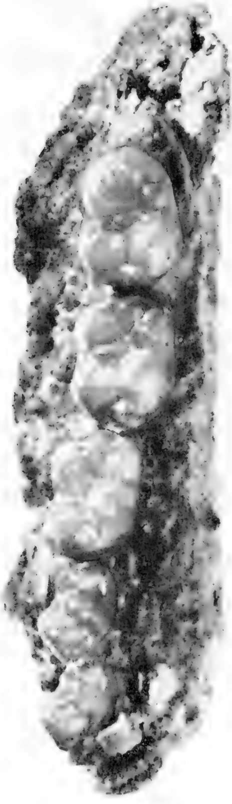

Figure 3. Right mandibular ramus of *Apidium moustafai*, Y.P.M. 18009. x 6 approx.

Figure 4. Crown view of dentition, *Oligopithecus savagei*. Type, Y.C.P.E. 207. x 6 approx.

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Postilla

YALE PEABODY MUSEUM

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Number 65 August 24, 1962 New Haven, Conn.

STUDIES ON SPECIATION IN MALDANID POLYCHAETES OF THE NORTH AMERICAN ATLANTIC COAST

I. A taxonomic revision of three species of the subfamily Euclymeninae.

CHARLOTTE PRESTON MANGUM*

The three species of the polychaete family Maldanidae to be treated below are among the most common marine annelids of the Atlantic coast. Despite their abundance and familiarity, persistent confusion has led to an undue multiplication of taxa and the shuffling of species between them. Since Leidy (1885) described *Clymene torquatus*, the first American member of the subfamily Euclymeninae, these three species have been referred to at least nine genera and probably twice as many species.

It will be noted that their morphology is indeed similar. However, it is possible to distinguish them with certainty even in the field. The present effort is intended to provide a means of proper identification as well as a taxonomic grouping indicative of evolutionary status.

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METHODS AND LOCALITIES

The specimens considered were in all cases collected by the author. These collections extend over the entire Atlantic range of the various species. A preliminary effort was made to compare them with holotypes and paratypes in the collections of the Peabody Museum of Natural History, Yale University; the American Museum of Natural History, New York; and the U. S. National Museum, Washington, D. C. It soon became apparent, however, that the conditions of the type specimens would not permit analysis with the precision desired. As an alternative, the author has reinvestigated many of the type localities.

Collections were made at:

Passamaquoddy Bay, New Brunswick (45°N), intertidal to about 1.5 meters below Mean Low Water.

Cape Cod Bay, Mass. (41°30′N), intertidal.

Vineyard Sound, Mass. (41°30′N), intertidal to about 1 meter below M.L.W. Type locality for *Clymenella torquata* (Verrill, 1873) and *Clymene producta* (Lewis, 1897).

Long Island Sound, Conn. (41°15′N), 0 to about 1.5 meters below M.L.W.

Isle of Wight Bay, Maryland (38°20′N), 1.5 meters below M.L.W.

Newport River, North Carolina (34°40′N), intertidal to 3 meters below M.L.W.

Summer River, Florida (29°50′N), intertidal to about 1 meter below M.L.W.

Bahia Parguera, Puerto Rico (18°N), 0.5 to about 1.5 meters below M.L.W.

Specimens were killed in 5% formalin in seawater, and later transferred to 70% ethyl alcohol. Setae were dissected out and mounted in Permount.

Specimens listed under the new combinations have been deposited in the Yale Peabody Museum of Natural History.

Genus *CLYMENELLA* Verrill 1873

Clymenella torquata (Leidy, 1855)

Taxonomic summary:

Clymene torquatus Leidy, 1855. New Jersey.

Clymenella torquata (Leidy), Verrill, 1873.

Paraxiothea latens Webster, 1879.

The genus *Clymenella* was erected by Verrill (1873) for *Clymene torquatus* Leidy, thus removing this species from the European genus *Clymene* Savigny.

Description: Fully formed adult with 22 segments: single prostomial achaetous segment, 18 setigerous and 3 preanal achaetous segments. Cephalic plate present dorsally on prostomium, slanting away from more ventral proboscis and forming acute angle in lateral view of approximately 65° (Fig. 1A). Slightly elevated border of cephalic plate with four indentations: two dorsal and two ventrolateral. Central depression of plate bisected by median keel. Keel bounded on either side by deep furrow (nuchal organ), and extending anteriorly beyond border as small papilla. No dark pigment spots between prostomium and papilla.

First three setigerous segments with notopodial fascicles of long slender setae and 6-7 neuropodial rostrate uncini (Fig. 2A). Fourth setigerous segment extends for short distance over third as distinctly flanged collar. Four pairs of nephridia lying in coelom of setigerous segments VI through X (Paterson and Krewson, 1960) often visible as whitish ventrolateral masses. Mid-region translucent. Setigerous segments IX through XVIII greatly elongate, with increasing tendency for formation of highly vascularized ridge at posterior end of each segment. Number of neuropodial rostrate uncini increasing to about 30-40. Three preanal achaetous segments reduced in length, giving appearance of longitudinal compression.

Conical papilla perforated by anal opening and surrounded by caudal funnel with cirrated posterior margin. Relative lengths of cirri size-dependent; smaller animals or recently regenerated tails with irregularly long and short cirri; larger animals or older tails with equally long cirri. No single cirrus outstanding in relative length. Number of cirri variable, 10-30.

Color highly variable. Basic body color slightly iridescent yellow-orange, interrupted longitudinally by bright red dorsal and ventral blood vessels, and transversely in posterior segments by capillary beds concentrated in each segmental ridge.

Basic body color tinged by dull brown in certain localities, or obscured by accumulation of green pigment in others (Mangum, 1962). Overall appearance of entire population may be green or orange, but microgeographic population consistent with regard to color phase.

Length and length-frequency variable. Size range of adults over entire geographic population approximately 1-16 cm, but range of

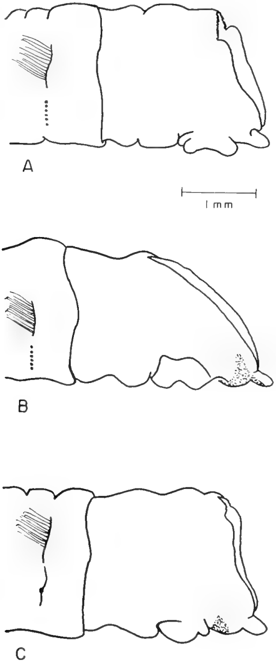

Figure 1. A. Prostomium of *Clymenella torquata.*
B. Prostomium of *Clymenella mucosa.*
C. Prostomium of *Clymenella zonalis.*

local population much smaller. Mean length of Newport River, N.C., summer population 4.2 cm (±0.9 S.D.); Nantucket Harbor, Mass., summer population 11.4 cm (±2.3 S.D.).

Straight, vertical tubes of sand and mucus, approximately 20 cm in length. Material cohesive; tubes removable intact from sediment No gelatinous egg masses.

Geographic range on North American Atlantic coast from New Brunswick to northern Florida; recent immigrant to southwestern England (Newell, 1949). Sand or mud, intertidal to about 110 m.

A distinct subspecies from the Gulf of Mexico has been described by Hartman (1951) as *C. torquata calida.* Its deviation from the Atlantic stem species may be somewhat exaggerated, for she believed *C. torquata* to possess 1) a cephalic plate with an entire. uncrenulated border, and 2) alternate long and short caudal cirri. However, the number (8-9) of crenulations or indentations that she attributes to Gulf populations is twice that (4) consistently found in Atlantic populations. If constant, this morphological difference may indicate genetic divergence, and therefore a valid subspecific distinction.

Material deposited at the Yale Peabody Museum: YPM No. 1482. W. Pivers Island, Newport River, N.C.

Clymenella mucosa (Andrews, 1891)

Taxonomic summary:

Axiothea mucosa Andrews, 1891. North Carolina.

Clymenella (Axiothella) mucosa (Andrews), Verrill, 1900

Axiothella mucosa (Andrews), Arwidsson, 1907.

The distinction between the original material and *C. torquata* (Leidy) was made on the absence of a well-developed collar on the fourth setigerous segment of the former (Andrews, 1891). The species was placed in the genus *Axiothea* Malmgren, which was later found to have been in prior use for a genus of Coleoptera (Verrill, 1900). On re-examination of the type species of Malmgren's genus, *A. catenata*, Verrill (1900) found that a fleshy fold was present on the third and fourth setigerous segments, but that it was much less developed than *C. torquata.* He concluded (1900:657): "The collar is doubtless much narrower in life than the latter (*C. torquata*), but it is of the same nature."

He thus extended his genus *Clymenella* to include *Axiothea* Malmgren which he renamed *Axiothella* and regarded as a subgenus. The occasional presence of a collar on the third and fifth segments is also diagnostic. It was noted here that the collar is not peculiar to *Clymenella* but is scattered throughout the family.

The generic separation of *Axiothella* and *Clymenella* Verrill was made by Arwidsson (1907), who simply reversed Verrill's decision that the two kinds of collars were worthy of only subgeneric distinction. Although his classification has persisted since that time, the extensive morphological similarities of the two genera have caught the attention of a number of workers (Hartman, 1945; Bookhout and Horn, 1949; Moment, 1951). At least one (Moment, 1951) has questioned the validity of separating the two as genera.

The present author now proposes a return to Verrill's (1900) original classification, on the premise that the differences that do exist do not warrant separation of *C. torquata* and *C. mucosa* on the generic level.

Description: Mature adult with 22 segments; relative lengths of segments and distribution of setae identical with *C. torquata*.

Flanged collar of *C. torquata* on fourth setigerous segment represented here by fleshy rim, only slightly more developed than comparable ridges on contiguous segments.

Cephalic plate slanting more abruptly than that of *C. torquata;* angle of prostomium in lateral view approximately 45° (Fig. 1B). Border of cephalic plate with only two indentations, dorsal and ventral; other features of plate identical with *C. torquata*. Ventral area between plate and proboscis bulb speckled with dark pigment spots.

Gonads visible through body wall of setigerous segments IX through XIV as opaque whitish masses; present during summer months. Nephridia obscured.

Caudal funnel cirrated, the longer processes alternating irregularly with the shorter. Median ventral cirrus always longer than others (up to 1.5 mm in very large specimens).

Color variable. Basic body color yellow to white. Red pigment diffusely localized in setigerous segments IV to IX, giving pink to pale red appearance. Red coloration obscured in certain localities by accumulation of green pigment in these segments and in setigerous segments X to XIV as well (Mangum, 1962). Walls of major blood vessels and parapodial capillaries also green in these populations, resulting in transverse green crescents along posterior surfaces of neuropodia in setigerous segments X to XVIII.

Length variable. Range approximately 1.5 to 7.5 cm. Newport River, N. C., population 5.4 cm (±1.5 S. D.); Bahia Parguera, P. R., population 2.7 cm (±0.7 S. D.).

Tubes sandy, vertical, not sufficiently cohesive to permit removal intact from sediment. Tubes of females Y-shaped, with round gelatinous egg masses protruding from one arm during summer months.

Geographic range from North Carolina to West Indies and Gulf of Mexico. Sand, intertidal and subtidal.

Material deposited at the Yale Peabody Museum: YPM No. 1483. W. Pivers Island, Newport River, N.C.

Clymenella zonalis (Verrill, 1874) new comb.

Taxonomic summary:

Praxilla zonalis Verrill, 1874. New England.

Praxilla elongata Webster, 1879. New Jersey.

Clymene producta Lewis, 1897. Massachusetts.

Euclymene (Euclymene) zonalis (Verrill), Verrill, 1900.

Euclymene (Macroclymene) producta (Lewis), Verrill 1900. Mass.

Possibly ?*Macroclymene elongata* (Webster), Hartman, 1951. Louisiana.

This species is perhaps the most problematic of the three. In addition to the synonymies noted above, it has been identified by innumerable names in various ecological surveys of the Atlantic coast. It is known as *Euclymene collaris* in the checklist of the Marine Biological Laboratory, Woods Hole, Mass. It was not included by Hartman (1945) in her survey of the area surrounding Beaufort, N.C., where it is common on local sandflats. Assignment to *E. collaris* Claparède is incorrect, since it is a Mediterranean species with differing morphology (Claparède, 1870).

In his original description, Verrill (1874) named the species *Praxilla zonalis.* The genus *Praxilla* was placed in synonymy with *Clymene* Savigny, subsequently found to have been preoccupied (Verrill, 1900). Verrill (1900) offered *Euclymene* as a new name, and extended the generic description to include *Praxilla.* Although the description of the expanded genus appears in the same work as that of *Clymenella,* Verrill does not emphasize the basis of generic distinction. Comparison of the descriptive texts reveals that the character of the neuropodial setae of the first three setigerous segments is the sole diagnostic feature (1900:654 and 658):

> *Euclymene:* ". . . especially by having on about three anterior setigerous segments, one or two stout, bent spines, replacing the rostrate uncini of the ventral parapodia (of *Clymenella*)."
>
> *Clymenella:* ". . . rows of ventral rostrate uncinate anterior setae having a series of apical hooks and a beard, on all the anterior setigerous segment."

The present author is aware that categorical distinctions in polychaete taxonomy are frequently made on the basis of setal structure. However, it is felt that the differences in this case are so slight that they do not override the importance of other morphological similarities. The same difference, *i.e.*, rostrate uncini vs. a single bent spine, is used to separate groups of species within the genus *Clymenella* (see discussion by Munro, 1937). Hartman (1961) has recently recognized *?Clymenella cincta* St. Joseph, 1899, as a valid species, although it bears the anterior spines characteristic of *Euclymene* Verrill.

It may very well have been his pre-occupation with segment numbers that led Verrill to seek generic differences, although this is only implicit in the text. He proceeds to discuss "a very aberrant species from near Vineyard Sound, Mass.," described by Lewis (1897) as *Clymene producta.* After examination of the type he concludes that it differs from *E. zonalis* only in the segment number. But the increase from 25 segments in his *E. zonalis* type to ca. 70 segments in Lewis' type was sufficient, in Verrill's judgment, to erect the sub-genus *Macroclymene* with *E. (M.) producta* (Lewis) as the type.

Hartman implied the elevation of *Macroclymene* Verrill to generic standing in her tentative identification of a Gulf of Mexico fragment (Hartman, 1951) as *?Macroclymene elongata* (Webster), which had been previously synonymized by Verrill (1900) with his *E. zonalis. Macroclymene* Verrill was subsequently listed as a separate genus in her authoritative *Catalogue of the Polychaetous Annelids of the World* (Hartman, 1959).

From the present author's collections it is apparent that the segment number of an individual and its range in a microgeographic population are simply size-dependent. The animals continue to proliferate additional segments so long as growth occurs, unlike the species whose adult growth consists only of the enlargement of a definite number of segments. The entire range described in the literature may be found within a single microgeographic population, *e.g.*, Vineyard Sound, Mass. It hardly seems likely that intrapopulational reproductive isolation exists concomitant with continuous differences in segment number. Therefore all of the Atlantic types should be regarded as members of a single species.

The author was unable to find specimens on the Atlantic coast south of North Carolina, and has not collected on the Gulf coast. Judgment must again be withheld on the specimen identified by Hartman (1951) as *?M. elongata* (Webster).

Description: Segment number variable. Range: 18 to ca. 70. Prostomial segment achaetous, followed by 15-ca. 65 setigerous and 3-4 preanal achaetous segments. Cephalic plate slanting dorsally forming prostomial angle of approximately 65° (Fig. 1C). Border of cephalic plate with five indentations: two dorsal, two ventrolateral and one ventral. Plate otherwise identical with *C. torquata.* Dark pigment spots present ventrally, but fewer than *C. mucosa.*

First three setigerous segments with dorsolateral fascicles of long slender setae, and 1-3 ventrolateral bent spines (Fig. 2B). 10-20 rostrate uncini beginning on setigerous segment IV and continuing posteriorly.

Condition of collar identical with *C. mucosa;* fleshy rim on setigerous segments III through V. Beginning with X and continuing up to preanal achaetous segments, posterior segments greatly elongated and swollen at terminals. Paired nephridia visible through body walls of setigerous segments VII through XIV as elongate ventrolateral whitish masses. Preanal achaetous segments compressed longitudinally.

Anal opening at center of conical papilla surrounded by cirrated caudal funnel. Number and relative length of cirri variable, resembling *C. mucosa.* Median ventral cirrus always longer than rest (up to 0.5 mm total length), but not so long as that of *C. mucosa.*

Color constant. No green populations found as yet. Basic body color slightly iridescent yellow-orange, resembling *C. torquata.* Distinct red bands surround portions of setigerous segments IV through IX, and sometimes X in larger individuals. Transverse crescents of red (lateral blood vessels) on posterior surfaces of

TABLE 1. COMPARISON OF CHARACTERS

Character	*Clymenella torquata*	*Clymenella mucosa*	*Clymenella zonalis*
Segment number	22 constant	22 constant	18-70 variable
Angle of prostomium	65° constant	45° constant	65° constant
No. indentations in cephalic plate border	4, 8-9 variable	2 constant	5 constant
Prostomial pigment spots	absent	present	present
Flanged collar on fourth setigerous segment	present	absent	absent
Neuropodial uncini on setigerous segments I-III	rostrate constant	rostrate constant	bent spine constant
Relative lengths of caudal cirri	all variable	median ventral longer constant	median ventral longer constant
Basic body color	yellow-orange constant	yellow-white variable	yellow-orange constant
Red bands in mid-region	absent	pale, diffuse constant	bright, distinct constant
Green dichromatism	present but variable	present but variable	absent
Gelatinous egg mass	absent	present	absent

Figure 2. A. Rostrate uncini from anterior setigerous segment of *Clymenella torquata.*

B. Neuropodial spines from anterior setigerous segment of *Clymenella zonalis.*

neuropodia from setigerous segment X to last setigerous segment.

Length variable; range 1.5 to ca. 20 cm.

Tubes sandy, sufficiently cohesive to permit removal from sediment intact. Straight, vertical for approximately 15-20 cm, then frequently curved, becoming J-shaped. No gelatinous egg masses.

Geographic range from Maine to North Carolina. Intertidal to 50 m; in sand.

Material deposited at the Yale Peabody Museum: YPM No. 1484. W. Pivers Island, Newport River, N.C.

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SNAILS ON A PERSIAN HILLSIDE

Ecology—Prehistory—Gastronomy

CHARLES A. REED

The archeologist who is prehistorian may expect snail shells in his excavations. Sometimes, even though the site may be far from the nearest seas, such shells are marine and often were used as decorations, indicating the continuity of human vanity through the ages. Generally, the archeologist has had little interest in such shells as snails, or even in the generic and specific identifications furnished him by a malacologist; instead, the archeologist is interested in any cultural uses of the shells, and is intrigued by problems of their geographic origin and the possibility of tracing prehistoric trade routes.

However, to the ecologically-oriented archeologists and the various natural scientists with them working the past fifteen years in Iraq and Iran, some of the local terrestrial snails have become of prime interest, particularly as potential indicators of past environmental conditions (including climate), and as a source of food for past populations. Thus the continued presence in archeological sites of the same species of snails in the same localities in northern Iraq, for periods sometimes measured in the tens of thousands of years, has been used, with other evidence, to make a tentative reconstruction of the environments of that area over those periods (Reed and Braidwood, 1960).

This environmental reconstruction, based primarily on zoological data, is partly in conflict for some time-periods with the glaciological evidence of Wright (1961) and the palynological evidence of Solecki and Leroi-Gourhan (1961). Wright's studies indicate a colder climate for the period of the Würm maximum of the late Pleistocene than postulated by Reed and Braidwood for those parts of this period for which they had zoological remains, mostly of mammals and snails. Conclusions derived from study of the pollen-grains recovered from Shanidar Cave in northern Iraq do not contradict Wright's glaciological evidence, but do indicate more fluctuating climatic phases during the periods of the Baradostian and Mousterian cultures than postulated by Reed and Braidwood.

Obviously if zoological remains, such as snail shells, are to be useful in assessing past environments, the ecological conditions of life –and particularly the environmental limitations within which each species can live—must be known. At present, such ecological data are not known precisely for any animal population of southwestern Asia; while in general the botanical assessment of past environments is probably capable of more exactitude than is one based on zoological evidence, the latter should not be ignored, and this present paper is a preliminary effort toward an understanding of the ecology of some of the snails excavated in various of the archeological sites in Iraq and Iran.

To be useful as a climatic indicator, an animal population should have narrow and definite environmental limitations, and these should be known. For instance, a snail which ranges from the Dead Sea to the Iranian Plateau, as does *Helicella langloisiana* Bourguignat, is obviously useless as a climatic indicator (Biggs, 1962).[1]

However, as our knowledge of the ecologic tolerances and limitations of each animal and plant species increases, we can

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[1] The same criticism might be brought against the use of *Helix salomonica* as an environmental indicator, since it had been reported (Biggs, 1960) from Jericho in the lower Jordan valley. However, it is now believed that this identification was an error (Biggs, personal communication).

use the data derived from combinations of species, each with varied requirements and with different present geographical ranges, to clarify our concepts of the changing environments of the past.

In all such attempts at environmental reconstruction we begin with the assumption that a biologic population of a past period, as represented by identified remains, had the same ecological requirements as do members of a species with the same morphology as studied today. In general, these assumptions of

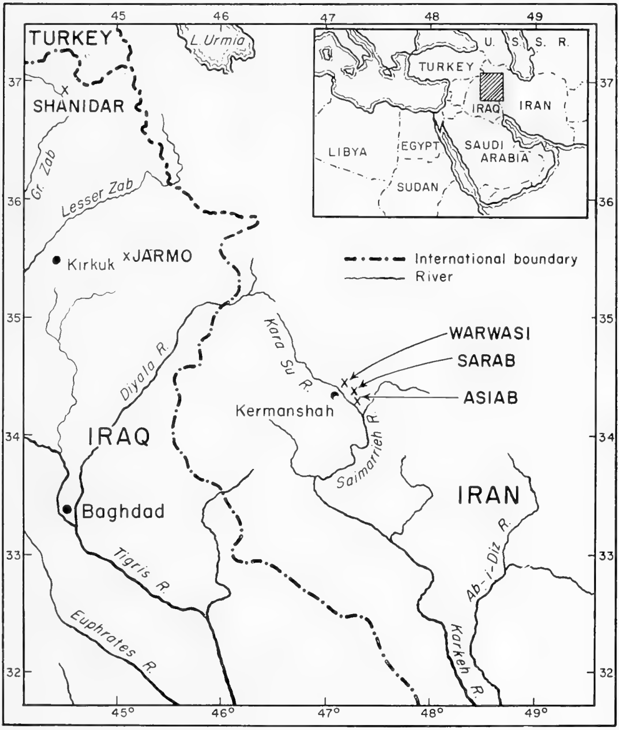

Fig. 1. Map of the area discussed, showing the archeological sites mentioned.

evolutionary stability and ecological uniformitarionism upon which we build our paleo-ecological reconstructions are probably more valid than is the loose framework of our present knowledge, but we are warned by Johnson (1960), even if in a different context, that these assumptions may be less valid for the more precise details we hope to learn in the future.

In addition to the climatic problems outlined above, the steady increase in numbers of one kind of snail, *Helix* (*Naegelea*) *salomonica* Naegele through the late Pleistocene and into the early Recent (post-Pleistocene) in all archeological sites of northern Iraq, is considered to be evidence for the increased use of these animals as food by a steadily-growing population (Braidwood and Reed, 1957; Braidwood and Howe, 1960). The same general pattern is evident in western Iran, and other species of *Helix* during this general period were similarly being used in northern Africa.

Thus by the time the fourth[2] southwestern Asiatic prehistoric expedition of the Oriental Institute of the University of Chicago was ready to go into the field in 1959, a preliminary field study of the snails important to the archeologists had become necessary.

Previous observations in northern Iraq and the problems posed by them were as follows (see Braidwood and Howe, 1960, as a general reference for geography, environment and chronology):

1. *Helix salomonica* is not common in archeological sites prior to the late cave-living period of the uppermost Pleistocene (i.e., the Zarzian, ca. 15,000-12,000 years ago), then increases in concentration to ca. 8,500 years ago, and was still numerous at 7,000 years ago, but after that it disappeared almost entirely from the archeological record of the area. It cannot be found at present in some of the regions where it was previously so plentiful, as for instance in the immediate area of Jarmo in northeastern Iraq. The appearance and increase of these snails

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[2] The previous expeditions had been in 1947-1948, 1950-1951, and 1954-1955, all in northeastern Iraq. The fourth, 1959-1960, went into western Iran. All four expeditions have been under the direction of Dr. Robert J. Braidwood of the Oriental Institute, University of Chicago. The present author was a member of the two last expeditions.

in archeological sites are undoubtedly to be correlated solely with changing human food-habits, but is their disappearance from the archeological record due solely to changing human food preferences? Possibly local destruction of the environment (deforestation and brush-cutting, cultivation, over-grazing and soil erosion) have destroyed the micro-habitat necessary for the species so that its present distribution is discontinuous. The species may thus be listed as "abundant" over much of northern Iraq at present (Harris, 1961), and have a number of localities listed (Biggs, 1959) while yet being locally eradicated in an area (as at Jarmo) where once numerous. Harris writes in general for the terrestrial gastropods which he has listed as abundant, "As long as some perennial plants are present, the supplement of annuals is quite sufficient to provide food for the limited faunas common today. Where perennials are absent, and only a poor annual flora is present, snails do not occur, even though the rainfall is adequate." However, the situation is not so simple, as there may well be a sequence of local eradication with the deterioration of the environment; for instance, as mentioned, *H. salomonica* now seems to be absent entirely from the area around Jarmo, whereas *Levantina kurdistana* (L.Pfr.) still flourishes there.

2. Different species of *Levantina* have been recorded from different archeological sites in northern Iraq. *L. mahanica* Kobelt is found, in at least one long-occupied site, that of Shanidar Cave, for several tens of thousands of years, where the shells of this species occurred earlier (ca. 60,000 or more years ago) than did those of *H. salomonica* (somewhat more than 50,000 years ago) and in greater numbers than the latter in the older deposits (prior to 27,000 B.C.). However, shells of *H. salomonica* are more numerous in the later, post-Würm deposits (Solecki's layers B and A) which coincide with the period when this latter snail was being gathered for food in other areas of southwestern Asia. In general, the concentrations of the shells of *Levantina* never become high in archeological remains in Iraq and Iran, and one assumes that it was rarely, if ever, used for food. One wonders, too, why it was not so used, since it is a large and meaty snail. However, the number of

L. spiriplana (Olivier) found together at Jericho, in the lower Jordan valley, suggested to Biggs (1960) that this species of *Levantina* was being eaten at one time at that site.

Levantina has managed to survive, as at Jarmo, where *Helix salomonica* cannot now be found. Moreover, at the three sites (Shanidar Cave, Jarmo, and Warwasi), where recent collections have been made, the species of *Levantina* reported from the prehistoric levels are the same (*L. mahanica*, *L. kurdistana*, and *L. diulfensis* [Mousson], respectively) as are those found in each of the areas now.

3. At the strictly taxonomic level, are the different species of *Levantina* reported from northeastern Iraq (*mahanica*, *kurdistana*, *guttata* [Olivier]) valid species, or are they—and the forms since collected from western Iran (*guttata* and/or *diulfensis*)—merely geographical variants (i.e., subspecies) in a wide-ranging and continuous population (one species), the different parts of which exhibit considerable morphological differentiation?

It was with such questions in mind that the members of the Iranian Prehistoric Project went into the field in west-central Iran in 1959. We cannot claim to have solved any of these problems, but we have added to our observations, and we feel that a presentation is due of these, as well as of our present level of understanding.

Unfortunately, late 1959 and early 1960 was a poor time for "normal" environmental observations. The season was an exceptionally dry one over all of southwestern Asia. In the area of Kermanshah, west-central Iran, where our group was located, unusual cold and snow in November was followed by a long period of winter dryness, during the greater part of what is usually the rainy season. Then there was more snow in March and finally some rain in April.

Observations to be reported were thus made in the area of Kermanshah under the above-described circumstances. The Kermanshah valley is a flat-bottomed alluvial valley, at a general level of 4,000-4,400 ft. (ca. 1,230-1,330 m), surrounded by mountains, some of them high, steep and rugged. The average annual precipitation is variously reported as 13.1 in. (Robison and Dodd, 1955) to nearly 17 in. (Bakker, 1956; Ganji, 1960: the latter's figures are for 15 consecutive years.) This precipitation occurs entirely during the typical Mediterranean "rainy season" (October to May, with March the month of heaviest rain). The "average" is, however, not the "normal," as wide annual fluctuations occur, from 9 in. to 24 in. (22.5-60.0 cm), although such extremes may not occur oftener than once in 35 years (Bakker, 1956). Even two seasons recorded as having the same precipitation could differ widely in the ecological results of that snow and rain, depending upon the temperature at the time, the intensity of the rain (or depth of snow), and particularly upon the seasonal distribution.

The valley floor and much of the adjacent valley walls are not now forested, and the botanists who have studied there seem agreed that probably the areas now unforested have mostly not been forested as long as present climatic conditions have prevailed. Actually, the area seems to be one of an environmental transition, as measured by floral zones (Bobek, 1951; Pabot, 1961). The valley floor is now intensively cultivated, and the valley walls heavily grazed and subjected to continuous bush-cutting (I do not say brush-cutting because the vegetation is too sparse to be called brush.) To what extent the human activities, continuous for several thousand years, have changed the original environment we cannot assess nor can we at present definitely reconstruct the pre-agricultural environment.

All of the above environmental factors, not available to museum malacologists intent on taxonomic identifications, are pertinent to the understanding of our problems. Actually, we need to know additional types of ecological information not yet gathered, such as the distribution, both geographically and environmentally, of each species represented. Precise data of this type would inform us concerning the limits within which the total environment might vary and yet allow combinations of certain species of snails to persist at one spot, as at Warwasi. However, not only is such information not yet available, but the nomenclatural confusions concerning certain of these species are such that one finds difficulty in interpreting some of the identifications as published. It would be most desirable to have the collecting, identifications, and ecological studies accomplished by one person or a coordinated team. Additionally, we should know the fewest number of feeding periods per year which will support each population of snail, and also the kinds of variables (maximum and minimum daily temperatures and maximum and minimum daily precipitations) which control the emergence, feeding and breeding of each species. Eiseley (1937) has considered in some detail other factors of the ecology of terrestrial gastropods which have bearing on paleoenvironmental interpretations, and several other authors have also considered different aspects of this general problem.

Some observations and collecting of empty shells had been accomplished prior to the April rains, and by that time data from several excavations could be added (Braidwood, Howe, and Reed, 1961). Our observations were concentrated on *Helix* and *Levantina*, for these alone (so far as we can see at present for the area of our studies) are part of our more general prehistoric archeological problems. These preliminary observations were as follows:

1. Shells of neither *Helix* nor *Levantina* were found anywhere on the open valley floor, on open rounded well-grazed hills, in areas adjacent to streams, or in the typical oak-hawthorn-pistachio forest (Bobek, 1951) of some of the nearby hilly areas.

2. Adjacent to the archeologic site of Warwasi (fig. 2) in the Tang-i-knisht valley, there is a southwesterly-facing, rock-strewn slope covered with thornbushes and with a cliff above. On the slope the most common shell was that of *Helicella langloisiana*, occurring by the thousands. Some of these were sharply-keeled, some almost rounded on the edges of the whorls, with all gradations between these extremes. The second shell, in frequency, was the high-spired *Jaminia* (*Euchondrus*) *albula* (Mousson). Next most common was *Levantina diulfensis;* the *Levantina* shells were accumulated at the base of the cliff and some scattered down the slope. Fourth in frequency were shells

of *Helix salomonica*, found only on the slope. Rarest were shells of *Buliminus* (*Buliminus*) *egregius* Naegele and *Zebrina carducha* (Mertens), which were found only in cracks in the cliff and, presumably fallen from there, at the foot of the cliff.

3. Shells of *Helix salomonica*, but of no other snail, were found in open fields on the top of the low divide between the Kermanshah valley and the next valley to the south. The altitude was around 5,500 feet (ca. 1,700 m) and the shells were associated here only with a hardy ground-hugging perennial too soft to be called a shrub but yet too resistant to be removed by the primitive ploughs used in the area. This circumstance agrees with the observations in Iraq of Harris (1961) on the role of perennials in the survival of snails, but one wonders what factor in this particular locality led to the survival of *H. salomonica* and no other species.

4. Shells of *Helix salomonica* were found in great numbers in an archeological site (Tepe Sarab) located in the open Ker-

Fig. 2. The hillside and cliff at Warwasi, where living snails were collected in April of 1960. The Paleolithic archeological site of Warwasi is the dark overhang at the base of the cliff, almost directly above the car.

manshah valley (Braidwood, Howe, and Reed, 1961); Tepe Sarab is now dated at nearly 8,000 years ago and is thus probably somewhat more recent than is Jarmo. Large numbers of *H. salomonica* in a site of this period agree with our findings in northern Iraq. We are not suggesting that *H. salomonica* was the major food source at Tepe Sarab (nor at any other archeological site), as: a) in our experience, these snails can only be gathered during or following a rain, and; b) at Sarab, as at Jarmo, the people already had cultivated grains and domestic animals.

5. In a site (Tepe Asiab), probably some 2,000 years older than Tepe Sarab and less than a mile distant, but near a permanent stream (the Kara Su) in the valley's center, *H. salomonica* is extremely rare; the major molluscan protein source here seemingly was a clam, *Unio tigridis* Bgt. (So far as we know, these earlier people at Tepe Asiab did not have cultivated grains or domestic animals.) In northern Iraq at the same time (ca. 10,000 years ago) we think *H. salomonica* was being eaten in some quantities; perhaps the easy availability of the fresh-water clams, still present in the river adjacent to Tepe Asiab, made the gathering of snails unnecessary.[3]

6. In the rock shelter of Warwasi (Braidwood, Howe, and Reed, 1961), adjacent to the slope and cliff mentioned in paragraph 2 above, snail shells are found sparsely but continuously through most of the Zarzian and through all of the deeper Baradostian and Mousterian levels (these latter at least 40,000 years old and probably older). Shells of *Helix salomonica* become numerous in the uppermost Zarzian layers (about 12,000

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[3] It is obvious, thus, that local biotic and/or cultural patterns change the local archeological findings, making widespread archeological exploration necessary before a total picture emerges. In the excavations at Tepe Sarab, for instance, *Unio tigridis* is rare, although the clam-laden Kara Su is no more than a half-mile away. Within some 2000 years a major shift in food-habits had occurred and the people simply didn't gather clams anymore. Similarly today in the same region, we were told that the people will not eat clams or snails, even under conditions of extreme starvation. There is no truth to the assertion sometimes made by some prehistorians that primitive people ate anything and everything they could gather. There is now, and seemingly has always been, the important factor of the "cultural filter" in the collection of human food-stuffs, and consequently in the comparative archeologic record.

years ago), at which time these snails probably were being gathered for food. Throughout these tens of thousands of years of the later Pleistocene the species represented are the same as those still present on the hillside and, except for the *H. salomonica* of the more recent Zarzian levels, are considered to be no more than random strays into the cultural deposits. In levels below the upper Zarzian, *Levantina* is the most numerous, and occurs earlier than any of the others; at its earliest occurrence it was exactly the same *L. diulfensis* as found on the hillside today.

Subsequent collections of living snails, on April 9 and April 18, 1960, were made on the slope and cliffs immediately adjacent to the site of Warwasi in the Tang-i-knisht valley, which is a lateral side-valley opening southerly into the main Kermanshah valley close to the town of Kermanshah. The mouth of the secondary valley is bounded by high limestone cliffs, with steep slopes of soil and talus rock at their bottoms. It was on such a slope (fig. 2), southwesterly facing, that we did our collecting. Toward the base of the slope there was relatively little fallen rock, but higher and closer to the cliff the tumbled rock was thick. Thorn-bushes, rarely over 10 inches high and spaced some 10 or 15 feet apart, dotted the hillside, even growing among the fallen rocks but not up on the cliff. The ground between the thorn-bushes is quite bare since the slope is heavily overgrazed. This particular slope could be duplicated thousands of times around the Kermanshah valley; while we can say the slope is typical of the area today, we must also assume that the degenerate floral assemblage represents only a remnant of the "natural" vegetation (whatever that may have been) before intensive human use had removed most of the less hardy plants. Thus we cannot now imagine the appearance of these steep hillsides some 8,000 years ago.

On the two nights mentioned, there were continued gentle rains, followed by cool cloudy mornings (11°C-14°C ground temperature) with occasional drizzle. Living snails were asurface both mornings. Since the conditions and the collections were generally similar, the descriptions of the two events will be combined.

SPECIES ACCOUNTS

(Identifications were made by Rev. H. E. J. Biggs, from living specimens air-mailed to England; see Biggs, 1962.)

1. *Helix salomonica:* Most of these snails were found above ground, but under the thorn-bushes on the lower three-fourths of the slope. The snails were extended and moving, not up in a bush, but were generally on the accumulation of dead leaves and grass under a bush or at its edge. Only two individuals were seen out between bushes, on practically bare ground. A few were found under rocks (although none could be found under rocks between rainy periods). The population of *Helix* thinned out up the slope, and none were found in the upper fourth of the slope, although thorn-bushes occur on that upper fourth of the slope. On April 18 (although not on April 9) the snails were observed copulating; of 340 picked up on the slope on the latter date, 12 pairs were coupled, and many more of the living snails did so in the jars after being collected.

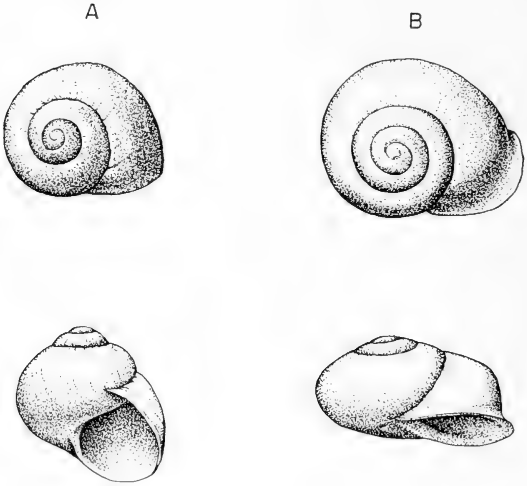

Fig. 3. A. *Helix salomonica.* B. *Levantina diulfensis.* Natural size.

2. *Levantina diulfensis:* These snails were first found about halfway up the slope, under identical habitat conditions (so far as could be observed) as the *Helix*. They became much more numerous on the upper parts of the talus slope and on the cliff itself and continued on to the top of the cliff, a near-vertical distance of at least 500 feet. On the upper parts of the talus slope, and on the cliff, they usually occur on bare ground or rock, or on occasional cliff-side patches of moss or grass but unprotected by thorn-bush.

3. *Jaminia* (*Euchondrus*) *albula* (Mousson): Although quite common as dead shells all over the hillside, living examples on these two mornings were rare. They were found coincident with the *Helix*, but also higher on the talus slope (not on the cliff), in similarly protected spots where detritus had accumulated.

4. *Buliminus* (*Buliminus*) *egregius* Naegele: As dead shells, these snails had been found on the surface of the highest part of the talus slope, but more frequently on the cliff-side itself, not only in protected crevices, but also out on small patches of grass or moss where such occur on the rough cliff. They seemingly did not continue to the top of the cliff, as the *Levantina* did. Whereas the living *Helix* and *Levantina* could easily be collected by the hundreds, *Buliminus* was rare, and only very few living *B. egregius* were found. (Three of these are those mentioned by Biggs (1962, p. 69) as being collected by Kent Flannery on April 17; the correct date is April 18.)

5. *Helicella langloisiana:* When collecting empty shells, this is by far the most frequent snail on the hillside, but the living examples were few on the two mornings specified. The *Helicella* were found on the slope under thorn-bushes and up the cliff on and under small vegetational patches.

6. *Zebrina carducha* (Mertens): The few individuals of this species were not distinguished by the collectors in the field from specimens of *Buliminus egregius;* the two have been confused even by experts, and the proper taxonomic position of the

species *carducha* has only recently been established on the basis of the internal anatomy (Forcart, 1962). As with *B. egregius*, individuals of *Zebrina carducha* were limited to the cliff-side niches. So far as can be determined in retrospect, the two species were collected together.

It is obvious that the ecologic notes made to date on these species of snails are not in themselves sufficient for valid paleoenvironmental conclusions. Still, a beginning has been made, and one continues to wonder how much different the climate could have been and yet have this same gastropod assemblage represented—as it is at Warwasi—for periods of tens of thousands of years of the late Pleistocene. During this time, a major period of glaciation occurred in the Zagros Mts. (Wright, 1961), with considerable depression of the mean annual temperature (possibly, but not necessarily as much as 12°C for the higher areas). The coincidental depression in altitude of the permanent snow-line has not been studied for the northeastern (interior) side of the Zagros Mts., as in the area of Kermanshah, where the annual precipitation is much less than on the outer (southwestern) aspect; in this latter area, the snowline some 20,000 years ago was to be found at approximately 2,100 m to 1,500 m (ca. 6,750-4,850 ft.), if Wright's conclusions are correct.

The permanent snowline on the inner side of the mountains would have been higher (even though the inner side is typically colder), due to a lower annual precipitation (a precipitation possibly no greater than that today [Bobek, 1954]). The mean annual temperature, however, would have been lower (possibly 5° C, possibly more) than that of today, so that evaporation would have been less than it is now with a resultant more humid environment.

Whatever the details of the climatological factors, which should be determined in major part by geological investigations, the snails at Warwasi remain the same. At Shanidar Cave, on the "outer" side of the mountains, there is a human occupation hiatus of some 17,500 years (between ca. 30,000 years ago and 12,500 years ago, as derived from C^{14} determinations), which period neatly coincides with that postulated for the Würm glacial maximum in North America and Europe. The assumption is that man, because of cold, depressed snowline, and coincidentally depressed treeline, could not live in the region of Shanidar Cave during this period (an assumption which is perhaps questionable for the latter part of the period, when conditions must have been warmer and both snowline and treeline higher).

However, no such occupational gap has been detected for Warwasi (although there are no C^{14} determinations as yet on any of the levels of this site). The inference is that man continued to live in the area of Warwasi, and thus of the Kermanshah valley as a whole, at an altitude of 1,300 m (4,200 ft.) and higher, during a long period when he supposedly was excluded from the region of Shanidar Cave at 700 m (2,200 ft.). One can only say from a study of the fauna (including snails) that there was no noticeable faunal change at Warwasi throughout this period of the last 40,000 years or so of the Pleistocene, and at Shanidar Cave there was no noticeable faunal difference between the last of the Baradostian cultural layers (at ca. 30,000 years ago, prior to the occupational hiatus) and those of Solecki's "Mesolithic" layer (following the cultural gap, and beginning ca. 12,500 years ago) (Reed and Braidwood, 1960).

Perhaps long-term experimental studies on the environmental limitations of the snails of the Tang-i-knisht hillsides, coupled with intensive field studies over varied environmental areas where these snails may be found today, would throw some light on these problems. There is, thus, much work for the future.

GASTRONOMIC EXPERIMENTS

Several kinds of *Helix*, are the edible snails of southern Europe, and the evidence of hundreds of thousands of similar shells in archeological sites of 12,000 to 8,000 years ago in northern Africa, as well as in Iraq and Iran, showed that snails of this genus were being eaten then as well. Obviously, these snails were good human food. Why, however, were the somewhat larger *Levantina*, occurring on the same slopes for at least some tens of thousands of years, and as numerous or almost as numerous as are the *Helix* on those slopes today—why were these snails *not* eaten? (At least they do not occur in any great numbers in any archeological site hitherto excavated by the Oriental Institute and so we must assume they were not often gathered in our area; an occasional *Levantina* shell at Jarmo or Tepe Sarab may, we think, be due to a mistake by some small child helping its mother in the gathering.)

It was with pleasurable anticipation, therefore, with respect to the *Helix salomonica* but with some apprehension with regard to the *Levantina diulfensis* that we took more than 300 of the former and more than 200 of the latter and prepared them for eating in the best French tradition (Rombauer, 1951, p. 257). All members of the expedition participated in the experiment (April 19, 1960); indeed, we had a festive occasion, with special "snail-picks" being provided, made from some of the microlithic bladelets from Tepe Sarab (fig. 4). (We are not claiming that these microliths were used originally as snail-picks; we only showed that they could be.) This gourmet experiment proved to our complete satisfaction that both the *Helix* and the *Levantina* are uniformly good.

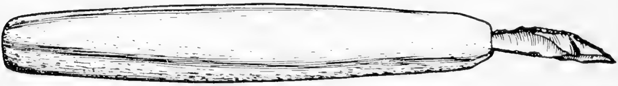

Fig. 4. Prehistoric microlith from Sarab, mounted to be used as a snail-pick for gastronomic experiments.

However, it was assumed that 8,000 years ago the techniques of French cooking were not available to the people of west-central Iran (although we have no way of knowing, of course, what variety of herbs they may have used to flavor their food), so a few hardier spirits tried a second experiment. Both *H. salomonica* and *L. diulfensis* were boiled 15 minutes, and then eaten hot, without salt or any other flavoring. Surprisingly, they are both acceptable food under these Spartan conditions; the *Helix* comes out of the shell quite easily, the *Levantina* perhaps a bit less so, and the latter retains maybe a bit more mucus (tasteless), but it seems hardly possible that such minor factors were those which restrained the prehistoric populations of the Zagros slopes from eating the *Levantina*. We found these snails quite tasty, and cannot imagine why they were not eaten in former times; the experiments, from the point of view of such "action archeology," were therefore a failure, although gastronomically a success.

The mode of preparation of the snails for eating under prehistoric conditions is a problem we have not solved. Since most of the shells are intact as we find them, the animals must have been killed prior to extraction, inasmuch as the living animals cannot be extracted from their shells without breaking these. Although the animals could be killed by drowning, we presume that the mode of killing was by cooking, but have no proof of this. We cooked them by boiling, for us a simple and effective method; the boiling does not affect the shells in any way that we could see, although Matteson (1959) noted that extended boiling of certain terrestrial snails from Illinois tends to cause the epidermis to flake away from the rest of the shell. However, extended boiling—if the snails *were* boiled—is not necessary for their preparation as food.

If the snails were cooked by boiling, as we first casually assumed, the question arises as to what were the containers in which they were boiled. Pottery is unknown prior to about 8,500 years ago, and for earlier times, we have no archeological evidence of containers in which boiling water could have been held. In answer to some who have suggested that this earliest pottery was too coarse to have been used to hold boiling water, Dr. Frederick Matson, who assisted in the excavations and has studied the ceramics from Jarmo and Sarab, has written, "The pottery from Sarab and Jarmo could easily withstand boiling water. The vessels are made of fired clay, and, aside from their porosity, would not react with the water. However, I doubt if they were used to boil snails or prepare stews because most of the larger flat-based vessels have very thin bases and there might be a problem with respect to the weight of the water unless the pots were nested in the fire with adequate support beneath them. Also, I do not recall seeing smudge and burning marks on the exteriors of the lower parts of the vessels that would suggest such firing. . . . A small amount of water in a pot full of snails would not require a lot of basal support for weight. If the pot were covered with a flat slab of some sort (skin, sherd, wood, or smaller jar that just fit the mouth) the snails could be steamed without requiring the presence of much water. . . . I would not want to rule out the boiling or steaming of the snails, because it would be physically possible, but I wonder if it wouldn't be easier to roast them in hot ashes" (Matson, personal communication).

However, as mentioned, pottery was unknown for much of the period for which we think eating of snails to have occurred, and actually for neither the pre-pottery or pottery-making cultures do we have any real knowledge of the mode of preparation of the snails.

In a similar situation in Alabama, where large numbers of snail shells were found in pre-pottery cultural associations, Morrison (1942, p. 381) thought that the snails were steamed in pits beneath a fire. Again, we have no archeologic evidence for or against such a hypothesis; we only know that, both for our sites in southwestern Asia and for those in Alabama (as well as those from prehistoric Jericho [Biggs, 1960]), the great majority of the shells show no signs of charring, and thus we assume the animals were not roasted on hot rocks.

SUPERSTITION

Our cook and two house-boys were town bred; they were familiar with snail-shells as shells, but were astounded to discover that each housed a living animal. They were of the opinion that no one of all the people they knew had any idea that these shells were anything other than what they were commonly regarded to be: snake pillows!

ACKNOWLEDGMENTS

My zoo-archeological work in southwestern Asia in 1954-1955 and 1960, upon which the present paper is based, was financed in large part by grants from the National Science Foundation to the Department of Anthropology and to the Oriental Institute of the University of Chicago. While in the field, all members of the expeditions assisted with the work in one way or another, and to each of these numerous people I extend my thanks. I am particularly grateful to Kent Flannery, Jim Knudstadt, and Gene Garthwaite for the gathering of

more than 500 live snails in the vicinity of Warwasi on the drizzling morning of April 18, 1960. I am most indebted to the Rev. H. E. J. Biggs, of Bromley, Kent, for his identifications, not only of the living snails sent him, but also of hundreds of dead shells collected from numerous recent surfaces and ancient dwelling-places. Additionally, he has spent many patient hours, initiating the present author (who is not a malacologist) into the mysteries of terrestrial snails from the region of the Zagros Mts. of Iraq and Iran.

SUMMARY

The finding of shells of certain terrestrial snails (particularly of *Helix salomonica* and several species of *Levantina*) in archeological context throughout the upper Quaternary of the slopes of the Zagros Mts. of southeastern Iraq and western Iran led to the speculations concerning: 1) the use of *Helix* as food by the prehistoric people involved, and: 2) the possible use of the presence of these shells and others as ecologic indicators of past environments.

Pleasurable gastronomic experiments indicated that both *Helix salomonica* and *Levantina diulfensis* were equally acceptable as food to modern archeologists and their colleagues; however, during the late Pleistocene and early Recent when snails were being gathered for food, all evidence indicates that, in the area studied by us, the *Helix* were eaten and the *Levantina* were rejected. We have no explanation for this choice by the prehistoric peoples involved.

The use (and possible mis-use) of terrestrial snails as paleoecologic indicators are discussed, and some preliminary ecologic notes are made on six species which have been found in late Quaternary archeological sites and which presumably may have importance to paleo-environmental studies. However, only a bare beginning has been made in this type of study, particularly for the area of the Zagros Mts., and much more intensive study is necessary before any valid paleo-environmental deductions can be made on the basis of the terrestrial snails.

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YALE PEABODY MUSEUM

OF NATURAL HISTORY

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NEW SUBSPECIES OF BIRDS FROM LUZON, PHILIPPINES

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During the course of my studies on Philippine birds, initiated in 1956 following an expedition to central Luzon, taxonomic revisions of several species have been undertaken, some of which have already been published. In the present paper, five additional subspecies from Luzon are described. Of these, two represent forms from Luzon as a whole, as distinct from those of other islands, while three reflect geographic variation within Luzon itself. The latter may be added to Gilliard's list (1950:473) of bird species geographically variable on Luzon, which I have already amended to some extent (Parkes, 1958: 2).

Gallicolumba luzonica griseolateralis, subsp. nov.

TYPE: Adult ♀ (Y.P.M. No. 48108) collected at Mt. Sicapo-o, Ilocos Norte Province, Luzon, Philippines, April 18, 1959, by D. S. Rabor (original no. 18557).

DIAGNOSIS: Similar to *G. l. luzonica* (Scopoli) of central and southern Luzon (type locality, vicinity of Manila), but crown darker gray, less clearly defined from back of head;

grays of wings somewhat darker; flanks and under tail coverts of females darker, the rufous much mixed with gray, and lower breast and abdomen purer white, less "stained" in appearance.

RANGE: Northern Luzon; I know of no specimens presently extant from areas where intergradation with *luzonica* might take place.

REMARKS: Sexual dimorphism in the Bleeding-heart Pigeon does not appear to have been described in the standard ornithological literature, and has been barely mentioned by aviculturalists. Delacour (1959:63) states that the female is "a little smaller and duller, with a thinner bill and a smaller head. Her underparts show more buff." There are actually several color differences between the sexes. Females have the edges of the flight feathers of the wing more strongly rufescent and are more heavily washed with rufous or pinkish-buff on the flanks and under tail coverts. There is a marked tendency for the iridescent color of the back to invade the area of the bend of the wing, which is clear gray in males. Males have, on the average, a somewhat larger red breast-spot, posterior to which is, in most individuals, a strong pinkish wash. In females of *luzonica* this wash is pinkish-buff mixed with gray, giving the underparts a stained appearance; this effect is less well marked in *griseolateralis*, as mentioned above in the diagnosis of that race.

Delacour and Mayr (1946:95-96) treated all of the Philippine representatives of *Gallicolumba* as subspecies of *G. luzonica*. Later, however, Delacour (1959:63-64) recognized at least two species (total number not clear from his discussion). Peters (1937:133-134) admitted five species. Certainly the level of differentiation represented by *luzonica* and *griseolateralis*, or by *criniger*, *leytensis* and *basilanica*, more closely corresponds to the usual Philippine (and continental) subspecies than does that represented by *luzonica* versus *criniger*. As is true of so many insular representative forms, the Bleeding-heart Pigeons have attained several stages of differentiation. To call all of these forms subspecies of *luzonica* is to use our admittedly imperfect trinomial system to mask certain obvious interrelationships. Within such a system it is impossible to avoid compromise. In this case the most useful solution seems to be the treatment of these pigeons as a single superspecies, divided into several species corresponding to what are usually specific levels of differentiation in appearance among continental forms. Some of these, in turn, exhibit geographical variation at the subspecific level.

Genuinely wild Bleeding-heart Pigeons from Luzon, with accurate locality data, are far outnumbered in museum collections by aviary specimens. All of the latter that I have seen have been referable to the southern race, so that it appears reasonably certain that the original material of *luzonica*, even if obtained in a Manila market, came from this population. A total of five northern and nine southern Luzon specimens with accurate data formed the basis for these notes.

Copsychus saularis heterogynus, subsp. nov.

Type: "♂" [= adult ♀] (Carnegie Mus. No. 139025), collected at Pangil, Laguna Province, Luzon, Philippines, in November, 1958, by N. A. Icarangal.

Diagnosis: Females differ from those of *C. s. mindanensis* (type locality, Mindanao) in being more heavily washed with buff on the posterior underparts, and in having this area, especially the flanks and under tail coverts, finely but distinctly barred with white. Males are not separable from *mindanensis.*

Range: Island of Luzon. No specimens from Polillo, Catanduanes or Marinduque were examined; these islands tend to be inhabited by Luzon subspecies of polytypic Philippine species.

Remark: De Schauensee and du Pont (1959:3) have mentioned the fact that Dyals from the Sulus have somewhat larger bills than those from the remainder of the Philippines. Actually the Sulu birds represent the extreme of a slight cline in bill size; although many specimens from both ends of the Philippine archipelago can be matched with one another, the individuals with longest and heaviest bills are mostly from more southern islands (Negros, Mindanao, Basilan, Sulus).

Of *C. s. heterogynus*, 14 males and 14 females from Luzon were examined, and of *C. s. mindanensis*, the following: Sibuyan, 1 ♂, 1 ♀; Mindoro, 1 ♂, 2 ♀; Samar, 1 ♂, 1 ♀; Cebu, 1 ♂ (juv., identified by probability); Negros, 4 ♂, 4 ♀; Mindanao, 4 ♂, 4 ♀; Basilan, 7 ♂, 1 ♀; Sulu archipelago, 4 ♂, 1 ♀.

Dicaeum aeruginosum striatissimum, subsp. nov.

TYPE: adult ♂ (Carnegie Mus. No. 95037), collected at Solsona, Ilocos Norte Province, Luzon, Philippines, December 8, 1923, by R. C. McGregor *et al.*

DIAGNOSIS: Differs from *D. a. aeruginosum* (type locality, Cebu) in being more heavily streaked below, with streaks extending farther back along flanks and on abdomen; dorsum sootier, with less contrasting greenish wash on upper tail coverts and edges of remiges and rectrices; white spot on inner web of outer rectrix larger but less sharply defined. Differs even more from *D. a. affine* of Palawan, which is markedly greenish above and sparsely streaked below.

RANGE: Specimens examined from islands of Luzon and Sibuyan.

REMARKS: I follow Salomonsen (1960a:5-6) in considering *D. aeruginosum* to be specifically separable from *D. agile*, with which it has been associated by recent authors. Salomonsen believed that "*D. a. aeruginosum* shows no geographical variation within its range," but had examined only Luzon and Mindoro specimens.

There is a cline in the Philippines from north to south in decrease of ventral streaking and increase of greenish on back and wings. Thus, although Luzon birds as a group are sufficiently distinct from those of the more southern islands to be worthy of nomenclatorial recognition, the characters of *striatissimum* are best developed in northern Luzon; the type selected is therefore a northern bird. In some species (cf. *Dicrurus*) the Mindoro population is most closely related to that of Palawan, lying to the southwest. In *Dicaeum aeruginosum*, on the other hand, Mindoro lies on the main north-south cline, and Mindoro birds are almost exactly intermediate between *striatissimum* and *aeruginosum*. They are nearest the former in back color and nearest the latter in amount of ventral streaking (6 specimens examined). Of *striatissimum*, 16 Luzon specimens and 1 Sibuyan specimen have been examined. Of *aeruginosum*, 6 Cebu and 4 Negros specimens were seen. The one known specimen from Mindanao (Salomonsen, *op. cit.*:15-16) probably belongs here. Of *affine*, 4 Palawan specimens were examined.

Dicaeum hypoleucum lagunae, subsp. nov.

Type: adult ♀ (Carnegie Mus. No. 139066), collected at Pangil, Laguna Province, Luzon, Philippines, in November, 1958, by N. A. Icarangal.

Diagnosis: Similar to *D. h. obscurum* from northern Luzon, but underparts heavily washed with olivaceous green, brightest and yellowest on mid-abdomen, rather than almost neutral gray with relatively little greenish wash. Quite different from the southern races *pontifex*, *mindanense* and *hypoleucum*, which are progressively more bicolored, culminating in the sharply black-and-white *D. h. hypoleucum*, the only race with pronounced sexual dimorphism. In *lagunae*, as in *obscurum*, the sexes are alike in color.

Range: Presently known only from Laguna Province, south-central Luzon, Philippines.

Remarks: Several birds of the foothills and highlands appear to have an interrupted range in Luzon, with distinctive northern an dsouthern subspecies (*cf. Ptilinopus merrilli*, *Culicicapa helianthea*). This hiatus may be an artifact based on insufficient collecting, as there are still large areas of Luzon, especially in the eastern Sierra Madre, which are all but unknown ornithologically. In any case, *Dicaeum hypoleucum* is here shown to be still another species known from areas in northern and in southern Luzon, with a subspecies in either area. I have examined 28 specimens from various northern Luzon localities, in the collections of the American Museum of Natural History and the Yale University Peabody Museum. Of *lagunae* I have seen only the type, in Carnegie Museum, and three specimens in the American Museum (one each from Mt. Makiling, Los Baños, and "Southern Luzon").

Salomonsen (1960b:3), when reviewing this species, stated that he had seen specimens of *obscurum* from Mountain Province only, although he supposedly had available the material belonging to the American Museum of Natural History.

Dicaeum pygmaeum salomonseni, subsp. nov.

Type: adult ♂ (Y.P.M. No. 48608), collected at 1600′ on Mt. Sicapo-o (Mt. Simminublan), Ilocos Norte Province, Luzon, Philippines, April 4, 1959, by D. S. Rabor and R. B. Gonzales (original no. 21123).

Diagnosis: Similar to *D. p. pygmaeum* of central Luzon south to the Surigao Strait (type locality, "Luzon," here restricted to the vicinity of Manila), but males with dorsum blacker, less green, contrasting more with rump; flanks grayer, less green; sides of head duller gray, less sharply defined from the white of the throat. In both *pygmaeum* and *salomonseni* the breast color is highly variable, but in the latter race the orange is less often than in *pygmaeum* concentrated into a suggestion of a definite breast spot. Females of *salomonseni* are duller, grayer, less green above than those of *pygmaeum*, with the yellow-green area of the rump duller and less extensive; underparts with less buffy wash; flanks grayer, less green.

Range: Northern Luzon, known from Mountain and Ilocos Norte provinces.

Remarks: Negros males are slightly paler on the sides of head than males from southern Luzon, but are not subspecifically separable from *D. p. pygmaeum*. It is of interest to note that Salomonsen (1960b:15-16) found that specimens from the Babuyan Islands north of Luzon differed from "typical *pygmaeum*" in certain characters, some of which ("deeper orange vinaceus [*sic*] tinge on the under parts, slightly darker olive flanks, and the dark longitudinal patch on the center of the lower breast and abdomen more well marked and distinct") represent trends *opposite* to the differences observed between the south Luzon *pygmaeum* and the north Luzon *salomonseni*.

Of *D. p. salomonseni*, 6 specimens from Mountain Province, 16 from Ilocos Norte Province, and 1 from "North Luzon" were examined. Of *D. p. pygmaeum*, the following Luzon specimens were examined: Manila, 1; Bataan Prov., 5; Rizal Prov., 5; Laguna Prov., 3; "Luzon," 1. Also Marinduque, 1; Siquijor, 1; Mindoro, 5; Bohol, 2; Negros, 20.

This new flowerpecker is named for the eminent Danish ornithologist Dr. Finn Salomonsen, an authority both on Philippine birds and on the family Dicaeidae.

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The 1956 expedition in which I participated was part of a project of the Graduate School of Public Health, University of Pittsburgh, under the sponsorship of the Commission on Viral Infections, Armed Forces Epidemiological Board, and supported in part by the Office of the Surgeon General, United States Department of the Army. Dr. Canuto G. Manuel, then Chief Zoologist of the National Museum of the Philippines, was helpful in many ways, including arrangements for two visits to the Mount Makiling area in Laguna Province. Mr. Reuben G. Almazan, Officer in Charge of Makiling National Park, was kind enough to donate two specimens of *Gallicolumba luzonica* from a locally-trapped flock, and arranged for permission to collect birds in the Park.

Specimens for comparison were borrowed through the courtesy of the authorities of the American Museum of Natural History, Yale University Peabody Museum of Natural History, Chicago Natural History Museum, and United States National Museum. Specimens were also examined *in situ* at the first two museums named, and at the California Academy of Sciences and the Museum of Vertebrate Zoology, University of California. Study of Philippine specimens at the last two named institutions took place during visits primarily concerned with an unrelated project supported by a grant from the National Science Foundation.

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YALE PEABODY MUSEUM

OF NATURAL HISTORY

Number 68 September 24, 1962 New Haven, Conn.

STOMATOPOD CRUSTACEA COLLECTED BY THE YALE SEYCHELLES EXPEDITION, 1957-1958

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Although small in size and number of species, the collection contains several rare species as well as several new records from the Seychelles. Of particular interest is the discovery of an undescribed species allied to *Gonodactylus fimbriatus* Lenz and *G. brevisquamatus* Paul'son. In all, ten species in three genera are represented, with all but two of the species in *Gonodactylus*.

In the following account, complete synonymies are given only for the relatively rare species. In the case of common species, reference is made to the synonymies compiled by Kemp, 1913, and Holthuis, 1941, as well as more recent papers. The species are arranged as in Kemp, 1913. In addition to the material collected in the Seychelles proper, several specimens were collected in the Maldives, at Ceylon, etc., during the expedition, and these have been included in the account. Comparative notes and sketches of *G. fimbriatus* and *G. brevisquamatus* have been added in order to clarify their relationship to the new *Gonodactylus*.

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[1] Contribution No. 404 from The Marine Laboratory, University of Miami.

The measurement following the number of specimens is in all cases total length, measured from the apices of the submedian spines of the telson to the anterior margin of the rostral plate. All of the material has been deposited in the Yale Peabody Museum (YPM).

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I would like to express my thanks to Dr. Willard D. Hartman, Curator, Division of Invertebrate Zoology, Yale Peabody Museum for making this interesting collection available for study. I would also like to thank Dr. E. Deichmann, Museum of Comparative Zoology at Harvard, who kindly loaned 4 specimens of *G. fimbriatus* and Mr. R. W. Ingle, British Museum (Natural History), who loaned a specimen of *G. brevisquamatus* for comparative purposes.

The illustrations of the new species were drawn by my wife, Lilly Manning.

Thanks are due to the National Science Foundation for their support of stomatopod systematics under Grant G-11235.

Pseudosquilla ciliata (Fabricius, 1787)

Pseudosquilla ciliata, Kemp, 1913:96; Holthuis, 1941:261.

Material. 1 ♂, 51.3 mm; YSE Sta. 9; seined offshore, Point Elizabeth, north of Trincomalee, Ceylon; N. Mahadeva; 22 August 1957; YPM 4326.

Lysiosquilla maculata (Fabricius, 1793)

Lysiosquilla maculata, Kemp, 1913:111, pl. 8, figs. 86-91; Holthuis, 1941: 269, fig. 5.

Material. 1brk. ♂, 164.8 mm; Seychelles; collected by local inhabitants; YPM 4342.

Gonodactylus chiragra (Fabricius, 1781)

Gonodactylus chiragra, Kemp, 1913:155, pl. 9, fig. 107; Holthuis, 1941:277, fig. 7.

Material. 1 ♀, 51.2 mm; YSE Sta. 12; Foul Pt., Ceylon; W. D. Hartman; 28 August 1957; YPM 4328.

1 ♂, 46.7 mm; YSE Sta. 17; Funadu Is., N. Male Atoll, Maldives; shoreward edge of reef, living in cavities in coral; W. D. Hartman; 19 September 1957; YPM 4329.

1 ♂, 41.0 mm, 1 ♀, 23.1 mm; YSE Sta. 28; seaward reef, Île du Coin, Peros Banhos Atoll, Chagos Archipelago; A. J. Kohn, W. D. Hartman; 23 October 1957; YPM 4333.

1 ♀, 15.2 mm; YSE Sta. 35B; northwest of Moyenne Is., Seychelles; A. J. Kohn; 20 January 1958; YPM 4456.

1 ♂, 37.7 mm; YSE Sta. 41; seaward reef, Menai Is., Cosmoledo Atoll; A. J. Kohn; 10 December 1957; YPM 4338.

1 juv., 6.8 mm; YSE Sta. 53; Pasquère, Praslin Is., Seychelles; W. D. Hartman; 19 January 1958.

Gonodactylus platysoma Wood-Mason, 1895

Gonodactylus chiragra var. *platysoma,* Kemp, 1913:162, text-fig. 1; Holthuis, 1941:281.

MATERIAL. 1 ♀, 86.1 mm; YSE Sta. 25C; Gan Is., Addu Atoll, Maldives; A. J. Kohn; 18 October 1957; YPM 4331.

1 ♀, 46.8 mm; YSE Sta. 27; lagoon side, Île du Coin, Peros Banhos Atoll, Chagos Archipelago; W. D. Hartman; 22 October 1957; YPM 4332.

Gonodactylus spinosus Bigelow, 1893

Gonodactylus spinosus Bigelow, 1893:101; Bigelow, 1894:493; Nobili, 1906:330; Borradaile, 1907:210; Bigelow, 1926:519, figs. 1, 2.

Gonodactylus chiragra spinosus, Lanchester, 1903:454, pl. 23, fig. 14.

Gonodactylus demani spinosus, Kemp, 1913:165, pl. 9, fig. 112; Tattersall, 1921:361; Kemp and Chopra, 1921:311; Ramadan, 1936:9; Dollfus, 1938:215, fig. 17; Chopra, 1939:172.

MATERIAL. 1 ♀, 17.2 mm; YSE Sta. 30A; Bird Is., Seychelles; W. D. Hartman; 6 November 1957; YPM 4334.

REMARKS. As first pointed out by Kemp and Chopra (1921) and confirmed by Bigelow (1926), *G. spinosus* differs from *G.*

demani in having the inner branch of the uropod setose on all margins; in *G. demani* the inner margin is devoid of setae.

There is no reason to maintain *spinosus* as a variety or subspecies of *G. demani*, Varietal status does not have nomenclatural significance, and as both *spinosus* and *demani* are sympatric in the Red Sea as well as in other areas, they cannot be regarded as subspecies. No overlap or variation has been shown in the main character used to separate the two, so they must be regarded as distinct species.

Chopra (1939) records this species from Mauritius to the Gulf of Suez, Red Sea, and Persian Gulf, and from Zanzibar to the Sea of Java, and Borradaile (1907) reported it from the Seychelles.

Gonodactylus falcatus (Forskål, 1775)

Cancer falcatus Forskål, 1775:96.

Gonodactylus glabrous Brooks, 1886:62, pl. 14, fig. 5, pl. 15, figs. 7-9; Kemp, 1913:167, pl. 9, fig. 113.

Gonodactylus falcatus, Holthuis, 1941:284, fig. 9a.

Material. 1 ♂, 40.1 mm; YSE Sta. 9; seined offshore, Point Elizabeth, north of Trincomalee, Ceylon; N. Mahadeva; YPM 4327.

1 ♂, 28.3 mm; YSE Sta. 22; Hulule Is., N. Male Atoll, Maldives; W. D. Hartman; 5 October 1957; YPM 4358.

3 ♀ ♀, 29.7-35.9 mm; YSE Sta. 36; in coral cavities, Anse à la Mouche (northern reef), Mahé Is., Seychelles; W. D. Hartman; 24 November 1957; YPM 4335.

2 ♀ ♀, 35.0-43.3 mm; YSE Sta. 36; Anse à la Mouche (northern reef), Mahé Is., Seychelles; A. J. Kohn; 22 December 1957; YPM 4336, 4337.

Gonodactylus crinitus, new species

Figure 1

Holotype. 1 ♀, 27.5 mm; YSE Sta. 33; Beau Vallon, Mahé Is. Seychelles; A. J. Kohn; 1 February 1958; YPM 4459.

Paratypes. 1 ♀, 26.4 mm; data as in holotype; YPM 5510.

♀ ♀, 28.2-28.8 mm; YSE Sta. 55; La Passe, Silhouette Is., Seychelles; A. J. Kohn; 6 February 1958; YPM 4340.

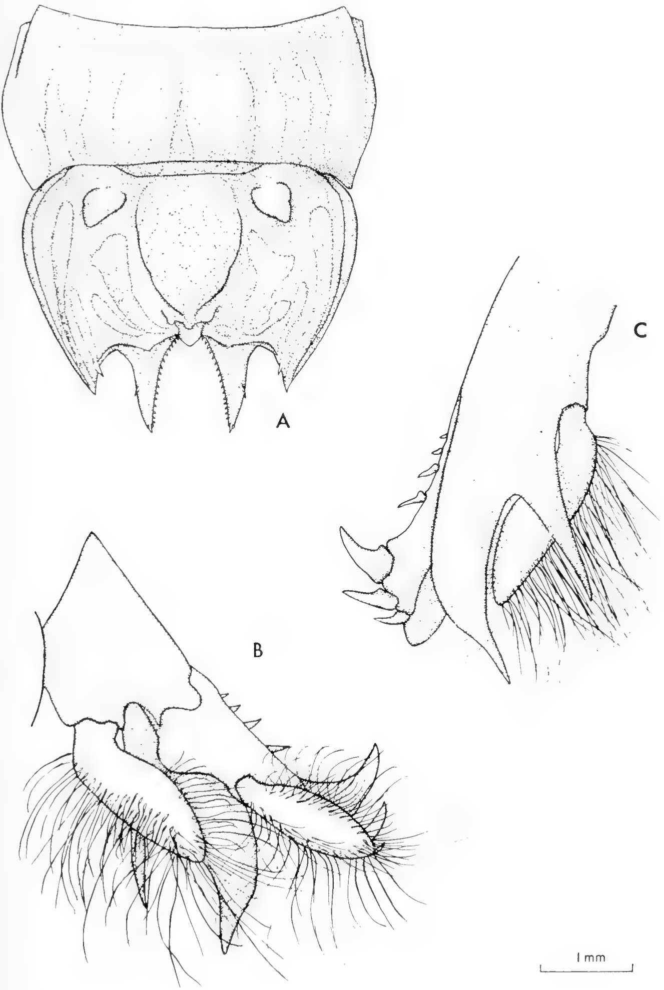

Figure 1. *Gonodactylus crinitus*, n. sp. Female paratype, Mahé Is., Seychelles. A. Sixth abdominal somite and telson. B. Dorsal view of right uropod. C. Ventral view of right uropod. Telson length = 2.9 mm.

Description. Rostral plate with three sharp anterior spines; median spine elongate, extending beyond base of eyes; lateral spines broader, shorter, extending to base of eyes; rostral width at anterolateral angles greater than median length.

Carapace with anterolateral margins distally truncate and extending well beyond base of rostral plate; lateral margins of carapace sinuate; posterior breadth greater than anterior.

Mandibular palp two- or three-segmented; five epipods present; antennal scale extending to or beyond middle of cornea.

First five abdominal somites wtih an impressed pit on upper median portion of pleuron; second to fifth somites with "reversed-L-shaped" groove anterolaterally; sixth abdominal somite with six longitudinal carinae, submedians broader than intermediates and all are swollen, with irregular margins.

Telson with eleven dorsal carinae and four posterior spines, submedians with movable tips; anterior pair of tubercles present; median carina swollen, with irregular margins; posterior margin of telson with a prominent median tubercle; above and anterior to this tubercle lie a pair of submedian tubercles; three carinae between median carina and carina of intermediate tooth; first pair not extending to anterior margin, flattening and widening anteriorly, converging posteriorly; second pair much shorter than first, converging posteriorly, not extending anteriorly past middle of telson; first and second pair (lateral to median carina) may fuse posteriorly in a transverse carina that runs toward median distal tubercle; third pair thinner, lying mesial to posterior portion of the carina of the intermediate tooth; carinae of intermediate tooth long, well-defined, extending almost to anterior margin of telson; marginal carinae sharp, fusing posteriorly with carina of intermediate tooth; a transverse, raised ridge, biconcave posteriorly, extends from base of third pair of carinae to base of carina of submedian tooth and from there to under the median tubercle; submedian teeth with movable apices and with 13-17 minute denticles on inner margin and a spinule on outer margin; intermediate teeth with a spinule on inner margin.

Uropods with penultimate segment of outer branch not setose, extending beyond distal segment; penultimate segment armed with seven lateral spines, first four small, movable, last three fixed, large, antepenultimate by far the largest; last three with tips corneous and strongly recurved; distal segment of outer branch elongate, paddle-shaped, dorsal margin setose on either side, median strip not setose, ventral margin not setose; inner branch elongate, outer margin convex, tapering to tip, inner half of dorsal margin setose, with proximal third of outer half without setae, ventral margin without setae; basal prolongation with proximal spine slender, almost as long as distal spine; distal spine recurved dorsally, outer margin concave distally.

Color. Largely faded in preservative; carapace and body mottled green and white; eyestalks with scattered dark chromatophores; mottling very pronounced on sixth abdominal somite and telson, carinae of telson appearing banded with white and green.

Measurements. Holotype: total length, 27.5 mm; carapace length 5.6 mm; telson length, 2.9 mm; telson width, 3.6 mm. Female paratype, YSE Sta. 33: total length, 26.4 mm; carapace length, 5.0 mm; telson length, 2.9 mm; telson width, 3.4 mm.

Discussion. *G. crinitus* is closely related to both *G. fimbriatus* Lenz and *G. brevisquamatus* Paul'son, but differs from both in having 11 dorsal carinae on the telson, lacking setation on the dorsal surface of the proximal segment of the uropod, and lacking ventral setation on the ventral surface of the uropod. Differences between the three species are summarized in Table 1.

G. fimbriatus has been synonymized with *G. brevisquamatus* since the remarks of Kemp (1913) and Tattersall (1921) based on an unpublished account by Patience in which the two were synonymized. The two species have not been directly compared since that time. Tattersall's action was followed by Kemp and Chopra (1921), Ramadan (1936), and Dollfus (1938). Serène (1949) kept the two species separate in his discussion of the position of *G. strigatus* Hansen. The two species are very closely related and in my opinion they are distinct. An adequate series might show that they deserve only subspecific status.

Four specimens of *G. fimbriatus* (all ♀♀, total length 21.4-30.7 mm; Zanzibar; Cooke, col.; MCZ 7817) and one of *G. brevisquamatus* (♀, 27.2 mm; Tella Tella Kebira, Sudanese Red Sea; C. Crossland, col.; B. M. (N. H.) registry 1936.9.30. 1-2) were examined; the latter specimen was one of those examined by Tattersall (1921). The following notes were taken from this material.

TABLE 1. Comparison of

Gonodactylus brevisquamatus Paul'son, *G. fimbriatus* Lenz, and *G. crinitus* n. sp.

	G. brevisquamatus	*G. fimbriatus*	*G. crinitus*
Telson			
Dorsal Carinae	9	9	11
Submedian denticles	± 14, in one series	10-12 in 2 series	13-17 in one series
Intermediate denticles	1 on submedian, 1 on intermediate tooth	6-10 in 2 series on submedian, 6-8 on intermediates	1 on submedian, 1 on intermediate
Uropods			
Exopod, prox. seg.	with a dorsal patch of setae	with a dorsal patch of setae	no dorsal patch of setae
Exopod, distal seg.	broadly rounded distally, outer and inner margins about equally convex; setose proximally on dorsal margin, all of dorsal setae short	tapering distally, outer margin much more convex than inner; setose proximally on dorsal margin, all of dorsal setae short	tapering distally outer and inner margins about equally convex; nonsetose prox. on dorsal margin, all of dorsal setae long
Endopod	short, rounded distally; completely setose ventrally	short, bluntly truncate distally; completely setose ventrally	elongate, tapering distally; no ventral setae
Basal prolongation	outer spine much larger than inner	outer spine much larger than inner	inner outer spine slightly larger than

G. fimbriatus and *G. brevisquamatus* are very similar in general appearance. They differ primarily in the number and arrangement of submedian and intermediate spinules on the telson (Table 1) and in the shape of the uropod segments. A ventral view of the uropod of each species is shown in Figure 2; setation is omitted for clarity. In *G. brevisquamatus*, the distal segment of the outer branch is broadly rounded and the inner branch tapers distally. In *G. fimbriatus*, the distal segment of the outer branch tapers and the inner branch is truncate distally. Both are similar in lateral spination of the proximal segment of the outer branch. The inner spine of the basal prolongation is comparatively longer in *G. brevisquamatus*. Both species have a pair of short submedian carinae on the ventral surface; these carinae converge anteriorly but do not meet.

Figure 2. A. *G. brevisquamatus* Paul'son, Red Sea, ventral view of right uropod; B. *G. fimbriatus* Lenz, Zanzibar, ventral view of right uropod. Smaller lateral spines present in both species; they are obscured by the basal prolongation in 2A.

The setation of the uropods is characteristic in both. The proximal segment of the outer branch bears a prominent, circular patch of setae on the dorsal surface. The ventral surface of the uropods is completely setose, with a thick, circular, proximal patch of strong setae.

G. fimbriatus has been reported from Zanzibar (Lenz, 1905: 38, pl. 47, fig. 11; 1910:572) and Coëtivy, Seychelles (Borradaile, 1907:211). Serène (1949:231, 235) mentioned a specimen from the Mergui Archipelago, perhaps from Kemp's (1913:175) reference to Patience's material.

Other than Patience's questionable record of *G. brevisquamatus* from the Mergui Archipelago, that species is known only from the Red Sea. Patience's specimens may actually have belonged to *G. fimbriatus* rather than *G. brevisquamatus.* The following papers record *G. brevisquamatus:* Paul'son, 1875: 127, pl. 21, fig. 3; Nobili, 1906:331; Kemp, 1913:174, pl. 10, figs. 115, 116; Tattersall, 1921:362, pl. 27, figs. 5, 6; Kemp and Chopra, 1921:311; Ramadan, 1936:10; Dollfus, 1938:222, fig. 21.

Remarks. The curious arrangement of setae and spines on the uropods of *G. brevisquamatus* and *G. fimbriatus* is perhaps worthy of further mention. The large, recurved spines on the uropod may be used by the animal to "lock" itself in its burrow. The uropods are curved ventrally, so that the telson and uropods together form half of a circle. The inner branches of the uropods recurve dorsally. The setae of the uropods are so arranged that, when viewed from behind the animal, they appear as a rounded "basket," as if they were utilized as a filtering apparatus. All of the specimens of *G. fimbriatus* had the setose areas loaded with detritus and sand which had to be washed away before the uropod structure could be observed.

The significance of these structures is not readily apparent. The mouthparts and raptorial claws appear unmodified, and it seems unlikely that these species are filter-feeders. Observations on these species in the field would be most welcome.

Characters based on the relative length of the rostral plate or antennal scale in relation to the eye must be used with some caution in the stomatopods. Such characters vary according to the state of contraction or expansion of the body at preservation. In future work, more attention should be given to the shape of the uropods and their investment of setae. These characters coupled with the configuration of the telson are apparently diagnostic in this group of *Gonodactylus* (Group II of Kemp, 1913).

Name. The specific name is from the Latin, "crinitus," fringed, and refers to the setation of the uropods.

Gonodactylus lenzi Holthuis, 1941

Protosquilla glabra Lenz, 1905:388, pl. 47, fig. 13; Lenz, 1910: 572 [listed only].

Gonodactylus glaber, Kemp, 1913:182, pl. 10, fig. 121; Kemp, 1915:186; Roxas and Estampador, 1930:124, pl. 3, fig. 5; Roxas, 1930:18; Chopra, 1931:42; Gravier, 1937:208; Serène, 1947:385, fig. 1, pl. 2.

Gonodactylus lenzi Holthuis, 1941:288; Tiwari and Biswas, 1952: 362; Serène, 1954:6 [larval stages, p. 34 *et seq.*].

MATERIAL. 1 ♂, 25.7 mm; YSE Sta. 33; Beau Vallon, Mahé Is., Seychelles; inhabiting dead corals; A. J. Kohn; 1 February 1958; YPM 4458.

REMARKS. The specimen agrees with Kemp's account in almost all respects. The posterior spines of the telson are of equal size. The corrugations of the lateral margins of the telson are not visible, but the three central bosses of the telson are faintly corrugated.

The specimen figured by Serène (1947) has the bosses of the telson much more inflated than in the present specimen; both Serène and Gravier (1937) commented on the variability of the median bosses of the telson.

The color pattern in preservative is striking. The antennular flagella are banded purple and white. The rostral plate, ophthalmic somite and the two distal segments of the raptorial claw are bluish with scattered dark chromatophores. The body is cream colored and densely covered with dark chromatophores which are aggregated in dark patches on the posterior portion of the carapace, sixth and seventh thoracic somites, and second to fourth abdominal somites. Kemp (1913) found these patches on the first, fourth, and fifth abdominal somites. The fifth and sixth abdominal somites, telson, and uropods are outlined in blue.

This species has not previously been recorded from the Seychelles. The records in the literature are: Zanzibar (Lenz, 1905); Ceylon (Lenz, 1910); Andamans (Kemp, 1913; Tiwari and Biswas, 1952); Nicobars (Chopra, 1934); Bay of Batavia (Holthuis, 1941); Poulo Condore Islands (Gravier, 1937); Nhatrang, Viet Nam (Gravier, 1937; Serène, 1947, 1954); Philippines (Kemp, 1913; Roxas, 1930; Roxas and Estampador, 1930).

Gonodactylus gyrosus Odhner, 1923

Gonodactylus gyrosus Odhner, 1923:11, pl. i, figs. 4, 5; Ward, 1942:56; Tiwari and Biswas, 1952:362, fig. 5; Holthuis, 1953:61.

Material. 1 ♀, 41.5 mm; YSE Sta. 55; La Passe, Silhouette Is., Seychelles; A. J. Kohn; 6 February 1958; YPM 4341.

Remarks. The rostral plate of this specimen is somewhat shorter than that illustrated by Tiwari and Biswas (1952), as the median spine does not exceed the cornea. The cornea is noticeably bilobed, and the eyes are comparatively shorter.

The color pattern is similar to that shown by Tiwari and Biswas. The background color is cream, with many dark chromatophores in patterns on the anterior part of the body. The fifth abdominal somite is lined anteriorly and posteriorly with green. The sixth abdominal somite and telson are mottled green and white.

The mandibular palp is present, apparently two-segmented.

This species has not previously been recorded from the Seychelles. The records in the literature are: Arno Atoll, Marshall Is. (Holthuis); Gilbert Islands (Odhner); Andamans (Tiwari and Biswas); Diego Garcia, Chagos Archipelago (Ward).

Gonodactylus guerini White, 1861

Gonodactylus guerini White, 1861:43, pl. 6; Bigelow, 1931:139 [and synonymy]; Townsley, 1953:423, figs. 20, 21a-f; Serène, 1954: 52 [discussion only].

Material. 1 ♀, 35.5 mm; YSE Sta. 41A; anchorage off Menai Is., Cosmoledo Atoll; 25 fms.; W. D. Hartman; 12 December 1957; YPM 4447.

Remarks. The specimen agrees well with the description given by Bigelow (1931). The right submedian elevation of the telson bears a curved row of six instead of five spines as in Bigelow's material.

The color is as noted by Bigelow, with two dark transverse bands on the carapace; each of the thoracic and abdominal somites are banded. The spines of the telson are flushed with pink.

Bigelow gave a complete synonymy, which will not be repeated here, and recorded the following distribution: Hawaii, Marquesas, Fiji, and Mauritius, in depths ranging from a few feet to 60 fms. Townsley (1953) reported on other Hawaiian specimens in depths of 50 to 120 fms. The present specimen extends the range 900 miles to the north of Mauritius.

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* Paul'son's rare 1875 paper on the Crustacea of the Red Sea originally appeared in Russian; an English translation of this work was published in 1961 for the National Science Foundation and the Smithsonian Institution by the Israel Program for Scientific Translations. It is available in the United States from the Office of Technical Services, U. S. Department of Commerce, Washington 25, D. C.

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Postilla

YALE PEABODY MUSEUM

OF NATURAL HISTORY

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NOTES ON SOUTH AMERICAN FLAMINGOS

Luis E. Peña*

INTRODUCTION

During the Chilean winter of 1957 we had our first contact with the Andean species of flamingos on an expedition organized by the Yale University Peabody Museum of Natural History to the high ranges of the Andes in the province of Antofagasta, Chile. Later, in the summer of 1957-1958, we visited this region with Dr. Roger Tory Peterson and stayed there for a month studying these birds. In the summer of 1960, together with Dr. William G. Conway, Director of the New York Zoological Park and Mr. Bates Littlehale of the National Geographic Society, we spent another month on this work, and later, during the month of March of 1960, we extended the expedition for an additional few weeks traveling through the Patagonian region of Argentina. Recently, between October 1960 and March 1961, we made another expedition to the Patagonian region, including Tierra del Fuego.

DESCRIPTION AND DISTRIBUTION

Three species of flamingos that live and nest in the mountains in the province of Antofagasta, Chile and the neighboring

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* Casilla 2974, Santiago, Chile.

Figure 1. Outline maps of South America showing distribution of *Phoenicopterus chilensis* Molina, *Phoenicoparrus andinus* (Philippi) and *Phoenicoparrus jamesi* (Sclater).

region of Bolivia have been identified and observed (a fourth species called "Guajchatata" by the natives was not identified):

Phoenicopterus chilensis Molina is characterized by the lack of black coloration on the sides and back of the body when it is at rest. The reddest part is on its tail (figure 3 A and B). Geographically it is the most widely spread, having been found on the high Andean ranges of Peru and Bolivia, in the Patagonian region of Chile and Argentina including Tierra del Fuego, in Southern Brazil and in Uruguay. It is the only species that during certain months lives close to the sea. The natives call this bird the "Tococo," named for its cry.

Phoenicoparrus andinus (Philippi) has a black fringe on its tail and has been called the "Black Tail Flamingo." The winey coloration is very marked at the base of the neck and part of the chest (figure 4 A and B). This species is characteristic of the Andean region between 15° and 27° latitude south. It permanently inhabits the marshes and lakes of brine or of fresh water. It has been found throughout the year in the

Figure 2. The camp at Lejía Lake (Antofagasta Andes Range) at 12,200 feet above sea level where *Phoenicoparrus jamesi* (Sclater) was found in large numbers.

Atacama lake in Antofagasta, Chile, in Champaja, Argentina and in Lake Titicaca in Peru and Bolivia. The native name for this species is "Jetete" or "Jititi."

Phoenicoparrus jamesi (Sclater) has two red stripes which fall gracefully over its wings; they are almost plume-like and arise from the upper part of the back. The black plumes are seen only as spots on the sides. The neck and chest are of a very winey color (figure 5 A and B). The colors of the feet and beak as distinguishing features are of less importance, as from a distance one is all too likely to make a mistake, these parts of the body being often covered with mud. This species is typical of the high shallow Andean salt lakes, where they nest in large colonies. It has been observed in the Laguna Colorada, Bolivia, in the Laguna de Lejía, Antofagasta, Chile, and in the Salar de Atacama, Antofagasta, Chile in July 1957. It has also been collected in Lake Titicaca, Peru and Bolivia, and in Abrapampa, Argentina. The native name for this bird is "Chururu."

MIGRATION

Nesting colonies, always homogeneous as to species, on Laguna Colorada and in the Laguna Verde, both on the Bolivian-Chilean border, were visited on different occasions in the months of December, January and February. In general we were able to determine that the resident species of the regions of high altitude is *Phoenicoparrus jamesi;* of the regions of intermediate altitude, *Phoenicoparrus andinus;* and of the lower regions, *Phoenicopterus chilensis*, which wanders into the higher altitudes at intervals.

Phoenicoparrus andinus (Philippi) and *Phoenicoparrus jamesi* (Sclater) are both extremely common, numbering in the thousands while *Phoenicopterus chilensis* Molina did not seem to form such large flocks, except perhaps in the Patagonia of Argentina. At the end of spring (November and December) both species of *Phoenicoparrus* are around the high marshes and salt lakes which are over 4,000 meters high and frozen during the winter. At the end of February, March or April they return to the areas of milder climate, the Andean marshes and lakes of lower altitude (2,300 to 3,500 meters). Although

Ph. andinus prefers to nest in the marshes of lower altitudes, we have not confirmed that personally.

Phoenicopterus chilensis Molina invades the Chilean and Argentine Patagonian region up to Tierra del Fuego, the central region of Chile (coast of Santiago province to the island of Chiloé), disappearing totally during the summer months, taking shelter to nest, possibly in the hidden lakes of the central Andean region and the south of Chile and Argentina, but this has not been proved. Nesting colonies of these species are only known in the high mountain range of Antofagasta and the region of Natales, Magallanes (Chile). Formerly there existed a large colony in Laguna del Maule (Chile), but this has disappeared owing to construction work on a dam.

Some strays or small flocks of immatures may be found in the high lakes and marshes in the winter just as they may be found in the low marshes of the Patagonian region in the summer. The few flocks that actually winter in the high region of the Andes lakes and marshes make use of the moderate temperature springs occasionally found there, but these examples are relatively rare. The rest of these marshes are completely frozen and uninhabitable by these birds.

RELATIVE ABUNDANCE OF THE THREE SPECIES

When we were with Dr. Peterson at the Laguna Colorada (Bolivia) during the month of January 1958, we had been able to observe that the number of flamingos that were inhabiting this lake was in the vicinity of 6,000. Of these the following are the approximate percentages:

Ph. jamesi	97 per cent
Ph. andinus	2 per cent
Ph. chilensis	1 per cent

During the last expedition from January 25 to the first of March 1960, the concentration of flamingos on this lake had diminished to possibly not more than 4,500. Making a reasonable estimate, based on the daily visits of flocks that were arriving in the vicinity of our camp, we arrived at the following percentages of the species:

Ph. jamesi	86 per cent
Ph. andinus	2 per cent
Ph. chilensis	12 per cent

As is seen the percentage of *Ph. chilensis* grew noticeably. From our observations, we feel that this is owing to the fact that while it was the egg-laying period for all the birds, it was the final one for *Ph. chilensis,* before they banded together to seek a more temperate climate. For the constancy of the percentage of *Ph. andinus,* the logical conclusion is that this species is only a visitor to these high lakes and that its nesting is probably carried out elsewhere.

As the data that we gathered on our trip to Salar de Aguas Calientes (Chile) illustrated, we found only small groups of flamingos, though this is possibly due to our inability to distinguish the species from the great distances that separated us or to the short time at our disposal (end of February 1960). In the Laguna de Lejía, around the said marsh, we found about 1,500 flamingos, the relative occurrence of the different species being as follows:

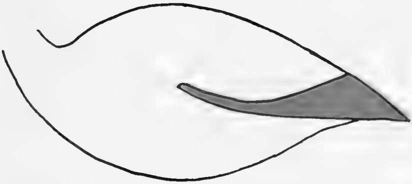
Ph. jamesi	1 per cent
Ph. andinus	98 per cent
Ph. chilensis	1 per cent

Plate

Figure 3. A. Schematic drawing showing lateral view of the body of *Phoenicopterus chilensis* Molina and the position of red coloration. B. Dorsal view of *Phoenicopterus chilensis* Molina showing positions of red coloration on its tail.

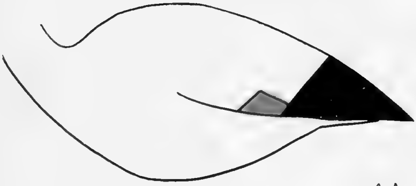
Figure 4. A. Schematic drawing showing lateral view of the body of *Phoenicoparrus andinus* (Philippi) and the distribution of the red and black coloration. B. Dorsal view of *Phoenicoparrus andinus* (Philippi), "The Black Tail Flamingo."

Figure 5. A. Schematic drawing showing lateral view of the body of *Phoenicoparrus jamesi* (Sclater) and the distribution of the red and black coloration. B. Dorsal view of *Phoenicoparrus jamesi* (Sclater) showing the two red stripes of plumes that fall over its wings and the small areas of black coloration.



3 A.

3. B.



4. A.

4. B.

5 A

5. B

It is possible that the non-use of this lake by *Ph. jamesi* is due to the fact that the great depth of the Laguna de Lejía, for example, is not favorable to them, as is true of other places. This great depth does not affect *Ph. andinus* because, as we had observed on many different occasions in the Laguna Verde and the Laguna de Lejía, one of their customs is to swim and look for food while submerging the head, neck and part of the body, in a manner similar to ducks. This custom was not observed in the other species of flamingos. *Ph. chilensis* when looking for its food effects a type of dance, slowly kicking his feet in the mud, turning around and keeping his head submerged in the turbulent and muddy water.

MEASUREMENT OF EGGS

From the colonies of *Ph. jamesi* we obtained 13 eggs which were measured. The data in millimeters are recorded below:

9.8 x 5.1	9.0 x 5.8
9.2 x 5.6	8.8 x 5.4
9.2 x 5.7	8.7 x 5.7
9.1 x 5.2	8.6 x 5.5
9.1 x 5.6	8.5 x 5.6
9.0 x 5.5	8.5 x 5.2
9.0 x 5.5	

As can be seen from the measurements, there is an enormous variation in size of *Ph. jamesi* eggs, only two having the same dimensions.

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Postilla

YALE PEABODY MUSEUM

OF NATURAL HISTORY

Number 70 November 5, 1962 New Haven, Conn.

A NEW CAVERNICOLOUS PSEUDOSCORPION BELONGING TO THE GENUS *MICROCREAGRIS*

William B. Muchmore

University of Rochester, Rochester, New York

This remarkable new form was found among collections in the Peabody Museum lent by Dr. C. L. Remington.

Microcreagris grandis, n. sp.

Material: Holotype male [Holotype No. E 101] (WM 403.01001) found July 6, 1946 by T. O. Thatcher "on formations in cave," Lehman Caves National Monument, White Pine Co., Nevada. Paratype tritonymph (WM 402.01001) found June 8, 1937 by T. O. Thatcher and R. Loir "on stalagmite in cave," also in Lehman Caves National Monument. Types in the Peabody Museum of Natural History.

Diagnosis: Male. A very large species for the genus, modified for cavernicolous life by considerable attenuation of the appendages, but not by loss of pigment or reduction of eyes. Color of carapace and palps a dark reddish-brown, the abdomen and legs much lighter. Carapace about one-third longer than broad, rather narrow at the anterior margin and greatest in breadth near the posterior end; broad, smoothly rounded epistome present; four well-developed eyes of nearly equal size present; surface smooth anteriorly, becoming rather scaly posteriorly and reticulated on the sides; carapacal setae 24 (4-5).

Abdomen elongate and typical of the genus; tergal chaetotaxy 5:9:7:11:8:10:9:9:12:9:?:mm; sternal chaetotaxy $28: (3\text{-}4)\frac{13}{(5)21(4)} : (4)\ 16\ (5) : 16 : \frac{2}{16} : \frac{2}{13} : 12:$?:?:?:mm; pleural membrane typically granulate; genital area typical. Chelicera of typical facies, about twice as long as broad; six setae on palm; fixed finger with 19 or 20 irregularly large and small teeth; movable finger with 20-21 such teeth; galea bifid just distad of the middle with each branch terminally divided into two short, pointed projections, reaching about to the end of the finger; galeal seta not reaching the tip of the galea; flagellum of 10 setae nearly all of which are deeply serrate on the anterior side; serrula interior with about 26 blades and serrula exterior with about 45 blades.

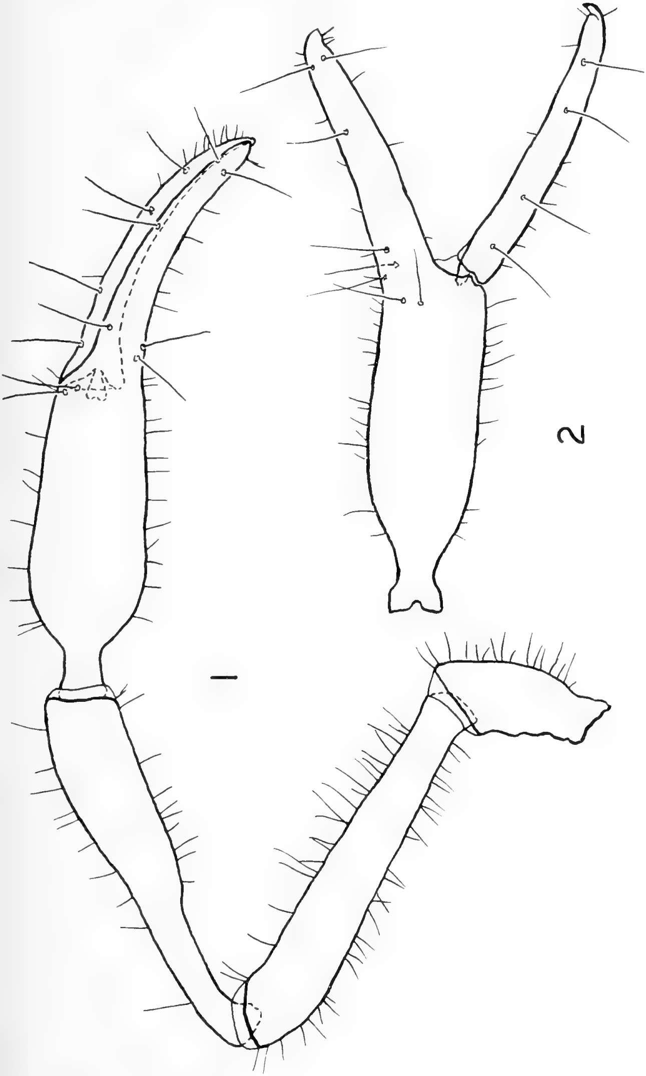
Palps very elongate for the genus; surfaces markedly granulate, except for the tibial pedicel, the pedicel and base of the chelal hand, and the chelal fingers; setae long and acuminate.

Maxillae with 4 or 5 terminal setae. Proportions of the podomeres as shown in figure 1. Tactile setae of chela as shown in figure 2; fixed finger of chela with a marginal row of 127 low, rounded or truncate teeth which are closely contiguous; movable finger with 118 similar teeth.

Trochanter 2.5, femur 5.9, entire tibia 5.0, tibial pedicel alone 5.2, chela 4.6, and hand 2.6 times as long as broad; movable finger 1.14 times as long as hand.

Legs. Legs generally similar to but more elongate and slender than those of other members of the genus. Each coxa of legs I and II heavily sclerotic but not produced into a definite process. Fourth leg with tactile setae on metatarsus 0.15 and on telotarsus 0.59 the length of the segment from the proximal end. Subterminal setae of all tarsi subequally bifurcated and each ramus with several spinose processes. Each claw with a small denticle on the dorsal side about one third the length of the claw from the proximal end.

Measurements. Body length 5.49 (in mm); carapace 2.05 long, anterior breadth 1.20, greatest breadth 1.50; abdomen



1

2

Figure 1. Dorsal view of left palp. x 25.

Figure 2. Lateral view of right chela. The terminal tooth of the fixed finger has been broken off. x 25.

3.43 long, 2.08 broad. Chelicera 1.04 long by 0.53 broad, and with movable finger 0.70 long; galea about 0.075 long. Palpal trochanter 1.31 long by 0.53 broad; femur 2.92 by 0.50; tibia 2.87 by 0.58 including pedicel, which is 1.24 by 0.28; chela without pedicel 3.83 by 0.84; hand 1.93 by 0.75; movable finger 2.19 by 0.29. Leg I: basifemur 1.27 by 0.27; telofemur 0.91 by 0.24; tibia 1.27 by 0.18; metatarsus 0.58 by 0.13; telotarsus 0.85 by 0.12. Leg IV: entire femur 2.15 long; basifemur 0.99 long by 0.42 broad; telofemur 1.23 by 0.40; tibia 2.28 by 0.23; metatarsus 0.75 by 0.17; telotarsus 0.96 by 0.15.

Female. Unknown.

Tritonymph: Similar to the adult male except that the appendages are much less attenuated and all parts are lighter in color. Carapace only one-sixth longer than broad; epistome and eyes as in adult; carapacal setae 23 (4-6).

Chelicera as in adult; six setae on palm; flagellum of 9 setae; galea well developed as in adult, but trifid in the distal third, and without terminal subdivisions.

Palpal podomeres not so attenuated as in adult, especially the tibial pedicel which is only 2.6 times as long as its least breadth; other ratios are: trochanter 2.1, femur 4.4, entire tibia 3.5, chela 4.1 and hand 2.1 times as long as broad; movable finger 1.05 times as long as hand; fixed finger with seven, and movable finger with three, tactile setae; fixed finger with 95 and movable finger with 93 marginal teeth.

Legs as in adult but stouter. Fourth leg with tactile setae on metatarsus 0.19 and on telotarsus 0.49 the length of the segment from the proximal end.

Measurements. Body length 3.15 (in mm); carapace 1.32 long, anterior breadth 0.87, greatest breadth 1.15; abdomen 1.82 long by 1.28 broad. Chelicera 0.77 long by 0.39 broad, movable finger 0.51 long; galea 0.068 long. Palpal trochanter 0.78 long by 0.37 broad; femur 1.62 by 0.37; tibia 1.53 by 0.44 including pedicel, which is 0.57 by 0.25; chela without pedicel 2.46 by 0.61; hand 1.24 by 0.61; movable finger 1.31 by 0.22. Leg I: basifemur 0.72 long by 0.19 broad; telofemur 0.54 by 0.17; tibia 0.69 by 0.12; metatarsus 0.37 by 0.10;

telotarsus 0.43 by 0.10. Leg IV: entire femur 1.35 long; basifemur 0.63 long by 0.29 broad; telofemur 0.71 by 0.29; tibia 1.28 by 0.16; metatarsus 0.45 by 0.13; telotarsus 0.59 by 0.13.

Remarks. Although the eyes are not reduced and the derm is heavily sclerotized and pigmented, *M. grandis* is certainly specially modified for life in caves by its large size and great attenuation of the appendages. In support of this contention is the fact that the specimens were taken "on formations" and "on stalagmite" within the cave where they obviously were at home. In proportions of the body and appendages it is rather similar to *M. cavernicola* Vachon (from caves in Portugal) which is undoubtedly a true troglobite. While reduction of the eyes and pigment usually accompanies increase in body size and attenuation of the appendages in adaptation of a pseudoscorpion to cavernicolous life, there is no reason to believe that all these modifications must *necessarily* proceed together. It is reasonable to suppose that *M. grandis* is exclusively troglobitic in spite of the retention of eyes and pigmented derm, features which have not proved disadvantageous and which have not yet been lost by random mutation. Indeed, it is difficult to imagine that such a form as *M. grandis* could live successfully in the epigean environment of a typical *Microcreagris*, where its size and attenuation would put it at a definite disadvantage.

It is impossible to fit *M. grandis* into the key given by Chamberlin (1962, p. 333) inasmuch as it has four eyes and an extremely slender tibial pedicel, a combination of characters which is not provided for in couplet 1. There is no difficulty, however, in separating it from other American species on the basis of its size and proportions.

It seems appropriate to note here that *Obisium cavicola* Packard from New Market Cave, Virginia, which Beier (1932) and Hoff (1958) tentatively place in the genus *Microcreagris*, does not in fact belong here. As will be shown in another place, it is a member of the genus *Chitrella*.

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Postilla

YALE PEABODY MUSEUM

OF NATURAL HISTORY

Number 71 November 14, 1962 New Haven, Conn.

SCOPELOGADUS (?) *CAPISTRANENSIS*, A NEW FOSSIL MELAMPHAID (PISCES: TELEOSTEI) FROM CAPISTRANO BEACH, CALIFORNIA

Alfred W. Ebeling

Melamphaidae, a family of bathypelagic fishes that hitherto has been known only from living material, comprises 5 genera and about 33 species. Regan (1911), followed by Ebeling (1962), referred it to the Stephanoberyciformes, an order of peculiar spiny-rayed deep-sea fishes allied with the Beryciformes, but having a hypertrophied open cephalic sensory canal system lined with delicate bony ridges, usually a single triangular supramaxillary bone, often a regressed lateral line, no orbitosphenoid bone, and possibly various other adaptations to life in the deep sea. Ebeling (1962) presented a key to the 5 melamphaid genera: *Melamphaes* Günther 1864, *Sio* Moss 1962, *Scopelogadus* Vaillant 1888, *Poromitra* Goode and Bean 1883, and *Scopeloberyx* Zugmayer, 1911. Ebeling and Weed (in press) revised *Scopelogadus*, which contains three living species, including two subspecies.

Scopelogadus, like other Melamphaidae, is mostly circumtropical at depths between 100 meters and the bottom. *S. beanii*, however, is antitropical and inhabits both the temperate

North Atlantic and the region of the Subtropical Convergence, which is an area of sinking of water masses at about 40°S lat. (Ebeling and Weed, in press).

Very few fossils of bathypelagic fishes have been reported. Only the Gonostomatidae, Paralepididae, and Myctophidae are listed in Berg (1940) as other than Recent ("Miocene to Recent"). To my knowledge, the only fossil melamphaids were collected by Dr. Andreas B. Rechnitzer on May 2, 1956, from Miocene shales along the sea cliff south of Capistrano Beach in Orange County, California. Because counts and measurements of these two small specimens generally agree with those of *Scopelogadus*, they are provisionally placed in this genus (Table 1).

The Capistrano Miocene locality consists mainly of finely laminated diatomaceous shale and mudstone. From the included Foraminifera fauna, Dr. M. N. Bramlette of the University of California, Scripps Institution of Oceanography inferred that the shale-mudstone deposits probably accumulated on the sea floor below 100 fathoms during the Upper Miocene Age (Miller, 1951). Dr. Carl L. Hubbs (pers. comm.), also of Scripps, added that although the lower parts contain algae (20 species thus far discovered), a few fish (herring), and many fish scales, the upper parts are bathypelagic deposits, in which have been found, besides the melamphaids, fossils of the bathypelagic fish *Cyclothone* and of the pelagic crustacean *Pleuroncodes*. Miller (1951) described a new fossil species of petrel, *Oceanodroma hubbsi*, which was also found near the bathypelagic site. More recently, a grunion-like shallow water fish (Atherinidae) was uncovered. As suggested by Dr. Hubbs, it would appear from this stratification of faunas that the deposits originated in a shallow basin, which gradually deepened as a result of either a rise in sea level or a depression of the bottom.

Scopelogadus (?) *capistranensis*, new species

Fig. 1

The following description is mainly of the holotype. Information from an impression of a second, smaller specimen compliments data on numbers of pectoral and pelvic rays and

Table 1. Comparison of *Scopelogadus* (?) *capistranensis* with the 5 genera of Melamphaidae.

Proportions are in per cent standard length.

	S. capistranensis	*Scopelogadus*	*Melamphaes*	*Sio*	*Scopeloberyx*	*Poromitra*
Greatest depth of body	33	23-33	25-34	25-30	23-32	26-34
Predorsal length	52	43-54	39-47	45-52	46-56	44-57
Origin of dorsal to caudal base	50	54-60	57-64	53-56	50-58	50-61
End of dorsal to caudal base	32	32-40	29-37	....	26-33	27-38
Head length	45?	33-46	33-44	34-42	30-45	33-46
Tip of snout to back edge of preopercle	28?	19-28	21-28	22-26	25-34	23-35
Greatest depth of head	30	24-30	23-31	26-27	22-32	24-31
Snout to base of pectoral	47	34-43	34-42	34-40	28-47	35-45
The dorsal ray (no. from last) under which anal originates (±, directly under last ray; —, slightly behind)	4-5	3-6	(—)-5	(±), (—)	(±) 2 or 3	3-9
Snout to anal origin	64	55-66	62-75	65-68	61-75	56-74
Length of caudal peduncle	30	28-40	18-30	25-32	23-29	22-37
Depth of caudal peduncle	11	9-14	9-13	10-13	8-12	8-14
Length of upper jaw	17?	13-19	16-20	13-15	15-23	15-22
Total dorsal rays	12 or 13	12-13	17-21	12	13-15	13-17
Total anal rays	9 or 10	9	9-10	9	8-10	9-12
Precaudal vertebrae	10	10	11-12	10	10	9-10
Caudal vertebrae	14	13-17	14-18	16-17	14-17?	15-20
Serrations on angle of preopercle	Numerous small	Numerous small	Absent or few and large	Numerous, minute	Absent	Numerous or small or large
Total number of disagreements with genus	....	2	7	10	4	2
Number of meristic disagreements	....	0	3	1	1	1

the position of the pelvic fin relative to that of the pectoral. Additional characters are given in Table 1.

Body with greatest depth, at pelvic insertion, about 0.33 standard length. Caudal peduncle with length 2.5 times its least depth. Distance from tip of snout to base of first anal ray almost 0.7 standard length. Head large, 0.45 standard length; its depth about 0.7 its length; 3 or more weak spines faintly visible at posteroventral angle of preopercle. Branchiostegal rays at least 6.

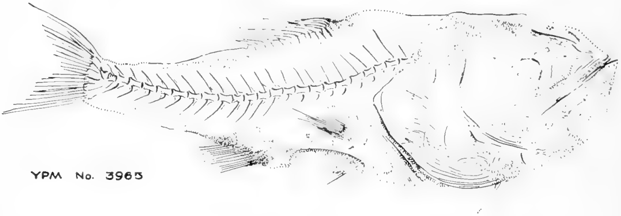

Fig. 1. *Scopelogadus* (?) *capistranensis,* holotype YPM No. 3965, 38.7 mm standard length.

Dorsal fin with about 13 rays (total); origin at middle of body: distance from tip of snout to base of first ray equals distance from this ray to base of caudal fin, which also equals distance from tip of snout to base of pectoral fin. Anal fin with 9 or 10 rays (total); originates under fourth from last dorsal ray. Pectoral fin with more than 12 or 13 rays, possibly 15. Pelvic fin with about 8 rays; inserts directly under pectoral. Caudal fin with 19 principal rays.

Vertebrae on holotype 10 precaudal plus 14 caudal (the first caudal vertebra overlies the first distinct haemal spine, the urostyle is counted as one element); in smaller specimen about 24 to 26. The arch of the first haemal spine apparently lacks the anteroventrally projecting spurs characteristic of some species in *Melamphaes* and *Scopeloberyx.*

MATERIAL

The types are two impressions of whole specimens, catalogued Yale University, Peabody Museum Paleontological Collections No. 3965. The larger, standard length 38.7 mm, is selected as holotype. The vertebral column and most of the fin rays are easily discernible on the holotype (Fig. 1). The impression of the smaller specimen is much fainter and therefore difficult to interpret. On the holotype are impressions of various head bones, including the line of fusion of the hyomandibular with the front of the preopercle, sections of the opercular series, parts of the jaws, branchiostegal rays, fin supports, and the caudal skeleton.

DERIVATION OF NAME

The species name *capistranensis* refers to the locality of discovery of the fossils.

IDENTIFICATION WITH *Scopelogadus*

The fact that *Scopelogadus* (?) *capistranensis* has 19 principal caudal rays and thoracic pelvic fins places it with the berycoid-like fishes. Its general shape, positioning of fins, numbers of fin rays, etc. further refer it to the Melamphaidae. A definite identification of the fossils with *Scopelogadus* was impossible, although the specimens are provisionally referred to this genus by virtue of comparisons with each melamphaid genus. In Table 1 are listed the only characters measureable on the fossils, along with ranges of values for all five melamphaid genera. At the bottom of each "genus column" are: first, the total number of characters whose ranges exclude values for *S. capistranensis* and second, this number of disagreements for meristic characters only. Both *Scopelogadus* and *Poromitra* had only two disagreements. Even though the next lowest proportion of disagreements, 4/18, of *Scopeloberyx* is not significantly different from 2/18 $X^2=0.20$ with one d.f., $0.75>p>0.45$), the fossils agree with *Scopelogadus* in both meristic counts and general overall shape, which associate them most strongly with this genus.

ACKNOWLEDGMENTS

I am indebted to Dr. Andreas B. Rechnitzer, formerly of the Scripps Institution of Oceanography, La Jolla and the Naval

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Postilla

YALE PEABODY MUSEUM

OF NATURAL HISTORY

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A MEROITIC TOMB INSCRIPTION FROM TOSHKA WEST

Bruce G. Trigger

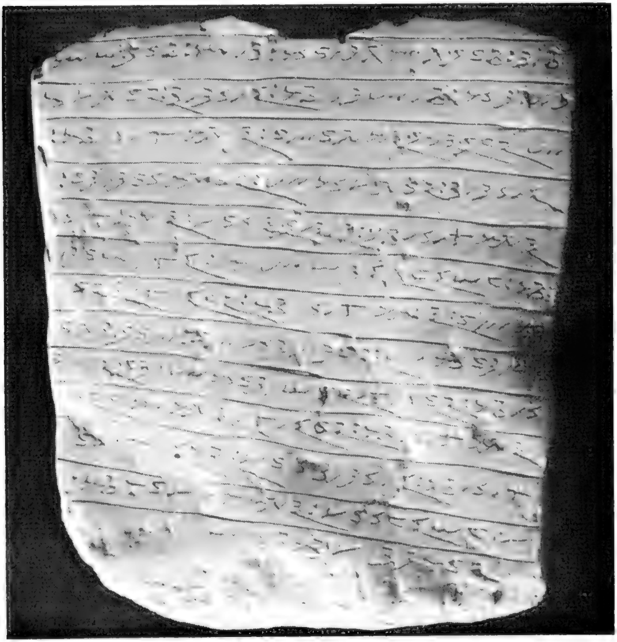
The Meroitic inscription presented herewith is the only funerary inscription to have been discovered by the University Museum of the University of Pennsylvania—Peabody Museum of Yale University Expedition to Egypt in the large cemetery (called TW-A) just north of the winter Post Boat station at Toshka West. The cemetery is in the north part of Toshka opposite Gebel Agg, and lies between the river and the hamlet of Duki Dawur. It was found to contain several hundred graves of the late Meroitic, X-group, and Nubian Christian periods. No reference to this cemetery is found in Emery's and Kirwan's (1935) report on their archaeological survey of this region. A description of the cemetery and of the work done there in 1961 and 1962 can be found in two preliminary reports on the work of the expedition written by its director, Professor William K. Simpson of Yale University. These have appeared in the *Illustrated London News* (1961) and in *Expedition*, the bulletin of the University Museum of the University of Pennsylvania (1962). The inscription, which was found during the 1962 field season, is illustrated on page 38 of the second article and on the cover of the issue.

The stela, on which the inscription was carved, was found face up and reused among the blocks in the largely denuded superstructure of a Christian grave numbered TW-A 198. The superstructure was of the type found by Monneret de Villard (1935: 132-141) at er-Rammal. Without much question the stela had been plundered from one of the Meroitic graves nearby for use as a building block. Since none of the Meroitic superstructures were preserved, however, it is impossible to discover from which grave it came. Funerary inscriptions were generally written either on offering tables or on stelae, more commonly the former. The stelae have a variety of shapes and apparently were set up in little shrines which projected from the front walls of the Meroitic superstructures (Griffith, 1911: 29). Sometimes representations of the deceased were painted or carved on these stelae, but more often there was only a text.

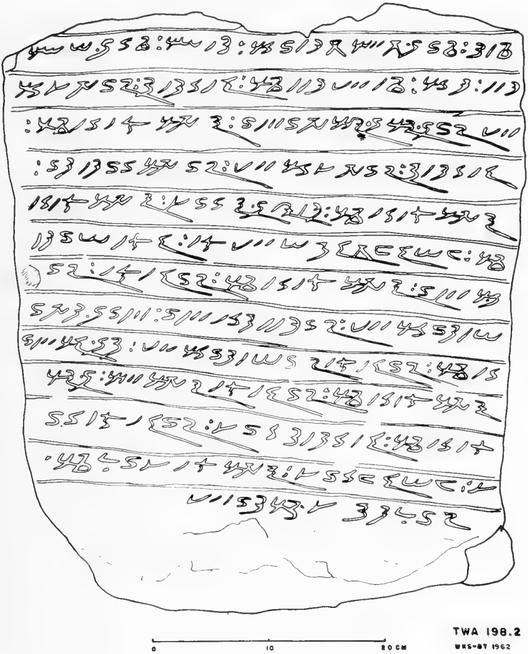
The Toshka West inscription is engraved on a block of grey, fine to medium grained Nubian sandstone. It has been given the Pennsylvania—Yale expedition number TW-A 198.2, and was assigned to the expedition for a subsequent division of finds between the University Museum and the Peabody Museum. The block is roughly rectangular, though the left side tapers slightly toward the base. Its measurements are: height 52 cm, width 40-45 cm, thickness 6.5-11 cm. The inscribed surface undulates slightly but is smooth except for some ridges in the lower right hand corner. These antedate the inscription. There is no evidence that this face was artificially worked, and it seems to be merely the natural, sand-scoured surface of a local rock exposure. This contrasts sharply with the carefully leveled surfaces of the fragments of two funerary stelae found by the expedition at Arminna West. The block was apparently quarried by scoring it along the sides and top edge and then prying it horizontally along the lines of natural bedding. The back is domed where large flakes were knocked marginally from the top and sides in order to lessen its weight. The sides were then smoothed near the upper face though traces of the scoring and prying still remain visible underneath. The upper edge, which suffered accidental chipping at a later time, was probably meant to be convex. Below the inscription the face of the block was quite rough, and no attempt was made to square this section. Presumably when the stela had been set up this part was covered over with mud plaster.

The rows of letters, which read from right to left, are separated by incised lines 2 mm wide and 2.5-4.5 cm apart. The ninth line from the top appears to have been engraved from both sides. The letters, which average about 1.5 cm in height (omitting tails) are engraved to a depth of 1 to 1.5 mm, about the same depth as the lines. The lines and the letters still have traces of the red paint used to accent the text. The whole surface of the stone, especially towards the bottom, is reddened, the coloration being clearly artificial and distinct from the natural pink color found in some of the Nubian sandstones. This no doubt represents the working out of pigment from the letters rather than a deliberate coloring of the whole surface of the block. A pronounced red line under the final row of letters, where presumably the stone was embedded in the superstructure, marks the termination of this reddening. This suggests that the pigment had been weathered while the stone was still *in situ.*

The similarity of some Meroitic letters, particulary *e* and *l*, and *m*, *š*, and *ẖ* creates a danger of error in transliteration, although a comparison of the form of letters found in recognizable phrases and words clears up most cases of uncertainty. The greatest margin of doubt must remain in the transliteration of personal names. Meroitic tombstones do not carry dates. Nevertheless, changes in the style of the letters may offer clues as to the general date of the inscription. Griffith (1911: 17-21) was able to distinguish three stages in the development of cursive Meroitic, and Hintze (1959), working on materials from Meroë, has recently published a more detailed paleographic table which gives the forms of letters associated with various reign dates. Although the study of Meroitic paleography is not yet sufficiently advanced to provide a real basis for dating inscriptions, the conclusions resulting from a comparison of this inscription with the forms given by Griffith and Hintze are of some interest. The form of the letters showing the most marked changes through time (Griffith 1911: 11) all belong to the later stages of the writing. In general, the letters most closely resemble the forms found in Griffith's columns 14 and 16. Column 14 belongs to the Transitional phase and is dated 25 B.C. to A.D. 250; 16 is Late and is dated A.D. 250 to 400. The rather equal distribution of resemblances suggests a date close to A.D. 250. Hintze's system provides a greater variety of forms, so much so that different forms of the same letter on our stone can often be placed in several columns. The temporal distributions of these placements are not, however, such as to be damaging to Hintze's system. The majority of forms are to be found in the columns dated A.D. 170-350 and A.D. 246-266.This dating seems in accord with the conclusions reached using Griffith's system. Two of Griffith's (1911: 33; 1912: 57) paleographically dated inscriptions which also bear the same introductory formula as does this one are dated to



the late period. Although a detailed report on the material from the Toshka cemetery has not yet been prepared, a date in the third century A.D. would not seem out of keeping for many of the Meroitic graves there.



Transliteration and Commentary

The following transliteration of the text follows Hintze's system. The arrangement of lines is that of the original. Words which are carried over from one line to the next are indicated by a hyphen. The colon is used to represent the Meroitic word divider. The text is divided into sections, each of which is de-noted by a letter of the alphabet. These sections will be discussed individually in the commentary.

1. (a) *wêš : wetñyiñqli : šêri : wetrri*
2. (b) *qê : mli : wês qêwi :* (c) *pêlmêš : adbli-*
3. *s atkitnideye : kditelêwi :*
4. (d) *pêlmêš : adblis : adilemême :*
5. *kditelêwi :* (e) *qntkleb : kditelê-*
6. *wi :* (f) *ḫrpḫñpẖrste : pteremê*
7. *tiye : kditelêwi :* (g) *apête : a-*
8. *rêmelis : aqêẖlêye : yetmde-*
9. *lêwi :* (h) *apête arêmelis : ẖtpiye*
10. *kditelêwi :* (i) *apêtekdiyi : tki-*
11. *telêwi :* (j) *pêlmêšleb : apêtele-*
12. *b : ḫrpḫleb : kditebetêwi :*
13. (k) *atêmšb : ẖ/š - i - ẖ/š - es*

Like all funerary texts this one consists of three sections, 1) an invocation usually addressed to Isis and Osiris, 2) the name and description of the person commemorated, and 3) a terminal formula or formulae, sometimes called a benediction.

Section (a) constitutes the introductory invocation. It is longer than the usual *wêši : šêreyi* (Isis, Osiris), since each of these god's names introduces another phrase terminating in *li* or *i*, which are believed to be vocative particles. The intervening phrases are apparently adjectives describing Isis and Osiris but their meaning is unknown (Griffith 1911: 34). There is a similar invocation on a stone of unknown provenience now in the Cairo Museum (Griffith 1912: 57). Another example occurs on funerary inscription 76 from Karanog, although here the second *ñ* is written *nê* and one stroke has been left out of the fifth letter of the second word. The first substitution is quite common, however, (Griffith 1911: 14) and in writing *yi* one stroke is commonly omitted (*ibid.*, 33). The alternative reading *wetñĉêinĉqeli* is impossible (*ibid.*, 13, section 3). A variant also occurs in inscription 4 from Faras (Griffith 1922: 570) in the second half of which *mklẖ* [Great God? (Griffith 1912: 57)] replaces the name of Osiris.

Section (b). This section gives the name of the deceased, which is referred to in the literature as the A name. As in some other inscriptions the name is introduced by the expression *qê*, which Griffith renders tentatively as "the honorable." The expression *qêwi* regularly follows the name of the deceased and it is not often separated from it by a word divider. Hence the name is *Mli-wês*, the prefix *mli* indicating that it is a woman's name (Griffith 1911: 55). This prefix is often separated from the rest of the name by a word divider.

Following this we find eight parallel phrases listing people who stand in some sort of relationship to the deceased. In their fullest form these phrases consist of a title, the person's name, and a word describing the relationship between him and the dead person. Griffith (1911: 38) called this last word the descriptive phrase. Grammatically it stands in apposition to the name of the deceased. The terminal particle *lêwi* (which sometimes replaces *qêwi* in the preceding phrase may either represent a copula or be for emphasis (*ibid.*, 35). Two descriptive phrases which very frequently occur in funerary inscriptions are absent here. These are *tedḫelêwi* and *terikelêwi*. The former follows the name of the mother (the B word) of the deceased, and the latter that of his father (the C word) and they seem to give a reading: A borne by the woman B, begotten of the man C. On the other hand six of the sections in this inscription contain the descriptive phrase *kditelêwi* which is unrecorded in Griffith's word lists. Griffith (1911: 38, 39) lists two forms beginning with *kdi* (which is believed to mean "woman"), *kdisbetêwi* and *kditêwi*, both of which are associated with feminine A names. Taking the forms which are known, it would seem to be composed of *kdi* (woman?) and *telêwi* (the locative particle plus the copula? *lêwi*). *Telêwi*, however, seems to be added only to place names (Griffith 1911: 23, 40). If, as conceivably might be the case, *te* was written here as a variant for *tê*, the genitive suffix, then this word might be closely related to *kditêwi* and be read "a woman? of A." But this sort of comparison, which has constituted the main approach to the study of Meroitic grammar so far, tends to provide little in the way of satisfactory solutions to such problems in the absence of a more fundamental break-through in the study of the language.

Sections (c) and (d). Despite the lack of a divider, the initial *s* in line 3 undoubtedly belongs with the final word on the preceding line. *Pêlmêš*, a variant *of plmêš* or *pelmêš*, is derived from the Egyptian *pꜣ ỉmy-r mšʿ* meaning *strategos* or commander. The form *pêlmêš adblis* does not appear in the word lists but seems to be a variant of *pelmêš adblitê*, with a genitive particle *s* substituted for the alternative (?) genitive particle *tê*. The expression is translated "commander of the land" or as Zyhlarz (1956: 33) has suggested "commander of the deserts." The closely related term "commander of the water" is written *pelmêš atêlis* and *pelmêš atêlit* (Griffith 1912: 64). The last portion of the name *Adilemême* is the same as that of the name *Arlemême* occurring in inscription 24 from Faras (Griffith 1922:583).

Section (e). *qntkleb* may be a person's name or it may consist of the root *qntk* plus the plural particle *leb*. Neither form could be located elsewhere. The *leb* ending would seem to make a personal name less likely.

Section (f). *ḫrpḫñ* and variants, a civil title believed by Griffith (1922: 567) to refer to the governor or leading person of a community, in rank inferior to a *paqar* and a *pesatê*. *pẖrs* (Pachoris) is the old name of Faras; *te* is the locative particle. Hence "a civil official in Pachoris."

Sections (g) and (h). *apête*, from the Egyptian *ỉpwty*, messenger or envoy; *arêmelis*, "of (the) Rome." Presumably the so-called *s*-genitive here has the force of a dative, as Griffith (1911: 72) himself has suggested. The considerable number of people holding this title would suggest that it is applied to individuals having dealings with Roman Egypt, perhaps to government sponsored traders. Hence the title may mean something like "agent to the Romans." *yetmdelêwi* is a common descripive phrase rendered as "cousin of" or "kinsman of" (Griffith 1912: 65).

Section (i). The first word seems to consist of *apête* plus *kzi* which is sometimes added to a noun to give it a feminine form.

Hence it would appear to read "a female ambassador." Here, however, it may well be used as a person's name as Griffith (1911:59) shows a variant to be used elsewhere. The terminal *yi* is unaccounted for. *tkitelêwi* seems to be another unlisted descriptive phrase.

Section (j). The first three words have been made plural by the addition of the suffix *leb*. This list of titles may either be resumptive or refer to *Mli-wês's* relatives (?) in general. The descriptive phrase used here would seem to be a plural form, since it contains a *b*-infix. But such a form has occurred only once before in an inscription commemorating a single person. This is in inscription 99 from Karanog, and Griffith (1911: 70) believed it to have been written inadvertently. Moreover the *têwi*-ending normally becomes *tebkwi* in the plural. Hence a completely different word or form may be involved. The ending *betêwi* occurs in inscriptions 89 and 125 from Karanog (See Griffith 1911: 40).

Section (k). The form *atê* introduces the terminal formula Type A, the commonest and invariably the first of a number of such titles. *atê* is rarely separated by a divider from the following letters, which in almost all the variants of this formula are *mš*. *mšb* is found in Type Ae (Griffith 1911: 46) but here any resemblance between our inscription and any of the varieties listed by Griffith ceases. The second word is very carelessly written and may be read several ways. It does not bear resemblance to any other of the types of terminal formulae, except perhaps a crude and unconvincing one to type F (Griffith 1911: 52), and hence it would appear that we have here only one formula. Griffith (*ibid.*, 46) suggests that the general meaning of this phrase is "abundant water may you drink," this wish being made on behalf of the deceased for his afterlife. The formation of the various forms is exceedingly speculative and no purpose could be served in discussing them here

CONCLUSIONS

As can easily be seen in the preceding discussion, there exists at present only a rudimentary understanding of the Meroitic language. The sound values of the letters have been generally established, names can be read, and certain loan words, mostly from Egyptian, have been recognized. The meaning of a small number of native words and some of the basic elements of grammar have also been established. Griffith's lexicons, which systematically arrange the known forms, should someday provide a substantial base for further work. But until either bilingual texts are discovered or the linguistic affiliations of Meroitic are worked out so that known cognate languages can provide a sound basis for systematic investigation, the hope of much progress in the understanding of Meroitic appears dim indeed. Until such a time the "translation" of even relatively simple and well-studied formulae such as appear on tomb inscriptions must remain an identification of known words and grammatical forms eked out with many others of vague or uncertain meaning as well as with guesses and blanks. With these limitations in mind we offer the following translation of the Toshka inscription:

(a) O (unknown adjective) Isis! O (unknown adjective) Osiris!

(b) (the honorable) *Mli-wês* (is here commemorated)

(c) a kinswoman of the commander of the deserts (land?) whose name is *Atkitnideye*

(d) a kinswoman of the commander of the deserts *Adilemême*

(e) a kinswoman of *Qntkleb* [or of *qntk*s]

(f) a kinswoman of the governor [or civil official] of Faras *Pteremêtiye*

(g) a kin [or a cousin] of the envoy to the Romans *Aqêẖlêye*

(h) a kinswoman of the envoy to the Romans *H̱tpiye*

(i) a relation (?) of *Apêtekdiyi* [or of a female ambassador],

(j) a relation (?) of commanders, envoys, and governors (?)

(k) (Abundant water may you drink in the afterlife.)

Despite plundering and reuse, this Meroitic funerary inscription from Toshka West has been preserved virtually intact. It appears to date from the third century and commemorates a woman whose name was *Mli-wês*. She has no specific titles, although this is often the case when women are commemorated. Her name is followed by a list of the names and titles of a number of individuals whom we presume to be her relatives. In spite of orthographic peculiarities all the titles which are listed are known, with the possible exception of *qntk*, if it is a title. Although close parallels exist for the name *apêtekdiyi*, we are not sure that it is here being used as a personal name. A search of the literature has failed to turn up occurrences of the other personal names in the inscriptions from the Meroitic cemeteries at Karanog, Shablul (Griffith 1911), and Faras (*ibid.*, 1922). The inscription is somewhat unusual in that the formulae giving the names of the parents of the deceased are lacking. Also several new descriptive phrases are found here.

This text is of interest since it one of the very few Meroitic funerary texts to have come from the Toshka-Arminna region, and the only one preserved intact. Junker (1925: 104) found a few fragments of broken funerary inscriptions in the Meroitic cemetery at Arminna East, and a few more have been found by the Pennsylvania-Yale expedition at the village site at Arminna West. These are as yet unpublished. Apart from a few graffiti scratched on rocks and a number of inscribed potsherds from both Toshka and Arminna, these constitute the entire corpus of Meroitic writing from this section of Lower Nubia.

ACKNOWLEDGMENTS

The 1962 excavations of the Peabody Museum of Yale University and the University Museum of the University of Pennsylvania were directed by Professor William K. Simpson of Yale University and were supported by the E. B. Coxe, Jr. Fund of the University Museum, a grant from the Bollingen Foundation, established by Mr. Paul Mellon, to Yale University, and by a grant of the Department of State through Public Law 480. The author's participation in this year's work was facilitated by a grant of the Augusta Hazard Fund of

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Postilla

YALE PEABODY MUSEUM

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NEW BIRDS FROM PALAWAN AND CULION ISLANDS, PHILIPPINES

S. DILLON RIPLEY AND D. S. RABOR

INTRODUCTION

BY D. S. RABOR

The Palawan Expedition of 1962 was sponsored jointly by the Yale Peabody Museum, the Entomology Section of the U. S. Army Medical Research and Development Command of the Office of the Surgeon General, under the auspices of the Bernice P. Bishop Museum, and by Silliman University at Dumaguete City, P. I. Collections were made on Palawan Island March 26 until May 18, 1962, working in southern Palawan from March 26 until April 21, 1962, and in northern Palawan from April 25 until May 18, 1962.

The main collecting localities in southern Palawan included the forested areas in the vicinity of the municipality of Brookes Point, from the sea coast up to about 6,700 feet to the top of the main peak of Mount Mantalingajan. Collecting camps were established at Macagua (sea level to 500 feet), Pinigisan (2,100-2,500 feet), Magtaguimbong (3,600-4,350 feet), and on the ridge and top of the peak of Mount Mantalingajan itself (5,000-6,700 feet).

The collecting localities in northern Palawan included Sitio Malabusog (sea level to 500 feet) of Barrio Tinitian, municipality of Roxas, and Sitio Tarabanan (sea level to 1,000 feet) of Barrio Concepcion, municipality of Puerto Princesa.

A small collecting party worked on Balabac Island from April 17 until May 2, 1962, and rejoined the main body of the expedition party in northern Palawan on May 5, 1962.

Mr. Max Thompson, Research Fellow of the Bernice P. Bishop Museum, who was a member of the expedition party, headed a small group that carried on additional collecting for the Bishop Museum, on Busuanga and Culion Islands of the Calamianes Group, north of Palawan, from May 20 until June 20, 1962, after the main party had already left for home. His collections of 141 birds from both islands were included in our study.

It is interesting to note that six months earlier, in August and September, 1961, a small collecting party of the Danish "Noona Dan" Expedition, together with two Filipino collectors from the Philippine National Museum, worked in the same collecting localities where we collected later on, with the exception of the ridge and top of the main peak of Mount Mantalingajan itself, which they failed to reach. Our collecting party made camps on the very camping sites of the Danish Expedition collectors in the lower elevations of the Mount Mantalingajan Range and even employed the same head mountain guide for the work in the highlands of Mount Mantalingajan.

Salomonsen (1961, Dansk. Ornith. Foren. Tiddsskr., vol. 55, p. 219-221; 1962, vol. 56, p. 129-134) reported and described one new species of tree-babbler, *Stachyris hypogrammica*, and two new subspecies, a mountain tailor-bird, *Orthotomus cucullatus viridicollis* and a mountain leaf-warbler, *Phylloscopus trivirgatus peterseni*, from the collections made by the "Noona Dan" collectors in southern Palawan.

Salomonsen reported six forms of true mountain birds which were taken by the "Noona Dan" collectors, which included the following:

1. *Zosterops montana*
2. *Muscicapa westermanni*
3. *Seicercus montis*
4. *Phylloscopus trivirgatus*
5. *Orthotomus cucullatus*
6. *Stachyris hypogrammica*

Our Palawan Expedition Party secured very good series of most of the above mentioned mountain birds, except *Seicercus montis*, of which only 5 specimens were taken by us. In addition, two more true mountain birds were collected by our party, increasing the list of true mountain birds from Palawan to 8. These forms are *Brachypteryx montana* and *Cettia Montana.*

We are reporting six new subspecies of birds from our recent collections on Palawan, most of them from the highlands of southern Palawan in the Mount Mantalingajan localities, and from the Calamians. It is very possible that the highlands of northern Palawan, notably in the localities of Cleopatra's Needle, the high peak which dominates this area may still yield additional forms distinct from those that we have collected in the Mount Mantalingajan localities of southern Palawan. The highlands of northern Palawan remain as still another largely unworked locality.

We are indebted to the authorities of the American Museum of Natural History and of the Chicago Natural History Museum for the use of some of the comparative materials in our present study.

D. S. Rabor acknowledges his indebtedness to the Frank M. Chapman Memorial Fund of the American Museum of Natural History, to the Entomology Section of the U. S. Army Medical Research and Development command of the Office of the Surgeon General, and to the Yale Peabody Museum, for the research grants, which enabled him to come to the United

States to study and prepare the report on the present bird collections from Palawan, Balabac, and the Calamian Islands of Culion and Busuanga, in collaboration with Dr. Ripley.

NEW SUBSPECIES FROM PALAWAN

BY

S. DILLON RIPLEY AND D. S. RABOR

Ninox scutulata palawanensis, subsp. nov.

TYPE: Yale Peabody Museum No. 73202 from Tarabanan, Concepcion, Puerto Princesa, Palawan Island, Philippines, sea level to 1,000 feet elevation. Adult male collected May 8, 1962 by D. S. Rabor.

DIAGNOSIS: Similar to *N. sc. randi* of most of the larger Philippine islands in the reddish chocolate-brown upper- and underparts, but decidedly smaller. Slightly smaller than *N.* sc. totogo of Botel Tabago but lighter brown on upperparts with decidedly more reddish wash; light parts on the streaked individual feathers of underparts purer white with much less buff, and brown streaks darker: blackish tail bands similar in width, number and location on tail feathers, but brown bands in *palawanensis* tinged more ashy. Closest to *Ninox scutulata borneensis* in size, but upperparts slightly darker brown with more red wash; blackish tail bands much narrower, more in number and darker, and the brown bands tinged more ashy.

MEASUREMENTS: *N. sc totogo* from A'Oshima, Loo Choo Islands, and Okinawa: Wing ♂ (2) 214, 210, ♀ (5) 204-212.5 (av. 208.5); tail ♂ (2) 119, 115, ♀ (5) 111.5-118 (av. 115.6); culmen from base ♂ (2) 24.5, 23.5, ♀ (4) 23.5-25 (av. 24.5); tarsus ♂ (2) 26, 24.5, ♀ (5) 25-26.5 (av. 26 mm). *N. sc. borneensis* from Borneo: Wing ♂ (4) 176-184.5 (av. 179.6), ♀ (2) 182.5, 176, sex ? (4) 183-187.5 (av. 185.6) tail ♂ (4) 98-102 (av. 99.5), ♀ (2) 96.5, 96, sex ? (4) 94-104 (av. 100.1); culmen from base ♂ (4) 21.5-22.5 (av. 22.1), ♀ (2) 22, 22.5, sex ? (4) 21.5-24 (av. 22.2); tarsus ♂ (4)

23-25 (av. 24.4), ♀ (2) 24.5, 23.5, sex ? (4) 22.5-24 (av. 23.6 mm). *N. sc. palawanensis* from Palawan Island. Wing ♂ 195.5; tail 108; culmen from base 23.5, tarsus 25 mm.

Range: Palawan Island.

Remarks: The three races *totogo, borneensis* and *palwanensis* are lightly differentiated from one another, based on plumage coloration. In size, however, *palawanensis* is intermediate between *totogo* and *borneensis.*

Pitta erythrogaster thompsoni, subsp. nov.

Type: Yale Peabody Museum No. 73203 from 6.5 km southwest Culion, Culion Island, Philippines. Adult male collected June 7, 1962 by Max C. Thompson. Orginial field no. BBM-PI 3290, Bernice P. Bishop Museum.

Diagnosis: Closest to *P. e. propinqua* of Palawan and Balabac Islands but back, rump, tail and scapulars pale blue, not cobalt. Differs from *P. e. erythrogaster* in the much paler blue of back, rump, tail and scapulars, and in the much narrower dull green band on mantle, as in *propinqua.*

Measurements: *P. e. propinqua* from Palawan: Wing ♂ (3) 96-100 (av. 98); tail ♂ (3) 34-36.5 (av. 34.8); culmen from base ♂ (3) 13.5-14.5 (av. 14); tarsus ♂ (3) 32-33.5 (av. 32.8 mm); weight ♂ (3) 50.7-53.4 (av. 51.2 grams).

P. e. erythrogaster from Luzon: Wing ♂ (4) 96.5-99 (av. 97.5), ♀ 99.5; tail ♂ (4) 32-37.5 (av. 35.1), ♀ 34.5; culmen from base ♂ (2) 23.5, 23.5, ♀ 23; tarsus ♂ (4) 33.5-35.5 (av. 34.2), ♀ 35 mm; weight ♂ (4) 56.2-69 (av. 63.3), ♀ 55.2 g.

P. e. erythrogaster from Mindanao: Wing ♂ (2) 98.5, 100.5, ♀ (2) 95.5, 98; tail ♂ (2) 36.5, 33.5, ♀ (2) 32, 34; culmen from base ♂ (2) 23.5, 24, ♀ 22; tarsus ♂ (2) 35.5, 35.5, ♀ (2) 34, 34.5 mm.

P. e. erythrogaster from Negros: Wing ♂ (3) 98-100.5 (av. 99.5), ♀ 99; tail ♂ (3) 33-35.5 (av. 34.3), ♀ 32; culmen from base ♂ (3) 22-23.5 (22.6), ♀ 23; tarsus ♂ (3) 33-33.5 (av. 33.3), ♀ 33.5 mm.

P. e. erythrogaster from Samar: Wing (sex?) 94.5; tail 35.5; tarsus 33 mm.

P. e. erythrogaster from Bongao: Wing ♂ 95; tail 36.5; culmen from base 22; tarsus 35 mm.

P.e. thompsoni from Culion: Wing ♂ (2) 94.5, 94; tail 35, 36; culmen from base 22.5, 23.5; tarsus 33, 34.5 mm.

Range: Culion Island.

Remarks: The Negros population of *P. e. erythrogaster* comes closest to *P. e. thompsoni* in the intensity of the blue color on the back, rump, tail and scapulars, but the Culion form is still paler on these parts. Also, the dull green band on the mantle in the Negros birds is much wider as is characteristic of *erythrogaster.*

We take great pleasure in naming this form after Mr. Max C. Thompson, Research Fellow of the Bernice P. Bishop Museum, the young collector who was a great help in the field work in Palawan, Balabac, and the Calamians.

Brachypteryx montana sillimani, subsp. nov.

Type: Yale Peabody Museum No. 73204, from Magtaguimbong, Mount Mantalingajan, 3,600-4,350 feet, Palawan Island, Philippines. Adult male collected April 11, 1962, by D. S. Rabor.

Diagnosis: Closest to *B. m. poliogyno* of northern (northwestern) Luzon and Mindoro, and *B. m. andersoni* of southern Luzon, but differs in the following characteristics: a) Male averages much brighter and richer slate-blue upper- and underparts, with much less wash of gray on abdomen; b) female with much duller rusty brown undertail coverts; c) longer culmen.

MEASUREMENTS: *B. m. poliogyna* from northern Luzon: Wing, ♂ (3), 65-68.5 (av. 66.6); ♀ (2) 68.5, 62.5; tail, ♂ (3) 45.5-47 (av. 46.3), ♀ (2) 46, 40; culmen from base, ♂ (3) 15.5; ♀ (2) 16.5, 15.5; culmen from anterior margin of nostril, ♂ (3) 8.5, ♀ (2) 9, 8.5; tarsus, ♂ (3) 26-27.5 (26.5), ♀ (2) 28, 27.

B. m. poliogyna from Mindoro: Wing, ♂ (5) 65.5-67.5 (av. 66.7), ♀ (3) 60.5-64 (av. 62.3); tail, ♂ (5) 45-46.5 (av. 46), ♀ (3) 41-43 (av. 42); culmen from base, ♂ (5) 15.5-17 (av. 16.2), ♀ (3) 15.5-17 (av. 16.3); culmen from anterior margin of nostril, ♂ (5) 8.5-9 (av. 8.9), ♀ (3) 8.5-9.5 (9); tarsus, ♂ (5) 28-29.5 (av. 28.5), ♀ (3) 26-29 (av. 27.6).

B. m. andersoni from southern Luzon: Wing, ♂ (2) 71, 66, ♀ (2) 63.5; tail, ♂ (2) 45.5, 47, ♀ (2) 42.5, 43; culmen from base, ♂ (2) 16.5, 16, ♀ (2) 16.5, 16; culmen from anterior margin of nostril, ♂ (2) 9, 8.5, ♀ (2) 9; tarsus, ♂ (2) 28.5, ♀ (2) 28, 27.

B. m. sillimani from southern Palawan: Wing, ♂ (3) 68-70.5 (av. 69), ♀ (3) 63-68 (av. 66); tail, ♂ (3) 46.5-48 (av. 47.3), ♀ (3) 42-45 (av. 42.3); culmen from base, ♂ (3) 17-17.5 (av. 17.3), ♀ (3) 17-18 (av. 17.5); culmen from anterior margin of nostril, ♂ (3) 9-9.5 (av. 9.3), ♀ (3) 9-10 (av. 9.5); tarsus, ♂ (3) 27-29 (av. 28.1), ♀ (3) 27-28 (av. 27.6).

RANGE: The highlands of southern Palawan as far as known.

REMARKS: In the male, the Palawan form is the brightest and richest in coloration of plumage, with the least powdery gray wash on the slate-blue color, both on the upper- and underparts, when compared to males of other races of the species in the Philippines, Borneo, and Sumatra. The female of this race also averages brighter and richer slate-blue on the upperparts than those of the other races.

The Palawan birds resemble most closely those of northern Luzon

The species is recorded for the first time on Palawan Island

and is a new addition to the recently known mountain bird fauna of this island.

The various races of the species within the geographic unit of the Philippines include:

B. m. poliogyna—northern (northwestern) Luzon,
B. m. andersoni—southern Luzon,
B. m. brunneiceps—Negros,
B. m. mindanensis—Mt. Apo, Mindanao,
B. m. malindangensis—Mt. Malindang, Mindanao,
B. m. sillimani—southern Palawan.

Some of the larger islands with highlands attaining elevations of 3,000 feet or more may have representatives of this species that remain to be discovered. In southern Luzon, in the Mount Isarog localities, the species ranges as low as 2,200 feet along shaded banks of mountain streams.

The new race is named after Dr. Robert B. Silliman, Vice-President of Silliman University, Dumaguete City, Negros Oriental, Philippines, for his interest in and active stimulation of biological research in the university.

Muscicapa westermanni palawanensis, subsp. nov.

TYPE: Yale Peabody Museum No. 73205 from Mount Mantalingaian Peak, 5,500-6,000 feet, Palawan Island, Philippines. Adult female, collected April 14, 1962 by D. S. Rabor.

DIAGNOSIS: Like *M. w. rabori* and *M. w. westermanni* but differs in: a) bill decidedly more robust than that of either, as shown by the comparative index derived from the ratio between length of culmen from base and width of maxilla at level of frontal feathering; b) in the female, the upperparts being a purer, darker slate gray, and with the tawny-olive wash on the back and rump still further reduced; c) longer wing and tail.

MEASUREMENTS: *M. w. palawanensis*: wing ♂ (5) 58.5-61 (av. 59.5), ♀ (1) 55.5; tail ♂ (5) 42.5-44 (av. 43.3); ♀ (1) 40; culmen from base ♂ (5) 13-13.5 (av. 13.3) , ♀ (1) 13; width of bill at level of frontal feathering ♂ (5) 4.6-5.5 (av. 4.9), ♀ (1) 5.1; tarsus ♂ (5) 13.5-14.5 (av. 14 mm).

M. w. rabori: wing ♂ (9) 55.5-59.5 (av. 57.9), ♀ (3) 55-57 (av. 56); tail ♂ (9) 39-43 (av. 41.2), ♀ (3) 39-41, (av. 39.8); culmen from base ♂ (9) 12-13.5 (av. 12.8), ♀ (3) 12-13 (av. 12.3); width of bill at level of frontal feathering ♂ (9) 3.8-4.9 (av. 4.4), ♀ (3) 4-4.4 (av. 4.2); tarsus ♂ (9) 14-15.5 (av. 14.6), ♀ (3) 13.5-15 (av. 14.3 mm).

M. w. westermanni: wing ♂ (16) 55-57.5 (av. 56.2), ♀ (10) 52.5-58.5 (av. 54.7); tail ♂ (16) 39-41.5 (av. 40), ♀ (10) 37-39.5 (38.5); culmen from base ♂ (16) 12-13.3 (av. 12.5), ♀ (10) 12-13 (av. 12.5); width of bill at level of frontal feathering ♂ (16) 4-4.6 (av. 4.3), ♀ (10) 4-4.6) (av. 4.4); tarsus ♂ (16) 13.5-15 (av. 13.9), ♀ (10) 14-14.5 (av. 14.2 mm).

RANGE: Mountains of southern Palawan Island, Philippines, as far as known.

REMARKS: The Palawan males are indistinguishable from the males of the various Philippine races of the species, as is characteristic of this particular species if based on plumage coloration and color pattern.

The main bases for naming the Palawan population are: a) the decidedly more robust bill in both sexes compared to that of any other race of this species; b) the distinctive plumage coloration of the female; and c) the longer wing and tail lengths as compared to that of the other races in the Philippines. In order to arrive at comparative figures which determine the comparative degrees of heaviness of the bill in the various Philippine races, we are using the ratio of the length of culmen from base to the width of maxilla at level of frontal feathering. We call this figure the "index of bill heaviness." The lower this figure is, the more heavy or robust the bill. We included the figure for both sexes to arrive at indices which will give a general idea as to the average heaviness of the bill in either sex of a particular race.

The indices for bill heaviness of the races in the Philippines are:

M. w. palawanensis—2.70 (5 ♂, 1 ♀).
M. w. westermanni—2.87 (16 ♂, 10 ♀).
M. w. rabori—2.91 (9 ♂, 3 ♀).

Cettia montana palawana, subsp. nov.

Type: ♂ ad (Y.P.M. No. 54238), collected April 12, 1962, by D. S. Rabor on Mount Mantalingajan, 6,700 feet, Palawan Island, Philippines.

Diagnosis: This form differs strikingly in color from the other subspecies of *Cettia montana* from India east to Laos and south to Sumatra and Borneo. In olivaceous brownish tone this population is paler than *sepiaria* and more olive, less warm brown than *oreophila*, but altogether darker, more suffused than mainland birds. Olive yellow is on the throat and abdomen with warm olive brown on the flanks and invading the breast in a light wash in some specimens forming an incomplete breast band. These yellowish throat feathers tend to be streaked along the shaft and adjacent areas of the vanes with dull ashy, difficult to see on account of the make-up of the skins. This yellowish tone of the underparts is strikingly different from all other forms of *Cettia montana*. Like other Palawan animals, however, this warbler points up the Southeast Asian affinities of this island.

Measurements: Type: wing, 54.5; tail, 56; culmen from base, 15.5; culmen from anterior margin of nostril, 8.5; tarsus, 22 mm. Seven other males measure: wing, 54.5-57.5 (av. 55.8); tail, 55.5-60 (av. 57.6); culmen from base, 14.5-15.5 (av. 15.1); culmen from anterior margin of nostril, 8-8.5 (av. 8.4); tarsus, 20-22.5 (av. 21.6). Six females measure: wing, 51-55.5 (av. 52.4); tail, 47.5-54 (av. 51.5); culmen from base, 13.5-16 (av. 14.9); culmen from anterior margin of nostril, 8-8.5 (av. 8.4); tarsus, 21-22 (av. 21.3).

Range: Mountains of Palawan Island, Philippines.

Remarks: Stays singly or in pairs among the dense tangles and low stunted growth on the mountain ridges, always actively hopping from branch to branch, all the while giving out its very characteristic short note. Frequently the course of the bird may be followed by the sound of these notes, even though the bird itself may not be visible among the dense growth.

The species is recorded for the first time on Palawan, and in the Philippines, as a geographical unit and is a new addition to the recently known mountain birds of this island.

Lonchura leucogastra palawana, subsp. nov.

TYPE: Yale Peabody Museum No. 73206 from Macagua, Brooke's Point, sea level to 250 feet, Palawan Island, Philippines. Adult male, collected April 3, 1962 by D. S. Rabor.

DIAGNOSIS: Closest to *L. l. manueli* in the deep chocolate brown on chest becoming blackish brown to almost black on throat and chin, but differs in: a) having the deep chocolate brown on the chest, and the blackish brown or black on the neck, throat and chin occupying a decidedly much larger area up the sides of the neck and face; b) having a smaller bill.

MEASUREMENTS: *L. l. palawanas*: Wing ♂ (14) 48.5-51.5 (av. 50.3), ♀ (14) 49-52.5 (av. 49.9); tail ♂ (14) 33-36.5, ♀ (14) 31.5-37.5 (av. 35.4); length of culmen ♂ (14) 11.5 13 (av. 12.4), ♀ (14) 11-13 (av. 12); greatest width of culmen ♂ (14) 7.5-8 (av. 7.5), ♀ (14) 7-7.5 (av. 7.4); bill index ♂ (14) 19-20.5 (av. 19.2), ♀ (14) 18.5-20.5 (av. 19.5); tarsus ♂ (14) 12.5-13.5 (av. 13), ♀ (14) 12-13.5 (av. 13 mm).

L. l. leucogastra: Wing ♂ (7) 47.5-50 (av. 49.2), ♀ 50.5; tail ♂ (7) 27-35.5 (av. 33), ♀ 33; length of culmen ♂ (7) 10.5-12 (av. 11.6), ♀ 12; greatest width of culmen ♂ (7) 6.5-7 (av. 6.7), ♀ 6.5; bill index ♂ (7) 17-19 (av. 18.3), ♀ 18.5; tarsus ♂ (7) 12.5-13.5 (av. 13), ♂ 13.5 mm.

L. l. castanonota: Wing ♂ (2) 49.5, 50.5; ♀ (2) 49; tail ♂ (2) 33.5, 34, ♀ (2) 33.5, 36.5; length of culmen ♂ (2) 11.5, 12, ♀ (2) 12, 12.5; greatest width of culmen ♂ (2) 7, ♀ (2) 7, 7.5; bill index ♂ (2) 19.5, 20, ♀ (2) 20, 20.5; tarsus ♂ (2) 12.5, 13, ♀ (2) 13 mm.

L. l. everetti: Wing ♂ (9) 50-54 (av. 51.3), ♀ (7) 50-52 (av. 50.6); tail ♂ (9) 33-37.5 (av. 35.3), ♀ (7) 34-37.5

(av. 36.4); length of culmen ♂ (9) 12-12.5 (av. 12.3), ♀ (7) 11.5-13 (av. 12.3); greatest width of culmen ♂ (7) 7.5-8.5 (8), ♀ (6) 7.5-8.5 (av. 7.9); bill index ♂ (7) 19.5-21 (av. 20.3), ♀ (6) 19.5-20.5 (av. 20.3); tarsus ♂ (9) 12-13.5 (av. 13.1), ♀ (7) 12-13.5 (av. 13 mm).

L. l. manueli: Wing ♂ (7) 50.5-55 (av. 51.9), ♀ (4) 48-54 (av. 51.6); tail ♂ (7) 33-37.5 (av. 36.2), ♀ (4) 32.5-35 (av. 33.8); length of culmen ♂ (7) 12.5-13 (av. 12.8), ♀ (4) 12.5-13.5 (av. 13); greatest width of culmen ♂ (7) 8-8.5 (av. 8), ♀ (4) 7.5-8.5 (av. 8); bill index ♂ (7) 20.5-21.5 (av. 20.4), ♀ (4) 20-22 (av. 21.1); tarsus ♂ (7) 12.5-13.5 (av. 13), ♀ (4) 13-13.5 (av. 13.4 mm).

L. l. smythiesi: Wing ♂ 51.5, ♀ 50.5; tail ♂ 31, ♀ 33; length of culmen ♂ 12, ♀ 13; greatest width of culmen ♂ 7.5, 8; bill index ♂ 19.5, ♀ 21; tarsus 13, ♀ 13.5 mm.

We follow Parkes' measurement of the bill index, the index derived from the sum of the greatest length of culmen plus its greatest width.

Range: Palawan, Busuanga and Culion as far as known in the Philippines; the highlands of eastern and northern Borneo.

Remarks: Parkes (1958, Proc. U. S. Nat. Museum, vol. 108, no. 3402, p. 279-284) reviewed the taxonomy and nomenclature of this species and described two new races, bringing the total number of races that he recognized for the species to five. He gave the ranges of these various races as:

L. l. leucogastra—Thailand, Malay Peninsula, and Sumatra.

L. l. castanonota—Southern Borneo.

L. l. everetti—Luzon and the adjacent islands of Mindoro, Catanduanes, and Polillo, in the Philippines.

L. l. manueli—Southern half of the Philippine Archipelago and the highlands of northern Borneo, eastern Borneo, and Sarawak.

L. l. smythiesi—Known only from the vicinity of Kuching, Sarawak, Borneo.

Parkes had some Palawan specimens in his studies of this species and he included them with the variable *manueli*. In this connection he commented that "Although, as mentioned above, *manueli* is quite constant in its characters for a bird whose range encompasses so many islands, there is a certain amount of intraracial variation present. The most noticeable of these variations is a tendency for Palawan specimens to have smaller bills than those of the other islands within the range of *manueli* as here defined."

Our material, considering only the fully adult and properly sexed specimens, consists of 8 (7 ♂, 1 ♀) *L. l. leucogastra*, 4 (2 ♂, 2 ♀) *castanonota*, 16 (9 ♂, 7 ♀) *everetti*, 11 (7 ♂, 4 ♀) *manueli*, 2 (1 ♂, 1 ♀) *smythiesi*, and 28 (14 ♂, 14 ♀) *palawana*. Our material of *palawana* includes 23 birds from Palawan, two from Busuanga, one from Culion, and two from northern Borneo. In addition, we also examined but did not include the measurements, of two adult Palawan specimens of undetermined sex.

In studying the various races of *L. leucogastra*, especially those which are found in the Philippines, we made the following observations:

a) *Age of birds and their plumage.* Immature and subadult birds of the three Philippine races are indistinguishable from one another. Only fully adult birds show to the best advantage the characters which are of any value in differentiating the various races.

b) *Color of upperparts. L. l. castanonota* differs distinctively from the other races in having the deep rufous chestnut upperparts. The other races differ very slightly from one another in the general colors of the upperparts in being brown streaked with white on the back and crown. There is a tendency, however, toward a very gradual deepening in the intensity of the brown upperparts in the various races (excluding *castanonota*), starting from *everetti* as the lightest and ending with *leucogastra*, in the order *everetti* → *smythiesi* → *manueli* → *palawana* → *leucogastra*.

The degree of development of the white shaft streaks on the feathers of the back up to the crown is a very variable character, even within the same race, and depends much on the age of the individual bird and the freshness of its plumage. Within the same population, in any one race, there are individuals where these white shaft streaks have totally disappeared from the crown, giving this part a uniform color. These white shaft streaks are not as well pronounced on the back in some birds and yet are very distinct in others of the same race and from the same population of a particular locality.

c) *Upper tail coverts.* There is a gradual increase in the degree of intensification from the original plain brown upper tail coverts, which hardly contrast from the plain brown color on the rump and lower back in *smythiesi,* to deeper brown, blackish brown, blackish, and finally to black in *castanonota.* Among the races there is also a tendency for this color on the upper tail coverts gradually to invade the rump, thus increasing the area that it occupies. We summarize below the condition of the upper tail coverts in the various races:

L. l. smythiesi—plain brown, almost with no contrast to the rest of the rump and back.

L. l. everetti—plain brown with tendency to be slightly more intense than the rump and lower back, thus beginning to show a contrast.

L. l. manueli—darker brown, contrasting distinctly with the rump and the rest of back, but covers only a small area of the upper tail coverts.

L. l. palawana—blackish brown contrasting distinctly with the rump and rest of back, occupying a larger area on the upper tail coverts than in *manueli,* and in some specimens already beginning to show the tendency to invade the rump.

L. l. leucogastra—deeper blackish brown to almost black, this color having invaded the greater part of the rump or all of it, the whole area contrasting distinctly with the rest of back.

L. l. castanonota—very intense blackish brown to black, occupying the upper tail coverts and the rump, and contrasting distinctly with the rest of back.

d) *Anterior underparts.*

L. l. smythiesi—chocolate brown, becoming deeper and richer on throat and chin.

L. l. everetti—chocolate brown, becoming deeper and richer on throat and chin, as in *smythiesi.*

L. l. manueli—deep chocolate brown on the chest, becoming blackish brown on throat and chin, these colored areas being separated by a wide band of light brown on the sides of the chest and neck from the upperparts.

L. l. palawana—as in *manueli,* deep chocolate brown on the chest becoming blackish brown to black on throat and chin, but these colored areas occupying a decidedly much larger portion of the chest, neck, throat and chin, so that the plain brown band separating them from the upperparts is very much reduced.

L. l. leucogastra—the entire anterior underparts very intense blackish brown to black, this color extending up the sides of the chest, neck, throat and chin, coming in direct contact with the much lighter brown of the upperparts.

L. l. castanonota—as in *leucogastra,* with the tendency to be black instead of intense blackish brown.

The newly-described race is intermediate between *manueli* and *leucogastra* in color pattern. When the various races (excluding *castanonota,* because it is easily differentiated from the others) are arranged in the order of increasing intensity of the colors of the upperparts and underparts, the following arrangement results:

smythiesi → *everetti* → *manueli* → *palawana* → *leucogastra.*

We did not have the opportunity to examine specimens from the Sulu Archipelago but Parkes found the two birds that he examined to be small-billed. a condition similar to the

Palawan race. From this character and from geographic consideration we are inclined to include the Sulu Archipelago birds with the race *palawana*. The Philippine races of *L. leucogastra* have the following ranges:

L. l. everetti—Luzon and the adjacent islands of Mindoro, Catanduanes, and Polillo.

L. l. manueli—Central and southern Philippines.

L. l. palawana—Palawan, Busuanga, Culion, Sulu Archipelago.

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REVISION OF THE TYPE SPECIES OF THE ORDOVICIAN NUCULOID PELECYPOD GENUS *TANCREDIOPSIS*

A. LEE MCALESTER

ABSTRACT

The type species of the early Paleozoic nuculoid pelecypod genus *Tancrediopsis* Beushausen, 1895, is shown to be *Ctenodonta contracta* Salter, 1859, from Middle Ordovician rocks of southern Quebec, Canada. This species is redescribed from a series of 189 well-preserved silicified specimens, about half of which were collected at the original type locality. This large sample permits the definition of limits of variation in the species and reveals previously unknown morphologic features, among which are strong pedal muscle scars and external escutcheonal perforations. The species is easily confused with closely related sympatric species of *Tancrediopsis,* and criteria are discussed for distinguishing it from these similar forms. The correct name for *"Ctenodonta" contracta* Salter is shown to be *Tancrediopsis cuneata* (Hall).

INTRODUCTION

This paper is the first in a projected series to be devoted to generic-level revisions of the systematics and phylogeny of Paleozoic nuculoid pelecypods. As a vital first step toward clarifying the early history of this common and long-ranging group, a restudy is being made of the type species of each generic name that has been proposed for Paleozoic nuculoids.

This redescription of the generic type species is being patterned directly on a study of Paleozoic gastropod type species which has been compiled by Knight (1941). As in Knight's work, it is planned to make these redescriptions as objective as possible by basing them only on known original specimens of the species involved (see Knight, 1941, p. 1, for an excellent discussion of the value of objectivity in such work). An exhaustive search of the literature has indicated that about 60 names have been proposed for Paleozoic pelecypod genera which have at sometime been considered to show taxodont dentition or other evidence of nuculoid affinities.[1] The redescription of the primary types of the type species of these genera is now about half completed, and it is expected that these revisions will be submitted for publication as one unit within a year.

As a further step toward understanding the morphology, adaptations, and phylogeny of Paleozoic nuculoid genera, a much longer range program is planned for assembling and studying additional non-type material of the type species of many of these genera. In this program, particular emphasis will be placed on genera that cannot be adequately understood from the surviving original type specimens. Every effort will be made to assemble enough material of each species to permit the application of modern concepts of population systematics for determining the true nature and variability of specific and generic characters. It is planned to publish these more comprehensive revisions intermittently, one genus at a time, as adequate material of the type species can be assembled. This paper is the first of this series of type species revisions based on additional material that was not available to the original author of the species. It treats the common Ordovician nuculoid genus *Tancrediopsis* Beushausen (1895), whose type

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[1] The term "nuculoid" is used here in the broadest sense to include all *Nucula*-like forms from Paleozoic rocks. In practice, this means all Paleozoic pelecypods with taxodont dentition, because the convergent development of such dentition in other unrelated groups, such as arcids and the fresh-water genus *Iridina,* did not take place until after the close of the Paleozoic. As thus defined, "nuculoid" is approximately equivalent to the Subclass Protobranchiata (other than the Solemyidae) which has recently been suggested to include all pelecypods with protobranch ctenidia (see Cox, 1959).

species, *Ctenodonta contracta* Salter (1859), has never been adequately understood.

This revision of *Ctendonta contracta* is based on Salter's 15 original specimens from the Geological Survey of Canada collections, supplemented by an excellent series of 174 silicified specimens from the collections of the Yale Peabody Museum. About half of these additional specimens are from the original type locality of the species. The Yale material was collected in the early years of this century by C. E. Beecher and P. E. Raymond as a part of an ambitious program of restudy of important silicified early Paleozoic faunas of eastern North America. Many hundreds of pounds of rock from several localities were collected and etched, but the program was cut short by Beecher's untimely death in 1904, with the result that this great wealth of material has never been studied. The etched Middle Ordovician collections have now been sorted for pelecypods and have yielded about 1500 identifiable specimens. These collections are particularly rich in well-preserved nuculoid species, and it is expected that this material will provide a basis for future studies on the earliest evolutionary radiation of this important group of pelecypods.

I am most grateful to the National Science Foundation for support of these studies of Paleozoic nuculoid pelecypods under its Program for Systematic Biology, Division of Biological and Medical Sciences (Grant No. G19961). I am also greatly indebted to D. J. McLaren, T. E. Bolton, and G. W. Sinclair of the Geological Survey of Canada for the loan of Salter's types and for generous cooperation on this project. Finally, I wish to thank D. W. Harvey and Martha Erickson for their skillful preparation of the photographs and drawings, and C. J. Durden, who made the preliminary sorting of the silicified Peabody Museum material.

Genus *TANCREDIOPSIS*

Author. Beushausen, 1895, p. 70.

Type Species. *Ctenodonta contracta* Salter (1859, p. 37) [=*Tellinomya cuneata* Hall, 1856, p. 392] by subsequent designation of Cossmann, 1897, p. 94.

Discussion. Most Ordovician nuculoid pelecypods have been described under the generic name *Ctenodonta* Salter, 1852, which has as its type the large and distinctive, but rather uncommon Ordovician species *Ctenodonta nasuta* (Hall), 1847 (see Wilson, 1956, pl. 2 for illustrations of this species). In an attempt to subdivide further the complex of species traditionally assigned to "*Ctenodonta*," Beushausen proposed the subgeneric name *Tancrediopsis* for more common, smaller, early Paleozoic nuculoids typified by the Ordovician species *Ctenodonta contracta* Salter (1859) and the Silurian species *Nucula sulcata* Hisinger (1841), both of which were originally designated by Beushausen as the "types" of his new subgenus. The first subsequent designation of one of these species as the type of the subgenus was made by Cossmann two years after the original description (1897, p. 94), when he chose *Ctenodonta contracta* Salter as the type species. It will be shown later that the correct name for this species is *Tancrediopsis cuneata* (Hall).

Beushausen's name *Tancrediopsis* seems to have been ignored by all later workers on Ordovician pelecypods, but it has gained some usage as a generic name with workers describing Silurian and Devonian nuculoids (Prosser and Kindle, 1913; McLearn, 1924; Reed, 1931; Northrop, 1939; Sherrard, 1960). In this regard it should be noted that even though Beushausen originally named an Ordovician and a Silurian species as the "types" of the subgenus, the name was proposed to facilitate the description of Devonian species which were the subject of his monograph. While it is still too early to determine the final usefulness of the generic name, it appears likely that many of the post-Ordovician species to which it has been applied cannot be considered as congeneric with the type species, "*Ctenodonta contracta.*" The name *Tancrediopsis* will, however, probably prove useful in the future as a generic subdivision of the heterogeneous assemblage of Ordovician forms now included in "*Ctenodonta.*" Here again, a final determination of the value of the name must await further study of other genera and species of Ordovician nuculoids. In anticipation of such studies it appears that many Ordovician nuculoid species show closer affinities to

"*Ctenodonta contracta*," the type of *Tancrediopsis*, than to *Ctenodonta nasuta*, the distinctive and uncommon type of the genus *Ctenodonta*. For this reason, the transfer of many Ordovician species from *Ctenodonta* to *Tancrediopsis* may prove desirable in future revisions.

Tancrediopsis cuneata (Hall)

Figures 1-80

Tellinomya cuneata Hall, 1856, p. 392, figs. 6, 7. Hall, 1857a, p. 183, figs. 6, 7. Hall, 1857b, p. 143, figs. 6, 7. [not] Hall, 1862, p. 38, figs. 1, 2.

Ctenodonta contracta Salter, 1859, p. 37, pl. 8, figs. 4, 5. Logan, 1863, p. 175, figs. 160a, 160b. Wilson, 1956, p. 23, pl. 2, figs. 7-9.

Ctenodonta (Tancrediopsis) contracta (Salter). Beushausen, 1895, p. 70.

[?] *Tellinomya contracta?* (Salter). Walcott, 1884, p. 76, pl. 11, figs. 15, 15a.

Revised description. Shell of small size (median height of 136 measurable specimens 8 mm), equivalved, strongly convex, thick and massive, constricted posteriorly.[2] Shape variable, height ranging from 62 to 86 per cent of length (median of 86 measurable specimens 71 per cent). Surface sculpture of very fine, widely spaced concentric ridges which are commonly divided into rod-like pustules, especially near the outer margin (figs. 4-7, 18, 19, 24, 26, 28, 35, 37). Sculpture usually obscure or absent, probably because of difficulty of preservation rather than absence on original shell. The dorsal margin shows a prominent oval lunule anterior to the umbones and a more elongate and obscure posterior escutcheon (figs. 65-73). Lunule and escutcheon variable in size and shape. Strong, chevron-shaped, taxodont dentition with approximately equal num-

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[2] By analogy with living nuculoids, the smaller, contracted end of *T. cuneata* is considered to be posterior and the larger end to be anterior as shown in figs. 1 and 2.

bers of teeth on both sides of umbo, teeth decreasing abruptly in size but apparently continuous in umbonal region (figs. 46-64, 73-80). One well-preserved specimen shows several tiny perforations along the margins of the escutcheon, probably representing an extreme elongation of the dental sockets (fig. 71; see Sorgenfrei, 1937, and Trueman, 1952, for discussions of similar structures in Cenozoic nuculoids). Resilifer absent. Several specimens show a strong, external ligament structure preserved as a silicified replica along the anterior third of the escutcheon posterior to the umbones (figs. 65-67, 69, 70, 72, 80). Strong, subequal adductor scars deeply impressed into the thick shell material, bounded on interior side by thickened shell material making raised ridge which is most prominent behind the anterior scar (figs. 75-80). Two small but deeply impressed subequal pedal muscle scars occur just below the hinge plate at the dorsal end of these adductor ridges (figs. 74-80). A few well-preserved specimens also show faint impressions just below the posterior hinge plate which may represent other pedal or visceral muscle scars (figs. 75, 77). Pallial line not preserved, probably very faint or absent on original shell material. Original calcareous shell material unknown, replaced by amorphous silica in all specimens.

Types. Lectotype of *Tellinomya cuneata* Hall, here designated, the specimen shown by Hall, 1856, as fig. 7 (and fig. 6 if both figures represent the same specimen), p. 392; whereabouts unknown. Type locality: "Pauquette's Rapids on the Ottawa River" [between Allumette Island, Quebec and Ontario mainland, about three miles south of Waltham, Quebec, Canada (see Kay, 1942, pl. 6)]. Stratigraphic position: "Beds lying at the junction of the Trenton and Black River limestones" [Rockland beds of the Ottawa formation, Middle Ordovician (lower Trenton stage of Twenhofel, 1954)]. Lectotype of *Ctenodonta contracta* Salter, by designation of Wilson, 1956, p. 23, No. 1171b in the collections of the Geological Survey of Canada, Ottawa, Ontario, Canada. This specimen is one of Salter's original syntypes which was figured by him (1859)as pl. 8, figs. 5, 5a. Type locality: "Allumette Islands," Quebec [probably Paquette Rapids between Allumette Island, Quebec and Ontario mainland, about three miles south of Waltham, Quebec, Canada (see Kay, 1942, pl. 6)]. Stratigraphic

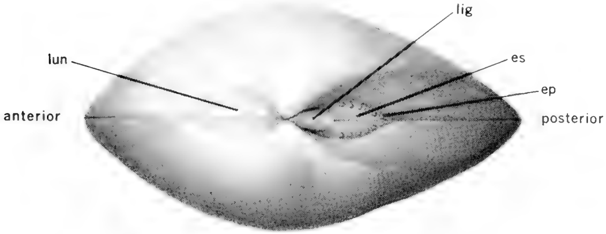

Figure 1. *Tancrediopsis cuneata* (Hall). Generalized dorsal view of articulated valves showing lunule (lun), ligament (lig), escutcheon (es) and escutcheonal perforations (ep).

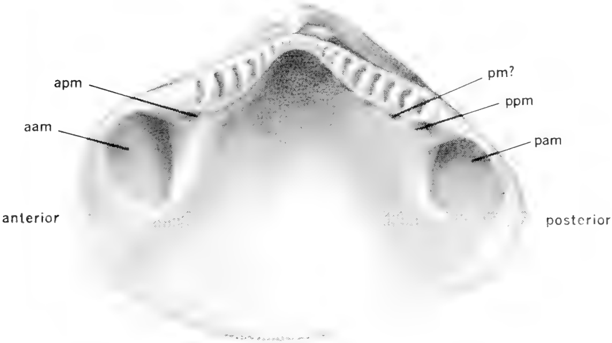

Figure 2. *Tancrediopsis cuneata* (Hall). Generalized interior view of right valve showing anterior adductor muscle scar (aam), anterior pedal muscle scar (apm), posterior pedal muscle scar (ppm), posterior adductor muscle scar (pam), and additional possible pedal or visceral muscle scars along posterior dorsal margin (pm?).

position: "Allumette limestones" [probably Rockland beds of the Ottawa formation, Middle Ordovician (lowest Trenton stage of Twenhofel, 1954)].

The location of Hall's original figured specimen is unknown, for it is not listed in the type catalogues of either the American Museum of Natural History or the New York State Museum (Whitfield and Hovey, 1898-1901; Clarke and Ruedemann, 1903), the two institutions which contain most of Hall's original material. The specimen may be as yet unrecognized among the non-type material at these or other institutions. Hall's original figure leaves little room for doubt, however, as to the identity of the species in question, and the designation of a neotype therefore seems unnecessary.

Material. This revised description is based on 189 silicified valves. Fifteen of these are Salter's original types of *Ctenodonta contracta* from the collections of the Geological Survey of Canada, Ottawa, Ontario, Canada (catalogue No. 1171). The remaining 174 specimens are from the collections of the Peabody Museum, Yale University, New Haven, Connecticut, U. S. A. All of Salter's specimens and almost half of the Yale material (75 specimens) were collected at Paquette Rapids (between Allumette Island, Quebec and Ontario mainland, about three miles south of Waltham, Quebec, Canada; see Kay, 1942, pl. 6) which is the original type locality of both *Tellinomya cuneata* Hall and *Ctenodonta contracta* Salter. The remaining Yale specimens (99) were collected from Middle Ordovician limestones of approximately the same age exposed at Pointe Bleue on the shores of Lake St. John, about five miles north of Roberval, Quebec, Canada (see Dresser, 1916, map 184A). Both Yale collections were made in 1903 by C. E. Beecher and P. E. Raymond. The original specimens studied by Salter were collected by W. E. Logan in 1845. The distribution of specimens of *Tancrediopsis cuneata* at these institutions and localities is shown in more detail in Table 1.

The material shows considerable variation in the quality of the silicified preservation. In some specimens the whole valve is preserved, but many valves were incompletely replaced by silica and do not show the entire outline. The fragile posterior extremity is commonly missing, but the heavy hinge plate and dentition are almost always preserved. The specimens from

TABLE 1

Distribution of specimens of *Tancrediopsis cuneata* (Hall) used in this study. For consistency, each valve of articulated individuals is counted as one "specimen."

Locality and Source	Right valves	Left valves	Articulated valves	Total specimens
Paquette Rapids				
Yale Peabody Museum...	44	29	2	75
Geological Survey of Canada..........	6	7	2	15
Pointe Bleue, Lake St. John (All Yale Peabody Museum)...........	19	20	60	99
Totals	69	56	64	189

Lake St. John are generally more coarsely silicified and show fewer morphologic details than do those from Paquette Rapids.

Occurrence. The species is known with certainty only from the type locality and the Lake St. John locality mentioned above, both of which probably represent horizons in the middle part of the Middle Ordovician (lowest Trenton stage of the American standard, approximately lower Caradoc of the European standard, see Twenhofel, 1954). Several additional Ontario and Quebec occurrences are listed by Wilson (1956, p. 23), and the species may be represented in the Ordovician of Nevada (Walcott, 1884). Restudy of other important Ordovician pelecypod faunas may prove the species to be more abundant and widespread than is apparent from the evidence now available. In most such faunas nuculoid forms are not silicified, but are preserved as internal or composite molds (see McAlester, 1962). For this reason, an artifical internal mold of a well-preserved, silicified specimen of *T. cuneata* has been figured here to facilitate comparison with other faunas (fig. 47).

Discussion. There has been considerable confusion in the identification of Salter's species "*Ctenodonta contracta*" and other closely related species from the Paquette Rapids locality. The Yale collections from this locality contain about 700 silicified nuculoid specimens, and an analysis of these specimens has revealed that at least seven species of nuculoids occur in appreciable numbers at Paquette Rapids. Several additional nuculoid species probably also occur in the fauna but are quite rare and are represented by only a few specimens from the Yale collections. Five of the seven common species are distinctive and cause little confusion in identification. Wilson (1956, pl. 2) illustrates four of these distinctive species, which are identified by her as: *Ctenodonta astartaeformis* Salter, *Ctenodonta levata* (Hall), *Ctenodonta nasuta* Hall, and *Ctenodonta logani* Salter. A fifth common species, a small *Palaeoneilo*-like form, is not mentioned by Wilson and may be as yet undescribed.

It is the final two common nuculoid species in the Paquette Rapids fauna which are easily confused. Both are medium-sized (for nuculoids), thick-shelled forms with contracted posterior extremities, strong adductor impressions, and similar patterns of dentition. Analysis of the large Yale collections shows that the two forms do, however, show consistent and distinct differences in shape, which are most obvious from comparing the shell exteriors. To facilitate comparison the two species will be referred to here as "Form A" and "Form B." Form A has more central umbones, a more elongate and gently-sloping posterior constriction, and a differently shaped anterior-ventral and anterior margin. Internally, the differences are less distinctive, but the more central umbones, less abrupt posterior constriction, and longer posterior dentition of Form A can usually be recognized. Form B also seems to have lacked the very fine, pustulose, concentric sculpture seen on well-preserved specimens of Form A. Form B also appears to have had weaker and somewhat differently oriented pedal muscle scars. In Form A the chevron-shaped teeth point toward the umbo, whereas they tend to point away from the umbo in Form B. These differences in shape and sculpture are shown in fig. 3.

There are no morphological intermediates between these two common forms in the Paquette Rapids fauna, and they certainly represent two closely related sympatric nuculoid species. Among approximately 700 identifiable nuculoid specimens from the locality in the Yale collections, about 250 (36 per cent) are form B, 75 (or about 11 per cent) are Form A, and the bulk of the remainder (about 375 specimens or 53 per cent) represent the five additional species mentioned above. The lectotype of Hall 's species *Tellinomya cuneata* is readily recognizable from the original figure as belonging to Form A (sub-central umbones, elongate posterior, etc.) as are also the lectotype and other original specimens of *Ctenodonta contracta* Salter. The lectotypes of both species are from Paquette Rapids, and there is little doubt that the two names are synonyms.

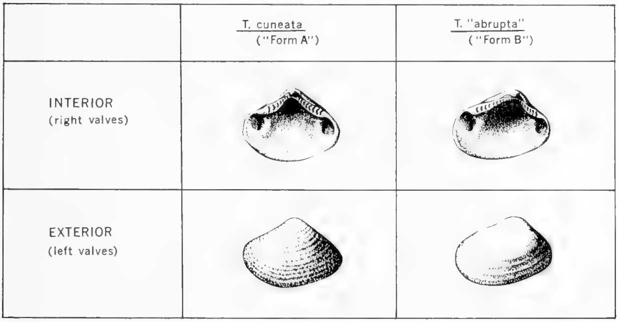

Figure 3. Internal and external views showing morphologic differences between the closely related sympatric species *Tancrediopsis cuneata* (Hall) and *Tancrediopsis "abrupta"* (Billings).

Hall's name "*Tellinomya cuneata*" was not formally proposed as a new species, but was merely first listed in explanation of figures of "*Tellinomya*" [=*Ctenodonta*] in a discussion of the genus (1856) which was later reprinted in two forms (1857a, 1857b). Characters of the species are, however, briefly mentioned in Hall's text (p. 392 in the original report). The figures and discussion of the species in Hall's report certainly constitute a valid description or "indication" of a new species as prescribed in the rules of nomenclature (see Stoll, 1961, p. 15), and Hall's name, which has three-years priority over *Ctenodonta contracta* Salter, is therefore accepted here as the correct name for the species. This strict usage of priority may violate the new "nomen oblitum" provision of the nomenclatural code which provides that "a name that has remained unused as a senior synonym in the primary zoological literature for more than fifty years is to be considered a forgotten name (nomen oblitum). . . [and] is not to be used unless the Commission so directs" (Stoll, 1961, p. 23). However, the application of the rule is ambiguous in this case because *Tellinomya cuneata* has appeared in what is presumably the "primary zoological literature" as an incorrectly suppressed senior synonym of *Ctenodonta contracta* within the past fifty years (Bassler, 1915, p. 302). In addition, the prescribed procedure for applying the rule is extremely cumbersome and in my opinion will do more to create nomenclatural instability than to correct it because every "nomen oblitum" must be laboriously referred to the Commission for action. For these reasons I prefer a strict interpretation of the Law of Priority in this case (for additional objections and comment on the "nomen oblitum" provision see the Bulletin of Zoological Nomenclature, Volume 19, Part 6, 28 December, 1962).

The name of the second common species ("Form B") is not yet certain, but it appears that the lectotype of *Ctenodonta abrupta* Billings (1862; see also Wilson, 1956) is a representative of "Form B," and this may be the correct name for the species. These two closely related species (*Tancrediopsis cuneata* and "*Ctenodonta abrupta*") are certainly congeneric and thus *C. abrupta* would become *Tancrediopsis* "*abrupta*" (Billings).

In addition to these two common species of *Tancrediopsis*, a few other specimens from the Paquette Rapids fauna may represent closely related but very rare species. Several such specimens in the Yale collections do not appear to fall within the range of shape variation of either *T. cuneata* or *T.* "*abrupta*," but at present these specimens are too rare either to warrant specific names or to cause confusion in the identification of *T. cuneata.* The original figured specimen of *Ctenodonta gibberula* Salter (1859, pl. 8, fig. 6) may represent one such species but, regrettably, the specimen appears to have been lost (see Wilson, 1956, p. 24). Pending the discovery of the original specimen or similar additional material, it does not seem prudent to recognize Salter's name. The two names *C. abrupta* Billings and *C. gibberula* Salter appear to be the only names proposed for Paquette Rapids specimens which are closely related to *T. cuneata.*

In comparison to the Paquette Rapids fauna, nuculoids are somewhat less common and more poorly preserved in the silicified fauna from Lake St. John, but the fauna does contain many articulated specimens which are rare at Paquette Rapids (see Table 1). The nuculoid species at Lake St. John all appear to be indistinguishable from those at Paquette Rapids, although the relative abundances differ at the two localities. At Lake St. John, *T. cuneata* is over three times as abundant as *T. "abrupta"* (99 vs. 30 specimens), whereas this situation is reversed at Paquette Rapids where *T. "abrupta"* strongly dominates (approximately 250 specimens vs. 75 specimens of *T. cuneata*).

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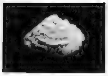
Figures 4-21. *Tancrediopsis cuneata* (Hall). A series of exterior views of silicified right valves showing variation in shape and sculpture. All figures are twice natural size. Precise locality information for the "Paquette Rapids" and "Lake St. John" localities is given in the text. YPM = Yale University Peabody Museum collections, New Haven, Connecticut, U.S.A. GSC = Geological Survey of Canada collections, Ottawa, Ontario, Canada.

Figure 4. YPM 22966, Lake St. John. Figure 5. YPM 22967, Lake St. John. Figure 6. YPM 22968, Lake St. John. Figure 7. YPM 22969, Lake St. John. Figure 8. YPM 22970, Lake St. John. Figure 9. YPM 22971, Paquette Rapids. The specimen lacks the anterior and posterior extremities. See also fig. 48. Figure 10. YPM 22972, Paquette Rapids. The specimen lacks the posterior extremity. Figure 11. YPM 22973, Lake St. John. Figure 12. YPM 22974, Lake St. John. Figure 13. YPM 22975, Paquette Rapids. The specimen lacks the anterior extremity. See also fig. 50. Figure 14. YPM 22976, Paquette Rapids. The specimen lacks the anterior and posterior extremities. Figure 15. YPM 22977, Paquette Rapids. See also figs. 52, 68. Figure 16. YPM 22978, Lake St. John. Figure 17. GSC 1171c, Paquette Rapids. One of Salter's original specimens of *Ctenodonta contracta*, figured by Wilson, 1956, as figs. 7 and 8 of pl. 2. See also fig. 70. Figure 18. YPM 22979, Paquette Rapids. The anterior part of the specimen is missing. Figure 19. GSC 1171k, Paquette Rapids. One of Salter's original specimens of *Ctenodonta contracta*, figured by Wilson, 1956, as fig. 9 of pl. 2. The specimen lacks the anterior extremity. Figure 20. GSC 1171e, Paquette Rapids. One of Salter's original specimens of *Ctenodonta contracta*. See also fig. 66. Figure 21. YPM 22980, Paquette Rapids. See also figs. 47, 55, 77, 79.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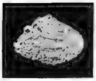
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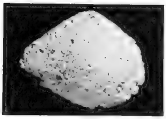
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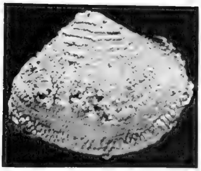
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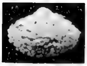
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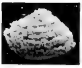
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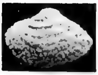
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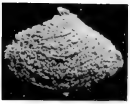
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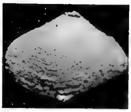
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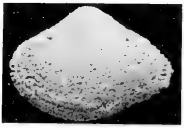
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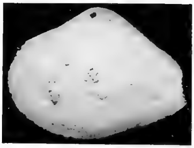
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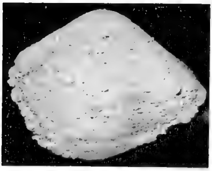
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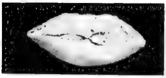
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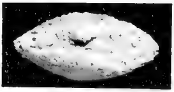
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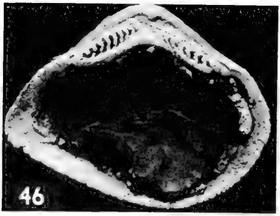
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Figures 22-47. *Tancrediopsis cuneata* (Hall). Figures 22 through 42 are a series of exterior views of silicified right valves showing variation in shape and sculpture. Figures 43 through 45 are dorsal views of three articulated silicified specimens (anterior end to left). Figure 46 is an interior view of the largest known specimen, a silicified left valve. Figure 47 is a latex internal mold of a silicified right valve showing the appearance of the species as normally preserved in non-silicified faunas. All figures are twice natural size. Precise locality information for the "Paquette Rapids" and "Lake St. John" localities is given in the text. YPM = Yale University Peabody Museum collections, New Haven, Connecticut, U.S.A. GSC = Geological Survey of Canada collections, Ottawa, Ontario, Canada.

> Figure 22. YPM 22981, Lake St. John. Figure 23. YPM 22982, Lake St. John. Figure 24. YPM 22983, Lake St. John. Figure 25. YPM 22984, Lake St. John. Figure 26. YPM 22985, Lake St. John. Figure 27. YPM 22986, Lake St. John. Figure 28. YPM 22987, Lake St. John. Figure 29. YPM 22988, Lake St. John. Figure 30. YPM 22989, Lake St. John. Figure 31. YPM 22990, Lake St. John. Figure 32. YPM 22991, Paquette Rapids. The specimen lacks the anterior extremity. See also fig. 58. Figure 33. YPM 22992, Lake St. John. Figure 34. GSC 1171L, Paquette Rapids. One of Salter's original specimens of *Ctenodonta contracta*. See also fig. 43. Figure 35. GSC 1171j, Paquette Rapids. Figure 36. YPM 22993, Lake St. John. See also fig. 44. Figure 37. YPM 22994, Lake St. John. Figure 38. YPM 22995, Lake St. John. See also fig. 45. Figure 39. Lectotype of *Ctenodonta contracta* Salter, GSC 1171b, Paquette Rapids, figured by Salter, 1859, as figs. 5 and 5a of pl. 8. The specimen lacks the posterior extremity. See also figs. 61, 67, 75, 80. Figure 40. GSC 1171m, Paquette Rapids. One of Salter's original specimens of *Ctenodonta contracta*. The specimen lacks the anterior extremity. See also figs. 60, 73, 76. Figure 41. GSC 1171i, Paquette Rapids. One of Salter's original specimens of *Ctenodonta contracta*. See also fig. 69. Figure 42. GSC 1171d, Paquette Rapids. One of Salter's original specimens of *Ctenodonta contracta*. Figure 43. GSC 1171L, Paquette Rapids. One of Salter's original specimens of *Ctenodonta contracta*. See also fig. 34. Figure 44. YPM 22993, Lake St. John. See also fig. 36. Figure 45. YPM 22995, Lake St. John. See also fig. 38. Figure 46. GSC 1171a, Paquette Rapids. One of Salter's original specimens of *Ctenodonta contracta*. Figure 47. Latex cast of YPM 22980, Paquette Rapids. See also figs. 21, 55, 77, 79.

Figures 48-64. *Tancrediopsis cuneata* (Hall). A series of internal views of silicified valves showing dentition and adductor musculature. Figures 48 through 56 are right valves; figures 57 through 64 are left valves. All figures are twice natural size. Precise locality information for the "Paquette Rapids" locality is given in the text. YPM = Yale University Peabody Museum collections, New Haven, Connecticut, U.S.A. GSC = Geological Survey of Canada collections, Ottawa, Ontario, Canada.

Figure 48. YPM 22971, Paquette Rapids. See also fig. 9. Figure 49. YPM 22996, Paquette Rapids. Figure 50. YPM 22975, Paquette Rapids. See also fig. 13. Figure 51. YPM 22997, Paquette Rapids. Figure 52. YPM 22977, Paquette Rapids. See also figs. 15, 68. Figure 53. YPM 22998, Paquette Rapids. Figure 54. GSC 1171g, Paquette Rapids. One of Salter's original specimens of *Ctenodonta contracta*. See also fig. 72. Figure 55. YPM 22980, Paquette Rapids. See also figs. 21, 47, 77, 79. Figure 56. YPM 22999, Paquette Rapids. See also fig. 74. Figure 57. YPM 23000, Paquette Rapids. Figure 58. YPM 22991, Paquette Rapids. See also fig. 32. Figure 59. YPM 23001, Paquette Rapids. See also fig. 78. Figure 60. GSC 1171m, Paquette Rapids. One of Salter's original specimens of *Ctenodonta contracta*. See also figs. 40, 73, 76. Figure 61. Lectotype of *Ctenodonta contracta* Salter, GSC 1171b, Paquette Rapids, figured by Salter, 1859, as figs. 5 and 5a of pl. 8. See also figs. 39, 67, 75, 80. Figure 62. YPM 23002, Paquette Rapids. Figure 63. YPM 23003, Paquette Rapids. Figure 64. YPM 23004, Paquette Rapids. See also fig. 71.


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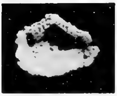
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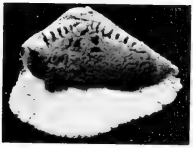
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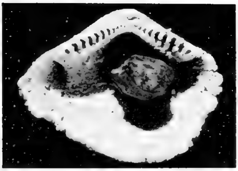
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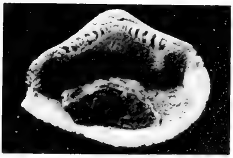
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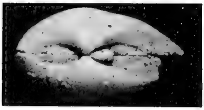

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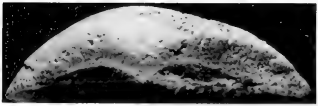

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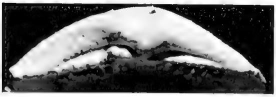

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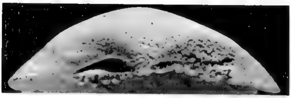

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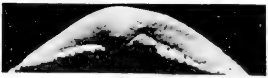

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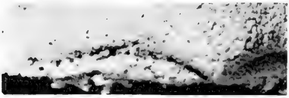

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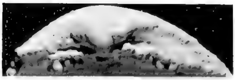

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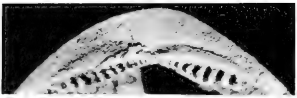

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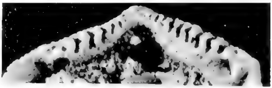

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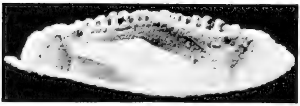

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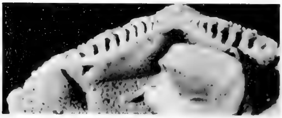

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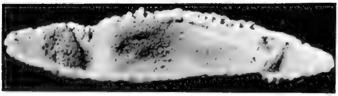

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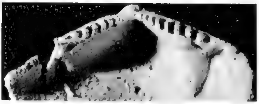

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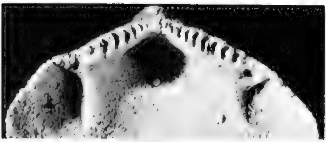

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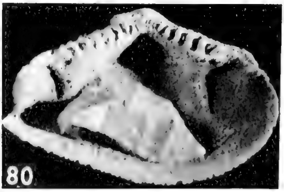

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Figures 65-80. *Tancrediopsis cuneata* (Hall). A series of enlarged views of silicified valves showing details of ligament, dentition, and musculature. All figures are three times natural size except Figure 65 (twice natural size) and Figure 71 (six times natural size). Precise locality information for the "Paquette Rapids" locality is given in the text. YPM = Yale University Peabody Museum collections, New Haven, Connecticut, U. S. A. GSC = Geological Survey of Canada collections, Ottawa, Ontario, Canada.

Figure 65. GSC 1171f, Paquette Rapids. One of Salter's original figured specimens of *Ctenodonta contracta,* illustrated by Salter, 1859, as figs. 4 and 4a of pl. 8. Dorsal view of articulated valves (anterior end to left) showing lunule, escutcheon, and silicified replica of ligament. Figure 66. GSC 1171e, Paquette Rapids. One of Salter's original specimens of *Ctenodonta contracta.* Dorsal view of right valve showing lunule, escutcheon, and silicified replica of ligament. See also fig. 20. Figure 67. Lectotype of *Ctenodonta contracta* Salter, GSC 1171b, Paquette Rapids, figured by Salter, 1859, as figs. 5 and 5a of pl. 8. Oblique dorsal view of left valve showing lunule, escutcheon, and silicified replica of ligament. See also figs. 39, 61, 75, 80. Figure 68. YPM 22977, Paquette Rapids. Oblique dorsal view of right valve showing lunule. See also figs. 15, 52. Figure 69. GSC 1171i, Paquette Rapids. One of Salter's original specimens of *Ctenodonta contracta.* Oblique dorsal view of left valve showing escutcheon and silicified replica of ligament. See also fig. 41. Figure 70. GSC 1171c, Paquette Rapids. One of Salter's original specimens of *Ctenodonta contracta,* figured by Wilson, 1956, as figs. 7 and 8 of pl. 2. Oblique dorsal view of right valve interior showing lunule, escutcheon, and silicified replica of ligament. See also fig. 17. Figure 71. YPM 23004, Paquette Rapids. Enlarged dorsal view of left valve showing lunule, escutcheon, and tiny perforations along posterior margin of escutcheon. See also fig. 64. Figure 72. GSC 1171g, Paquette Rapids. One of Salter's original specimens of *Ctenodonta contracta.* Oblique dorsal view of right valve showing lunule, escutcheon, and silicified replica of ligament. See also fig. 54. Figure 73. GSC 1171m, Paquette Rapids. One of Salter's original specimens of *Ctenodonta contracta.* Oblique dorsal view of left valve showing lunule, escutcheon, and dentition. See also figs. 40, 60, 76. Figure 74. YPM 22999, Paquette Rapids. Oblique ventral view of interior hinge region of right valve showing anterior and posterior pedal muscle scars and dentition. See also fig. 56. Figure 75. Lectotype of *Ctenodonta contracta* Salter, GSC 1171b, Paquette Rapids, figured by Salter, 1859, as figs. 5 and 5a of pl. 8. Ventral view of left valve interior showing dentition, adductor muscle scars, strong rounded anterior and posterior pedal muscle scars, and faint additional pedal? muscle scars below posterior dentition. See also figs. 39, 61, 67, 80. Figure 76. GSC 1171m, Paquette Rapids. One of Salter's original specimens of *Ctenodonta contracta.* Oblique ventral view of left valve interior showing dentition and posterior adductor and pedal muscle scars. See also figs. 40, 60, 73. Figure 77. YPM 22980, Paquette Rapids. Ventral view of right valve interior showing adductor muscle scars, strong rounded anterior and posterior pedal muscle scars, and faint additional pedal? muscle scars below posterior dentition. See also figs. 21, 47, 55, 79. Figure 78. YPM 23001, Paquette Rapids. Oblique ventral view of left valve interior showing dentition, anterior adductor muscle scar, anterior and posterior pedal muscle scars. See also fig. 59. Figure 79. YPM 22980, Paquette Rapids. Interior view of right valve showing dentition, adductor muscle scars, and pedal muscle scars. See also figs. 21, 47, 55, 77. Figure 80. Lectotype of *Ctenodonta contracta* Salter, GSC 1171b, Paquette Rapids, figured by Salter, 1859, as figs. 5 and 5a of pl. 8. Interior view of left valve showing dentition, adductor muscle scars, pedal muscle scars, and silicified replica of ligament. See also figs. 39, 61, 67, 75.

Postilla

YALE PEABODY MUSEUM

OF NATURAL HISTORY

Number 75 May 27, 1963 New Haven, Conn.

DAVID BALDWIN, O. C. MARSH AND THE DISCOVERY OF THE FIRST CONTINENTAL PALEOCENE FAUNAS OF THE NEW WORLD

Elwyn L. Simons

Recent reorganization of the collection of fossil vertebrates at the Yale Peabody Museum has brought to light material for establishing a hitherto unreported chapter in the history of western paleontological exploration—the time, place and circumstances of discovery of the first known land mammals of the New World Paleocene.[1]

David Baldwin, who was to make this outstanding discovery while in the employ of Professor O. C. Marsh of the Yale College Museum [Yale Peabody Museum], was first recommended to Marsh in 1876 by Lieutenant W. L. Carpenter. In the previous year both Carpenter and Baldwin, who held a position as packer, had taken part in paleontological activities of the Wheeler Survey of New Mexico on which expedition Professor E. D. Cope of Philadelphia was also present. According to Schuchert and LeVene (1940:179), Baldwin "began to collect for Marsh in New Mexico in May, 1876, and continued intermittently until 1880. Marsh was then concentrating on Eocene

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[1] Research reorganization of these collections was supported by National Science Foundation grants 14255 (1960) and GB-247 (1962).

mammals and the material of that age sent in by Baldwin—34 boxes and 20 packages—did not please him; moreover, with his customary absorption in the work at hand he failed to appreciate the value of the bones (14 boxes) collected by Baldwin from red beds, supposed to be Triassic age but later determined to be Permian. The terms under which Baldwin was to work were evidently not clearly defined by Marsh at the start, and a long wrangle resulted. The two finally agreed to submit their differences to Lieutenant Carpenter."

Eventually Carpenter arranged a settlement which was satisfactory to both, but Baldwin clearly had been irritated by the erratic nature in which he received payment from Marsh in support of his field activities and in 1880 shifted his employment and allegiance to Professor E. D. Cope. Baldwin then sent his collections made in the region in 1880-1881 to Philadelphia which formed the basis of the first report of the Paleocene (Lower Eocene) faunas of New Mexico, published by Cope 1881a and b). Between 1880 and 1888 Baldwin collected for Cope, and his work resulted in the Cope Collection of Paleocene mammals now located at the American Museum of Natural History, New York. Serving as it did as the basis for Cope's fundamental and extensive contributions on the nature and initial differentiation of Cenozoic Mammalia, this remains one of the most important collections of fossil Mammalia ever assembled, and it stands as a fitting memorial to Baldwin's diligence in the field.

While still working for Marsh, from July 1879 through the remainder of that summer, Baldwin began to find and send in to Marsh teeth of middle Paleocene mammals from the area which he had previously mapped and recovered mammalian bone fragments. His correspondence with O. C. Marsh, now preserved at the Peabody Museum as part of the extensive archive of Marsh's correspondence, makes it possible to learn much about his activities in opening up this great fossil field.

Although its importance was not recognized at that time, this discovery came as the culmination of three years' paleontological exploration of the San Juan and Gallinas River drainages by Baldwin. During 1876, 1877 and 1878 Baldwin was collecting almost continuously for Marsh, working particularly in Wasatch Eocene deposits of the Almagre and Largo formations in the drainage of Gallinas River, New Mexico. From these beds he sent in to New Haven a considerable collection of early Eocene Mammalia including much *Coryphodon* material. Nevertheless many of the specimens were fragmentary and incomplete and Marsh apparently was not particularly impressed by their quality. Very little was done with these shipments, many of which have only recently been sorted and identified.

An innovation relating to the history of recovery of fossil vertebrates was Baldwin's adoption in 1876 of the method of enclosing fragile fossil specimens in a clay paste prepared on the site of collection. A specimen of *Coryphodon molestus*, YPM 15239,[2] collected by Baldwin on Nov. 29/30, 1877 shows a further elaboration in that the clay-coated jaw was tied up between two cradle-like, hollowed and hand-carved boards (prepared by him) which effectively bandaged it for shipment. A note with the specimen by Baldwin states "N.B. Lower jaw done up in mud and boards in bottom of sack be careful very rotten." As far as can be determined from the Yale Peabody Museum records this is the first fossil vertebrate to have been housed for shipment in a manner foreshadowing modern methods. A letter from another of Marsh's collectors dated in the same year (1877) suggested that a coating of plaster of Paris would be useful in holding bones together during removal from a hard matrix in the field (see Schuchert and LeVene, 1940: 175). With these two suggestions in mind it only remained for Marsh to instruct his collectors to bandage fossil specimens in plaster jackets in the field—an invention for which he took (and is often given) credit (Schuchert, 1939:15).

By the spring of 1879 Baldwin had prepared a map of the rock types and river drainages of the San Juan Basin, New Mexico (Figure 1) and had begun collecting in horizons, which he regarded as Cretaceous, underlying the "*Coryphodon* beds." Actually these deposits were of Paleocene age but this could

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[2] Abbreviations used in this paper: YPM, Yale Peabody Museum, New Haven; AMNH, American Museum of Natural History, New York.

hardly have been realized at that time by either Marsh or Baldwin, inasmuch as continental deposits and faunas of this epoch were then entirely unknown in North America. During this period of his explorations David Baldwin shipped materials to Yale both from Animas City, Colorado and from Abiquiu a small town on the Rio Chama about twenty-five miles due north of Los Alamos, New Mexico. In June, 1879 Baldwin sent the following geological observations to his employer in New Haven.

Animas City Colorado

June 16th, 1879

"Prof. O. C. Marsh

Dear Sir:

Inclosed send you a list of the bones I send you by mail today. They are mostly weathered specimens. The mammals entirely so. In April I sent you the horizons of this basin cut in paper [figure 1]. The beds in which I have found these mammalian remains extend no farther west than about haff way between the Animas and La Plata rivers and their northern limit is about ten miles South of this place. They show themselves about twenty miles down the Rio Puerco from the head on the west side of Nacimento Mountain and from that point westward form a nearly continuous wall of bluffs nearly to the Eastern line of the Navajo Reservation. They do not extend to the road from Santa Fe to Fort Wingate. That road for the first forty miles west of the Puerco Crossing is on the Marine Cretaceous in part though mainly upon the Lignite and the Strata containing the reptillian remains on the San Juan river. These mammalian beds do not extend as far west as the Eastern line of the Navajo Reservation on the south side of the San Juan river but they extend far beyond what I have (untill this winter) considered as the limit of the Eocene basin. On the Gallina creek side to my mind everything is in confusion. I cannot believe that I have ever sent you a fossil from those beds from there. In your address at Nashville you spoke of the *Coryphodon* beds as being the oldest known Eocene and it was that statement that showed me that I had probably the best field in the world in which to look for Cretaceous Mammals it being a point where the oldest Eocene rested upon the newest fresh water Cretaceous. But I do not know but what you have had some other one sending you fossils from the New Mexican Eocene and probably these beds have been known to you for three or four years past.

Please tell me if I have ever sent you anything from the *Coryphodon* beds before. Are these last fossils from the *Coryphodon* beds?

I have not found any small reptiles above the coal yet though fragments of large bones are abundant. Please write to me at this place. I will work on these mammalian beds two or three weeks or perhaps a month before going back to Abiquiu.

Very truly yours,

D. Baldwin"

During the following month Baldwin continued to collect along the San Juan river and its tributaries the Animas and Canon Largo in the new extension of the "Eocene basin" which he had found, still supposing that these exposures were of Cretaceous age. Marsh's replies to Baldwin's letters during this period are not preserved, but it seems likely from the questions asked by Baldwin in the above letter of June 16, 1879 that he had not troubled to provide his collector with much information as to the nature of the fauna he was securing.

After searching in the New Mexican Paleocene for several months Baldwin at last succeeded in recovering mammal teeth which he sent to Marsh. In his letter of July 12 he discussed the occurrence of other fossils in these beds; his washing of sediments in an attempt to recover mammalian teeth may be the first time this technique, now widely applied, was used in America.

Animas City Colorado

July 12, 1879

"Prof. O. C. Marsh:

Enclosed you will find list of fossils sent to-day by mail.

I have found fragments of large Reptillian bones in the lower whitish beds resting upon the Reptilian Strata above the lignite and within 150 ft. perpendicular of the hard sandstone capping these lower whitish beds (See cut paper horizons sent you April 22nd, 79). This fact I suppose brings the Cretaceous to the hard sandstones capping the lower whitish beds.

A man living on the San Juan River has shown me where he picked up two years ago a piece of a small jaw having grinding teeth. He says it looked like the jaw of a man or monkey but says the teeth were smaller than A & B which I sent you today. The place where he found it was in the Reptillian horizon below the lower whitish beds the same horizon as the bones send in Box 2 1879 [YPM accession no. 1297] and about 400 yds. distant. I have packed dirt from the place where he said he found it 3 or 4 miles to the San Juan river and panned it out carefully to see if I could find a speck of a tooth or any fragment of small bone but could find nothing. It was a Cretaceous mammal but he has lost it. I have hunted for days and days in that vicinity and have found large reptiles in abundance but no small ones and no mammals.

I shall work my way from here down the Animas and up Cañon Largo to Abiquiu where I will try the Red rocks for a while.

Please write to me at Abiquiu and also please send me a check for $200 as I shall greatly need it.

Very truly yours,

With the exception of the 2nd part of Description of Jurassic fossils I have received nothing from you since yours of Nov. 2, 1878.

D. Baldwin

I shall order my mail to be sent from here to Abiquiu."

To this letter and a succeeding one of August 4th are appended the following field numbers, locality data and descriptions sufficient to confirm the identity of the Paleocene mammal teeth concerned which also still retain their original field designation slips (A and A, etc.).

List of Registered Package No. 6
Animas City Colo. July 12—1879

Package contains A & A, A & B, A & C, A & D, A & E [YPM accession no. 1247]

A. & A [YPM 11887] found west side Animas River, Taos Co., New Mexico, June 21st, 1879, near Cox's Ranch.

A & B [YPM 14459] one molar in piece lower jaw. Found south side San Juan River, Taos Co., New Mexico, June 28th, 1879, First Canon west of Cañon Largo.

A & C [YPM 14476] found on La Plata side of divide between Animas and La Plata rivers Ute Reservation Colorado July 9th, 1879—two molars in cement.

A & D Ute Reservation near A and C, July 9th, 1879.

A & E Ute Reservation La Plata side of divide July 10th, 1879 Piece of lower jaw teeth broken off—unmarked.

D. Baldwin

List of bones sent by mail from Abiquiu August 4th, 1879, [YPM accession no. 1259].

A & F [YPM 14461] from south side San Juan River, Taos Co., New Mexico four miles west of mouth of Cañon Largo—weathered fragments of skull mammal July 21st, 1879.

A & G [YPM 14477] south side San Juan River west of Cañon Largo. One back molar—and small bones, July 22nd, 1879.

D. Baldwin

Although the above listed localities are somewhat inexact, any locality data at all is rather unusual for the nineteenth century and is an evidence of the type of precision which Marsh consistently expected of his collectors. It must be remembered that some specimens secured in the 1870's (and even much later) by other institutions cannot now be located stratigraphically within the particular intermontane basin of their provenance. Taking the evidence of Baldwin's correspondence and the collection labels reproduced here, these initial finds of Paleocene Mammalia appear to have come from two different areas (Figure 1) about fifteen to twenty miles apart. The first being approximately between the towns of La Plata and Aztec, perhaps close to localities worked later by Granger in 1916 for the AMNH, while the second set of material apparently came from a spot six or seven miles north of Angel Peak on the south side of the San Juan River.

Although much of the material sent in at this time by Baldwin is insufficient for identification, three of the specimens of the July 12, 1879 shipment and two of the shipment of August 4 are adequate for generic and probable specific assignment. Although these scanty fragments provide little of morphologic or taxonomic interest, when taken together they do show that these initial discoveries are of species of Torrejonian rather than Puercan provincial age. The taxonomic position of these specimens is as follows: 1.) YPM 11887, *Periptychus rhabdodon*, fragmentary horizontal rami of both mandibles, with damaged left P_4 and right M_3; 2.) YPM 14459, *Periptychus rhabdodon*, mandibular fragment with left M_1; 3.) YPM 14461, *Periptychus* cf. *P. carinidens* maxillary fragment with a worn right M^2; 4.) YPM 14476, *Tetraclaenodon* cf. *T. puercensis*, left maxilla with M^{2-3} (M^3 larger than most *T. puercensis*, but close to *T. puercensis* AMNH 3937); 5.) YPM, 14477, *Neoclaenodon* cf. *N. procyonoides* M^2 and associated bone fragments.

The first of the above listed specimens, YPM 11887, was described by Marsh (1894:260) as the type of "*Eohyus robustus*." This was the only specimen from Baldwin's Paleocene collection at the Peabody Museum to which Marsh gave taxonomic attention. The latter, by 1894, had recognized that YPM 11887 and associated materials were from "the so-called Puerco deposits" (actually Torrejon horizons) thus lying considerably lower stratigraphically than the Wasatchian age beds to the east in which *Coryphodon* occurs as the commonest guide fossil. Marsh (1877:362) first mentioned the genus "*Eohyus*" from the "*Coryphodon* beds" but did not designate a species name and did not describe his material except to observe that "these remains are clearly Suilline in character, ..." In 1894 he designated a species for this Wasatchian, Eocene specimen, "*Eohyus distans*," the type of which consisted of a single upper right third molar figured by him (1894:261). In the opinion of Professor Marsh (1894: 260) Cope's genus *Periptychus* was a junior synonym of *Eohyus*. It is clear, however, that this is not the case. Whatever "*Eohyus distans*" is (the specimen cannot now be located), if from the "*Coryphodon* beds" as stated by Marsh, it cannot take priority over *Periptychus*, for the latter genus does not range into the Eocene. Moreover, Gazin (1955:10) regarded "*Eohyus*" as probably indeterminate. There can be little doubt that the "type" of "*Eohyus distans*" was from an Eocene horizon, for at the time of its first mention (1877) Baldwin had not yet begun to collect in areas which could have yielded Paleocene materials. Consequently, both Marsh's generic and species designations of "*Eohyus robustus*" are invalid. The "type" (YPM 11887) is a member of *Periptychus*, as was first noted by Sinclair (1914:267). The latter genus has clear priority over *Eohyus* through the description of *P. carinidens* by E. D. Cope (1881a:337). Moreover, YPM 11887 may be assigned with some confidence to *Periptychus rhabdodon*, a Torrejonian Paleocene species.

CONCLUSIONS

A small series of fossil mammals and other vertebrates, five of which can be taxonomically identified with some certainty, collected by David Baldwin for O. C. Marsh in the spring and summer of 1879, comprise the first continental Paleocene fauna to be discovered in the New World. Baldwin's pioneer collecting activities in Northwestern New Mexico are traced as they relate to this major discovery from his field label records, maps and correspondence preserved at the Yale Peabody Museum of Natural History. The species "*Eohyus robustus*" Marsh (1894) based on one of the specimens discovered in 1879 by Baldwin is a junior synonym of *Periptychus rhabdodon*, a Torrejonian, Paleocene condylarth.

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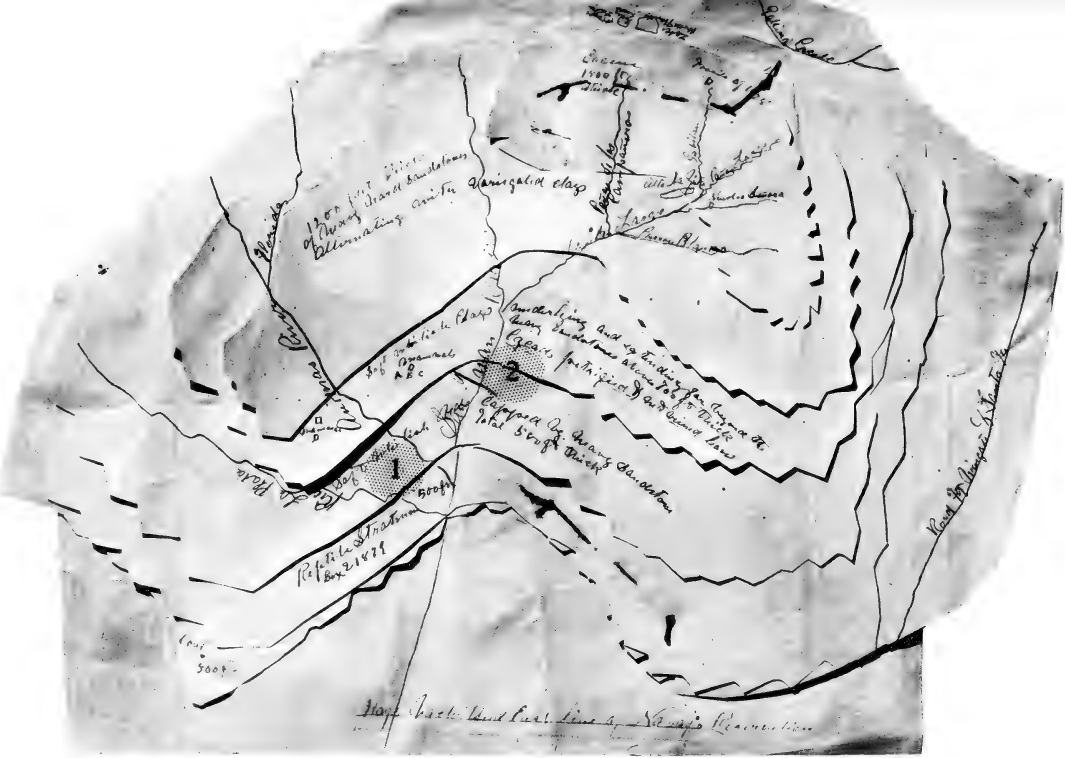
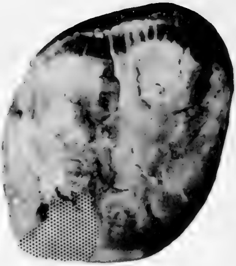
Figure 1.

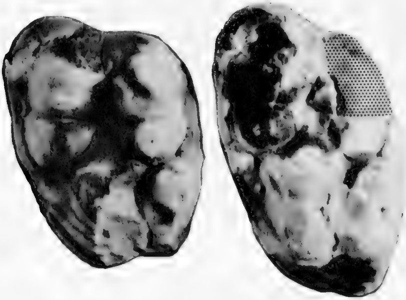
The first geological map of the North American Continental Paleocene, prepared by David Baldwin in April, 1879. The areas of two discoveries of Paleocene Mammalia made by him during that year are indicated by stipple.


Gallina Creek
1500 ft thick
1200 feet thick of heavy drab sandstones alternating with variegated clay
Puerco
Blanco
Soft white clay
Mammals
A B C
D
Underlying and extending far beyond the heavy sandstones above 700 ft thick
Cycads petrified & and Animal bones
Capped by heavy sandstone total 500 ft thick
2
1
500 ft
Reptile Stratum
Box 2 1879
Rio de la Plata
500 ft
Road to Abiquiu & Santa Fe
Map [illegible] Navajo [illegible]

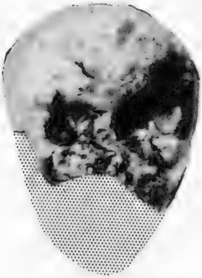
YPM 14477



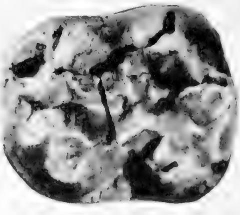
YPM 14461



YPM 14476



YPM 11887



YPM 14459

Figure 2. The initial five Paleocene mammals discovered in North America. Damaged areas stippled.

YPM 14477. *Neoclaenodon* cf. *N. procyonoides* M^2 and associated bone fragments.

YPM 14461. *Periptychus* cf. *P. carinidens* maxillary fragment with a worn right M^2.

YPM 14476. *Tetraclaenodon* cf. *T. puercensis,* left maxilla with M^{2-3} (M^3 larger than most *T. puercensis,* but close to *T. puercensis* AMNH 3937).

YPM 11887. *Periptychus rhabdodon,* fragmentary horizontal rami of both mandibles, with damaged left P_4 and right M_3.

YPM 14459. *Periptychus rhabdodon,* mandibular fragment with left M_1.

Postilla

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MOLT AND BREEDING IN POPULATIONS OF THE SOOTY TERN *STERNA FUSCATA*

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I have recently discussed (Ashmole, 1963) the breeding cycles of the Sooty Tern *Sterna fuscata* in all parts of its range. Although there are many areas for which adequate information is lacking, it appears that this species in different localities shows three different types of breeding cycle: namely, every twelve months, every nine and one half months, and every six months. In the places where breeding occurs every six months it has not yet been shown whether the same individuals breed in successive breeding periods, but I am at present carrying out work on Christmas Island (Pacific Ocean) designed to determine this.

During study of a large number of Sooty Tern skins in United States and British museums I observed an unexpected difference in the state of the primaries between samples of birds from populations where breeding is annual and from populations where breeding occurs every six months. This difference, described in the present paper, suggests that Sooty Terns in populations where six-monthly breeding occurs have

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evolved special modifications of the species' normal molt program, which enable them to breed at approximately six-month intervals and yet to replace their remiges often enough to maintain reasonable flying efficiency.

Sooty Terns in most populations appear to have a pattern of molt similar to that in a number of other tern species: that is, they undergo a postnuptial or "basic"[1] molt after breeding in which all feathers are replaced, and a prenuptial or "alternate"[2] molt shortly before the onset of breeding which does not involve the primaries or secondaries. Although Dwight (1901) says "The Terns undergo two complete moults in a year. . .," I know of no tern species for which there is adequate evidence that all the remiges are replaced twice each year. In some species none of the remiges are replaced more than once, while in others the inner primaries are replaced twice, the outer ones only once (Ashmole, in prep.). In the Sooty Tern I have found no indication that any of the primaries are replaced more than once between one breeding period and the next.

As in other terns, molt and breeding in the Sooty Tern are more or less mutually exclusive. (However, Brown Noddies *Anous stolidus* on Ascension Island and perhaps elsewhere sometimes breed and molt at the same time (Dorward and Ashmole, 1963).) Few museum specimens are accompanied by information as to whether the individuals were involved in breeding activities when collected, but Table 1 shows that most Sooty Terns collected on breeding grounds in all parts of the world have complete sets of primaries and rectrices. From some localities there are a few birds just completing the replacement of their primaries (primary molt scores 98 and 99), while from some breeding stations there are birds which have recently started a molt (primary molt scores nearly all below 30).[3] I have already shown (Ashmole, 1963) that on Ascension Island individuals complete a molt before starting to breed, but some at least start their postnuptial molt before their chicks

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[1], [2] These terms are those advocated by Humphrey and Parkes (1959).

[3] "Primary molt scores" are stages on the scale from 1 (= molt of primaries just started) to 99 (= molt of primaries almost completed); for details of the method of scoring see Ashmole (1962).

TABLE 1. Molt of primaries and rectrices of Sooty Terns collected on breeding grounds in different areas.[1]

Locality	Number of birds examined	Primaries: Proportion of birds molting	Primaries: Range in scores of molting birds[2]	Rectrices: Proportion of birds molting
GULF OF MEXICO AND W. INDIES				
Corpus Christi, Texas	17	0	—	0
Virgin Is.	12	0	—	0
EQUATORIAL ATLANTIC				
Fernando Noronha	33	.21	2-28, 98	.15
Ascension I.	107	.23	1-20	.13
SOUTH ATLANTIC				
Trinidade/Martin Vaz	11	0	—	0
INDIAN OCEAN				
Laccadive Is.	11	.18	2, 7	.09
NORTH PACIFIC				
Laysan	39	.03	98	.05
I. Isabela, Mexico	11	.18	2, 13	.09
I. Socorro	15	.20	4, 24, 48	.20
Clipperton I.	24	.04	99	.13
EQUATORIAL PACIFIC				
Christmas I.	16	.19	2, 98, 98	.06
Culpepper/Wenman, Galapagos	10	.30	All 98	.10
SOUTH PACIFIC				
Lord Howe I.	13	0	—	.23
Norfolk I.	10	.10	4	.10
Kermadec Is.	18	0	—	0
Tonga	11	0	—	0
Suvorov I.	40	.30	1-24	.15
Kauehi, Tuamotu Arch.	26	.04	98	.04
Marquesas Is.	19	.21	All 98	.05
Oeno	13	0	—	0

Notes. 1. Only breeding localities from which I have examined at least ten birds are included in this table.

2. See footnote in text for explanation of "primary molt scores."

become independent. Both on Ascension and elsewhere body molt of Sooty Terns occurs almost entirely while the birds are absent from the breeding grounds; I have so little information about it that I shall not consider it further in this paper.

PRIMARIES

Examination of molting birds on Ascension, and of skins of molting individuals, shows that in the Sooty Tern molt of the primaries normally starts with the first (innermost) feather and progresses outwards to the tenth (outermost long primary). Sooty Terns when breeding should thus have the innermost primaries oldest and the outer ones progressively newer, the whole series forming a smooth sequence. This was found to be the case in 86 per cent of all skins of birds collected on the breeding grounds and not in process of molt. However, in some birds there are striking differences in the condition of adjacent primaries; one finds a sudden break in the normal age-sequence part way through the series. This I have called a "discontinuity."[4] It should be emphasized that the discontinuities were not caused merely by molt in progress when the bird was collected; most individuals were not molting at all, and in the few which had recently started a molt the arrangement of old and new feathers at the discontinuity could not be explained as a result of the molt then in progress. It was evidently the result of an unusual molt sequence in the past, followed by a cessation of molt prior to breeding.

[4] Like many other species (Dwight, 1901) Sooty Terns have a pale "frosting" or "silvering" on the dark primaries and secondaries, which gradually wears off, thus making it easy to detect large differences in the age of adjacent feathers. I have recorded discontinuities only when the difference in the condition of adjacent feathers was sufficiently striking for there to be no doubt that they were of very different age. In badly set specimens it is difficult to assess the relative ages of the small inner primaries, especially as they tend to be protected from wear by the overlying secondaries. I may therefore have overlooked relatively new innermost primaries in some birds, and the figures for the occurrence of discontinuities between primaries 1 and 2 must be considered as minimum ones. Discontinuities further out in the series are not likely to have been overlooked, and there were few birds in which I was doubtful whether the feathers had been molted in regular sequence.

Discontinuities are found at all points in the primary series, but Table 2 (from which molting birds are excluded) shows that they are not distributed at random. Nearly all populations (see Table 3 for details) contain a small proportion of birds with first primaries much newer (occasionally much older) than the second, but in most populations (grouped in the bottom row of Table 2) discontinuities at other points in the primaries are rare. The sample from Ascension is separated since not only does it contain an especially large proportion of birds with discontinuities between primaries 1 and 2, but it also has a number with discontinuities between primaries 2 and 3;

Table 2. Distribution of discontinuities in the primaries of Sooty Terns collected on Ascension, on the Phoenix and Line Islands, on Bedout Island, and in the other localities mentioned in Table 3.

Locality	Number of wings examined		Number (above) and percentages (below) of wings with discontinuities at each point in the primaries									No. and % of wings with no discontinuities
			1/2	2/3	3/4	4/5	5/6	6/7	7/8	8/9	9/10	
Ascension Island	164 (=82 birds)	No.	20	8	1	2	0	0	0	0	0	133
		%	12	5	0.6	1	0	0	0	0	0	81
Phoenix and Line Islands	64 (=32 birds)	No.	2	0	2	2	5	6	8	7	12	34
		%	3	0	3	3	8	9	13	11	19	53
Bedout Island	10 (=5 birds)	No.	2	2	0	0	0	0	0	4	2	2
Other areas	946 (=473 birds)	No.	59	7	6	5	5	4	0	3	5	854
		%	6	0.7	0.6	0.5	0.5	0.4	0	0.3	0.5	90

Notes. 1. Molting birds are not included.

2. For each locality, the upper figures are the numbers of *wings* which show discontinuities at each point in the series of primaries. Wings are used rather than birds since the two wings on a single bird sometimes have discontinuities in different places.

3. The lower figures show the number of discontinuities at each position as percentages of the number of wings examined. Since there are sometimes two discontinuities in one wing, and both are included in the figures given, the percentages total more than 100 in some cases.

these are rare in other populations. Samples from two areas only contain an appreciable number of birds with discontinuities further out in the series than the second primary. One of these areas includes the Phoenix Islands and Line Islands in the central equatorial Pacific, while the other is represented by Bedout Island off the northwest coast of Australia. The distribution of discontinuities in the wings of birds from these areas (Table 2) seems certainly to indicate that many birds in these populations have a very different molt program from the birds breeding on Ascension and in the other localities from which specimens were examined.

Table 3 shows that, from population to population, there is no correlation between the frequency of occurrence of discontinuities between primaries 1 and 2 and that of discontinuities at other points in the series. Thus while 21 out of 38 birds from the Phoenix and Line Islands have discontinuities among pri-

TABLE 3. Occurrence of discontinuities among the primaries in adult Sooty Terns from different breeding areas.

	Occurrence of discontinuities only between primaries 1 and 2		Occurrence of discontinuities among primaries 2-10	
Geographical area	Number of specimens available	Number (and proportion) with discontinuities	Number of specimens available	Number (and proportion) with discontinuities
GULF OF MEXICO AND W. INDIES (incl. *Corpus Christi* (Texas), *Virgin Is.*)	74	13 (.18)	80	4 (.05)
EQUATORIAL ATLANTIC				
Fernando Noronha, Rocas Reef	34	2 (.06)	38	4 (.11)
Ascension I.	82	10 (.12)	106	6 (.06)
SOUTH ATLANTIC (*Trinidade/Martin Vaz*, St. Helena)	19	0 (—)	19	0 (—)
INDIAN OCEAN (incl. Gloriosa, Seychelles, Rodriguez, *Laccadive Is.*, Chagos)	21	2 (.10)	24	1 (.04)
NORTHWEST AUSTRALIA (Bedout I.)	5	1 (.20)	5	3 (.60)

Table 3 (Continued)

Geographical area	Occurrence of discontinuities only between primaries 1 and 2		Occurrence of discontinuities among primaries 2-10	
	Number of specimens available	Number (and proportion) with discontinuities	Number of specimens available	Number (and proportion) with discontinuities
Northwest Pacific Paracel Is., Philippines, Ryu Kyu Is., Bonin Is., Marianas)	13	3 (.23)	13	1 (.08)
North Central Pacific (Wake, Hawaiian chain incl. *Laysan*, Johnston)	79	2 (.03)	82	0 (–)
Northeast Pacific (Revilla Gigedo Is. incl. *Socorro*, *Clipperton*, Lower California, west coast of Mexico)	61	1 (.02)	63	2 (.03)
Equatorial Pacific				
Marshall Is.	5	1 (.20)	5	1 (.20)
Phoenix Is. (Howland, Baker, Canton, Enderbury, Phoenix)	9	1 (.11)	11	9 (.82)
Line Is. (Palmyra, *Christmas*, Jarvis, Malden, Starbuck)	23	0 (–)	27	12 (.44)
Galapagos Is. (*Culpepper/Wenman*)	10	1 (.10)	10	1 (.10)
Southwest Pacific (*Lord Howe*, *Norfolk*, *Kermadec Is.*, Fiji, *Tonga*, Samoa)	53	4 (.07)	55	1 (.02)
Southeast Pacific				
Cook Is., Society Is., Tubuai Is., Tuamotu Is. incl. *Kauehi*, *Marquesas Is.*, *Oeno*, Henderson, Ducie, Easter, San Felix	72	3 (.04)	73	1 (.01)
Suvorov, Tongareva	34	0 (–)	42	3 (.07)

Notes. 1. Only adult birds collected on the breeding grounds or within a few miles of them are included in this table.

2. Birds which were in process of primary molt are excluded, with two exceptions: (a) birds whose tenth primaries only were growing have been included, and (b) birds whose first and/or second primaries only were growing, have been used in the right-hand section but not in the left-hand section of the table: this accounts for the differences between the columns showing "Number of specimens available" in the two sections.

3. Where ten or more birds were available for examination of primaries 2-10, from one island or from a group of islands within a circle of radius 25 miles, the name of the island or group is italicized.

maries 2 to 10, only 1 out of 32—less than the average proportion—have discontinuities between primaries 1 and 2. Only on Ascension, as already mentioned, are there an appreciable number of birds in which primary 2, together with 1, is strikingly different in age from the rest. Probably in this case birds with the first and second primaries very different in age from the next outwards should be classed with those in which only the first primary is affected.

I suspect that discontinuities far out in the series are normally produced under quite different circumstances from those between primaries 1 and 2. I have already suggested with respect to the Ascension population (Ashmole, 1963) that birds with first (or first and second) primaries newer than the next outwards may be young birds breeding for the first time; in immature Sooty Terns successive sequences of primary replacement often overlap, so that as one sequence is nearing completion with the growth of the outermost primaries, another sequence is starting with the innermost ones. If molt stops for breeding at the completion of one sequence, the outermost feathers will be new, but so may be the innermost ones, with a discontinuity outside them.

It is not possible to explain in this way the extremely high incidence of discontinuities (Table 3) among the outer primaries in the samples from the Phoenix and Line Islands, while the small sample from Bedout Island may also require a different explanation. It can be no coincidence that it is on certain of the Phoenix Islands and Line Islands, alone of the places from which I have examined an appreciable number of specimens, that Sooty Terns are known to have two breeding periods each year (Ashmole, 1963).

It has been argued (Ashmole, 1963) that the Sooty Terns on Ascension are breeding as often as they can—that breeding, followed by a complete molt, occupies about nine and a half months. But if this is the minimum time needed by the Ascension birds, it is difficult to see how the birds in the Phoenix and Line Islands (where there are two breeding periods each year) could breed and undergo a complete molt in a period of only six months. It is therefore not surprising that it has been tentatively suggested in the past (Richardson and Fisher, 1950; Hutchinson, 1950; Chapin, 1954) that in the areas where breeding occurs every six months, different populations of birds might be involved in successive breeding periods, so that each individual would breed only once a year. I also felt that this must be the explanation, until I examined specimens of the Sooty Terns from the islands concerned, and found that many of the breeding birds had some old and some new primaries, and had evidently not undergone a complete molt between breeding periods.

As it has been pointed out, Sooty Terns in other parts of their range, where breeding occurs only once each year, have a straightforward complete replacement of all their remiges after breeding. If the individuals on the Phoenix and Line Islands were also breeding only once a year, how could one explain the fact that many of them do not have a complete set of new remiges when they start breeding? The most reasonable hypothesis seems to be that at least some individuals breed in successive breeding periods and replace only some of their wing feathers in the short interval in between. It is likely, however, that no one individual breeds in every breeding period.

The sample from Bedout Island (N.W. Australia) is very small, but three out of the five birds show discontinuities among primaries 2-10. Sooty Terns have so far only been recorded as breeding in autumn on Bedout. However, it would not be surprising if they were found to have two breeding periods there each year, since Serventy (1952) has shown that they breed in autumn on islands to the north of Bedout, but in spring on islands further south (see Appendix in Ashmole, 1963, for details). Bedout is at about the latitude at which several other species of sea birds change from autumn to spring breeding, and some of them are already known to breed in both seasons, on Bedout and certain other islands (Serventy, 1952).

Of the other localities from which there are reasonably large samples, Fernando Noronha (where the interval between successive breeding periods has not yet been determined) has most birds with discontinuities among primaries 2-10, but the proportion is far lower than in the samples from the Line Islands and the Phoenix Group. Of the latter, the Line Islands have the lower proportion, but even this is significantly higher than among the Fernando birds ($P < .01$). It is evident, therefore, that the populations from the Line and Phoenix Islands show peculiarities which are almost entirely absent in the other popu-tions sampled. This is expected on my hypothesis that peculiarities in the molt normally occur only in individuals which breed in successive breeding periods about six months apart.

Table 3 shows that although the proportion of birds with discontinuities among primaries 2-10 is far higher in both the Phoenix and Line Islands than in any other area apart from Bedout Island, it is appreciably higher in the small sample from the Phoenix Group than in that from the Line Islands. This difference as it stands is statistically significant (at the 5 per cent level), but both samples are heterogeneous (birds collected from several different islands, in different years and at different stages in the breeding periods), so I doubt whether it is meaningful.

Examination of the precise arrangement of new and old feathers in the primaries of birds from the Phoenix and Line Islands and from Bedout Island, may help towards an understanding of the molt program in these populations and of the way in which breeding and molt are interrelated; some actual examples are therefore given below. In the examples, N represents an apparently brand new feather, (N) a newish one, (O) an oldish feather, and O an old, worn feather. Where a series of adjacent feathers have been replaced in a regular sequence, they may grade from one category to another; in such cases the two terminal members of the series are joined by an arrow headed towards the newest feather. The figures 1, 2, 3 and 4 represent successive stages in the growth of a feather (see Ashmole, 1962:255).

		1	2	3	4	5	6	7	8	9	10
1. Suvorov	L.	N	N	N	O	O	O	O	O	O	O
	R.	N	N	N	O	O	O	O	O	O	O
2. Fernando Noronha	L.	1	(N)	(N)	(N)	(N)	(N)	(N)	(N)	(N)	O
	R.	1	(N)	(N)	(N)	(N)	(N)	(N)	(N)	(N)	O
3. Jarvis I.	L.	1	(N)	(N)	(N)	(N)	O	O	O	O	O
(Line Is.)	R.	(N)	(N)	(N)	(N)	(N)	O	O	O	O	O

		1	2	3	4	5	6	7	8	9	10
4. Enderbury I. (Phoenix Is.)	L.	(N)	——	——	——	——	——	——	——	——→	N
	R.	(N)	——	——	——	——	——	——	——→	N	O
5. Fernando Noronha	L.	O	——	——	——	——→	(O)	(N)	(N)	(N)	(N)
	R.	O	——	——	——	——→	(O)	(N)	(N)	(N)	(N)
6. Baker I. (Phoenix Is.)	L.	(O)	(O)	(O)	N	N	(O)	(O)	(O)	(O)	(O)
	R.	(O)	(O)	(O)	N	N	(O)	(O)	(O)	(O)	(O)
7. Jarvis I. (Line Is.)	L.	4	1	(N)	(N)	(O)	(O)	(O)	(N)	(N)	(N)
	R.	3	(N)	(N)	(N)	(O)	(O)	(O)	(N)	(N)	(N)
8. Palmyra I. (Line Is.)	L.	N	N	N	N	N	(O)	(O)	N	N	N
	R.	N	N	N	N	N	N	N	N	N	N
9. Christmas I. (Line Is.)	L.	(O)	——	——→	(N)	O	O	O	O	(N)	(N)
	R.	(O)	——	——→	(N)	O	O	O	O	(N)	O
10. Enderbury I. (Phoenix Is.)	L.	(N)	——	——	——→	N	(O)	(O)	(O)	N	(O)
	R.	(N)	——	——	——→	N	(O)	(O)	(O)	N	(O)

In most birds with discontinuities among primaries 2-10, both from areas where breeding occurs annually and from those where it occurs every six months, the feathers inside the discontinuity are newer than those outside it (see examples 1-4). This condition is the one which would arise if a normal sequence of primary replacement stopped part way through the series. Patterns of the type shown in example 5, in which there is a definite discontinuity between old feathers on the inside and newer ones on the outside, would result if, after primary replacement had stopped part way through the series for breeding, it later started again where it had left off, and then continued outwards.[5] However, the condition shown in example 5 is uncommon in all Sooty Tern populations. This suggests that normally, when a bird with the inner feathers newest (as in example 1) starts to molt again, the innermost primaries, rather than those immediately outside the discontinuity, are replaced first; this is in fact what is occurring in examples 2 and 3.

[5] Something equivalent to this certainly occurred in the replacement of the secondaries of some Black Noddies *Anous tenuirostris* on Ascension Island (Ashmole, 1962).

The other examples shown are of the more complex situation in which there is more than one discontinuity among the primaries in one or both wings. Patterns of this type, which are found in a significant proportion of the birds from areas where breeding occurs every six months, have not yet been found among birds from annual-breeding populations. They could not be produced during a molt program in which each primary was always replaced in regular sequence outwards through the series, but they could arise if an incomplete primary replacement was succeeded, after the breeding period, by another incomplete molt, and if feathers replaced late in the first of these molts tended to be skipped during the next. In this case the bird in example 1, if it underwent another incomplete molt, might in the next breeding period be in a condition similar to example 6, for instance:

	1	2	3	4	5	6	7	8	9	10
L.	(O)	(O)	(O)	N	N	N	N	O	O	O
R.	(O)	(O)	(O)	N	N	N	N	O	O	O

Another partial molt could lead to conditions comparable to those in examples 7-10, for instance:

L.	N	N	N	(O)	(O)	(O)	(O)	N	N	N
R.	N	N	N	(O)	(O)	(O)	(O)	N	N	N

or

L.	N	N	N	(O)	(O)	(O)	(O)	N	N	O
R.	N	N	N	(O)	(O)	(O)	(O)	N	N	O

It will be clear from what has been said that it is not necessary to postulate a random molt sequence to account for the complex patterns of old and new primaries found in the wings of some Sooty Terns. The indications are that in these birds as in all other terns molt in the primaries proceeds from the inside outwards, but that many individuals in populations where breeding occurs every six months fail to replace all their primaries between successive breeding periods, and that subsequent molts are modified by the presence in their wings of a mixture of old and new feathers.

SECONDARIES

As in other tern species, replacement of the secondaries in Sooty Terns starts much later than that of the primaries, but is completed at the same time or only a little later. Replacement normally starts at the two ends of the series of secondaries, and it is some of the middle feathers (often numbers 12 and 13 counting from the carpal joint inwards) which are the last to be replaced. After the complete replacement of the secondaries in this manner there should be no appreciable discontinuities within the series, but the feathers at the two ends of the series will be oldest, and the middle ones newest. This is in fact the situation found in nearly all specimens from most Sooty Tern breeding colonies, including Ascension Island (Table 4). This must imply that all the secondaries are replaced once between breeding periods. However, in several populations

Table 4. Numbers of Sooty Terns with discontinuities among the secondaries, in relation to the incidence of discontinuities among primaries 2-10, in different populations.

	Birds without discontinuities among primaries 2-10		Birds with discontinuities among primaries 2-10	
Geographical area	Number examined	Number with discontinuities among secondaries	Number examined	Number with discontinuities among secondaries
Gulf of Mexico and W. Indies	72	0 (+2?)	2	1
Ascension I.	74	1	6	1
Indian Ocean	22	0 (+1?)	1	1
Phoenix Is.	2	2	8	6 (+2?)
Line Is.	13	4 (+1?)	11	11
South Pacific (incl. Marquesas, but not Suvorov)	116	4 (+1?)	1	0
Suvorov	26	9 (+6?)	3	2 (+1?)

Notes. 1. Birds undergoing molt of primaries or secondaries are excluded, except for those in which only the first primaries have so far been shed.

2. Additional figures in brackets, followed by question-marks, represent birds whose secondaries show probable, but not striking, discontinuities.

birds are found which have some secondaries much older than the rest. I did not examine the secondaries of all specimens, and there were a good many doubtful cases, so I cannot give reliable figures for the frequency of this peculiarity in all populations. However, Table 4 gives the information for those populations from which the secondaries of a fair proportion of the available specimens were examined.

As might be expected, the populations in which many birds show discontinuities in the primaries (Phoenix and Line Islands) also contain many birds with discontinuities among the secondaries. However, in these populations some of the birds without discontinuities in the primaries, nevertheless have secondaries which do not seem to have been replaced in a smooth sequence: evidently the molt cycle is not entirely normal even in these birds.

Among localities where discontinuities in the primaries are rare, the island of Suvorov, south of the equator in the central Pacific, is the only one from which I have a fairly large sample, in which many birds have discontinuities among the secondaries (Table 4). In these birds some of the middle secondaries tend to be much older than the rest, suggesting that the secondary molt has stopped before completion. This situation invites comparison with the Black Noddies on Ascension Island (Ashmole, 1962), where the primary molt was apparently never cut short at the start of breeding, but some of the old middle secondaries, which are normally molted slightly later than the last primaries, were sometimes retained through the breeding period and replaced immediately after it. The occurrence of a similar phenomenon among the Sooty Terns on Suvorov suggests that the breeding cycle there may be abnormal in some respect, but there is very little information on the times of breeding (Ashmole, 1963).

RECTRICES

Replacement of the tail feathers of Sooty Terns normally starts with the outermost feathers (number 6 on each side), the central pair (number 1) being molted next; molt probably then continues in the sequence 2, 3, 5 and 4. It is possible that in the annual-breeding populations all the rectrices are then replaced again before the next breeding season, but in the Ascension population there was evidence that the outer pair alone are replaced twice (Ashmole, 1963). In the Ascension birds the outer webs of the outermost feathers are normally white in the breeding period, but are more often, if not always, dark in the non-breeding period. In other populations there is much variation in the color of these feathers, and samples from different populations sometimes also differ markedly. In some areas nearly all the birds taken on the breeding grounds have entirely white outer webs to the outer rectrices (69 out of 82 birds from the North Central Pacific), but in other places (e.g. Fernando Noronha, the Southeast Pacific, the Phoenix and Line Islands, and Suvorov) the proportion is much lower. It is likely that in the populations in which breeding occurs every six months not even the outermost rectrices are always replaced twice between successive breeding periods. I cannot suggest any explanation of the different frequencies with which dark color is present in the outer webs of these feathers in other populations.

DISCUSSION

The data presented in this paper, together with the information on the times of breeding of various Sooty Tern populations given by Ashmole (1963), show that the schedule of breeding and molt evolved among the Sooty Terns of the Phoenix and Line Islands is remarkable both in that breeding occurs every six months, and in that the program of molt is flexible to a unique degree. It appears that an individual sometimes undergoes a complete molt without interruption but at other times replaces only some of its primaries and secondaries between one breeding cycle and the next.

I have already mentioned that in the populations where breeding occurs every six months, individuals which have undergone only a partial molt before breeding generally have the outer primaries older than the inner ones. Since the outer primaries are also more subject to wear, it is not surprising to find some individuals with outer primaries in extremely poor condition while breeding. These birds are doubtless below their maximum flying efficiency, but if the curtailed molt has enabled them to breed in a breeding period which they would otherwise miss, the disadvantage may on balance be outweighed. However, it is clear that the molt program in the Phoenix and Line Island populations, in which the inner primaries are on an average replaced more often than the outer ones, although the latter get more wear, is not the most efficient that might be evolved. More birds would be close to maximum flying efficiency for more of the time if molt always started from where it had left off, so that the primaries were always replaced in order of age. This evidently happens sometimes but cannot be common.

Although I have argued that the presence of discontinuities among the primaries of breeding individuals from the Phoenix and Line Islands implies that these birds were involved also in the previous breeding period only six months before, I am not suggesting that individuals breed *every* six months. It seems unlikely that a pair could raise a chick successfully in one breeding period and yet be ready to breed again in the next breeding period only six months later. With the time required for courtship plus incubation for a month and feeding the young for two to three months (longer if the juveniles are not independent as soon as they leave the colony), very little time would be left before the next breeding period. I would guess that birds which raise a chick in one breeding period may then undergo a complete molt, missing the next breeding period: this would account for the proportion of birds from the Phoenix and Line Islands which appear to have undergone a perfectly normal and complete molt. Many of the birds, however, losing their eggs or their chicks while fairly young, could be ready to try again in the next breeding period, after only a partial molt.

This reasoning is of course highly speculative, and further discussion of the factors controlling the schedule of breeding and molt in the Sooty Terns of the Phoenix and Line Islands will be profitable only when we have more information on the sequence of events in individual birds from one of these populations.

ACKNOWLEDGMENTS

This account of molt in populations of *Sterna fuscata* forms a complement to my study of the species on Ascension Island during the course of the British Ornithologists' Union Centenary Expedition (Ashmole, 1963). The present paper is a product of my examination of a large number of skins of *Sterna fuscata* during the summer of 1960, while I was the holder of a Seessel fellowship at Yale University. I am most grateful to Professor G. E. Hutchinson who suggested a study of specimens of the species and who with Dr. S. Dillon Ripley enabled me to visit Yale. I must also thank Dr. Philip S. Humphrey, who gave me much of his time during my work in the Yale Peabody Museum, and whose wide knowledge of molt was a constant stimulant. My visit to Yale was made while I was a member of the Edward Grey Institute of Field Ornithology, Oxford; it is a pleasure to thank the Director, Dr. David Lack, for encouraging me to go to Yale, for helpful discussion of my work and for reading a draft of this paper. My wife has also made many helpful criticisms of the manuscript.

Tern specimens were studied in the collections of the following institutions: Peabody Museum of Natural History, New Haven (which contains the bulk of the collections made by the "Blossom" South Atlantic expedition, sponsored by the Cleveland Museum of Natural History); American Museum of Natural History, New York (which has fine series of Sooty Tern skins collected by the Whitney South Sea Expedition); United States National Museum, Washington, D.C.; Museum of Comparative Zoology, Cambridge, Mass.; Museum of Zoology, Ann Arbor, Michigan; Department of Conservation, Cornell University; British Museum (Natural History), London. I am grateful to the curators of all these collections for the facilities they offered me. In addition, skins were generously loaned by the authorities of the California Academy of Sciences, the Los Angeles County Museum, the Carnegie Institution, Pittsburgh, the Academy of Natural Sciences of Philadelphia, the Museum of Zoology, Ann Arbor, Michigan, the Kansas University Mu-

seum of Natural History, the Chicago Natural History Museum, the United States National Museum and the Bernice P. Bishop Museum, Hawaii.

SUMMARY

The Sooty Tern *Sterna fuscata* in most parts of its range breeds at the same season in each year, and study of museum specimens shows that the individuals replace all their remiges and rectrices between breeding seasons. On Ascension Island, where breeding occurs every nine and one half months, there is also a complete molt between successive breeding periods. However, among birds from the Phoenix Islands and Line Islands in the central equatorial Pacific, where breeding occurs every six months, many individuals have "discontinuities" among the primaries and secondaries, indicating that they have not undergone a complete molt between successive breeding periods. These populations have apparently evolved a uniquely flexible molt program, such that under certain circumstances (perhaps the successful rearing of a chick) breeding is followed by a complete molt, but often molt stops and the bird breeds again before all of the primaries and secondaries have been replaced. It is suggested that because of this flexibility in the molt, individuals are sometimes able to take part in successive breeding periods only six months apart.

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YALE PEABODY MUSEUM
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A NEW PEREGRINE FALCON FROM THE CAPE VERDE ISLANDS, EASTERN ATLANTIC OCEAN

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In the course of preparing a survey paper on the peregrine falcons, *Falco peregrinus*, of Eurasia and North Africa, we had occasion to examine three falcons taken in Cape Verde Islands a number of years ago by the "Blossom" Expedition of the Cleveland Museum of Natural History. On the basis of these same specimens, the peregrine was recorded as a migrant on the Cape Verde Islands by Bourne (1955) who also saw "large hawks . . . around the rocks of S. Thiego" and suggested that "the species may breed." More recently, Abbé Réné de Naurois saw peregrines nesting on Cima, one of the Rhombos Islets between Raza and Fogo (pers. comm. 1963). We thank both these authorities for their assistance.

The Cape Verde specimens are as large as *F. p. peregrinus* and *F. p. calidus* of the northern Palearctic, but they differ radically from these two subspecies in showing a strong rufous wash on the head, mantle and underparts as in some specimens of the smaller Mediterranean race, *brookei*, and all specimens

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of the North African desert subspecies, *pelegrinoides.* We, therefore, describe the Cape Verde breeding population of the peregrine falcon as:

Falco peregrinus madens, subsp. nov.

Type: Adult ♀ (Y.P.M. 44551), collected at Provocão, Brava, Cape Verde Islands, in 1924, by John da Lomba and Robert H. Rockwell on the "Blossom" Expedition.

Diagnosis: The adult female differs from typical European *Falco p. peregrinus* in being much more brownish and saturated, with the crown and nape feathers strongly tinged with brown and rufous producing an irregular rufous nuchal collar. The brownish shading extends down onto the mantle but disappears on the lower back and rump which are grey as in *peregrinus.* The black "moustaches" are edged rufous and the light cheek patches are suffused with the same color. The general appearance is of a tawny wash or suffusion throughout the underparts including the flanks and thighs but not the lower abdomen and vent which are isabelline.

The adult male also differs from *peregrinus* in having the crown, nape and mantle washed with brown and rufous to produce a distinct rufous nuchal collar. Below, there are traces of rufous wash on the black edges of the "moustaches" and the underparts are suffused throughout with dull pinkish buff. The immature female has a pronounced rufous nuchal patch and rufous edging to the feathers of the anterior part of the crown. It is heavily streaked below and roughly similar in tone of color to immature specimens of *brookei* although the rufous wash on the brownish black "moustaches" is striking.

This population differs from the migrant tundra form, *calidus,* in being darker, blackish brown, not grey or slaty on the upperparts, and in being washed with rufous on the head and cheeks and isabelline or pinkish buff on the remainder of the underparts.

Compared with the darkest specimens of the smaller Mediterranean subspecies, *brookei,* the two adult birds are as dark or even darker on the upperparts, less slaty, more blackish, with the dark shade extending further down the back. There is a much more pronounced rufous wash over the head, nape, cheeks and underparts, but the dark spots and barring are somewhat reduced below.

From *pelegrinoides*, which it resembles in having a rufous wash about the head, *madens* differs by being larger and altogether darker, more blackish above, and more heavily washed with darker buff below. The spotting on the underparts is heavier, especially in the male.

MEASUREMENTS:		Wing (mm)	Tail (mm)	Culmen (mm)
YPM 44551 (Type)	ad. ♀	340	156	54.5
YPM 44553 (paratype)	ad. ♂	320	151	60.0
YPM 44552 (paratype)	juv. ♀	315	152	54.5

RANGE: Cape Verde Islands; recorded so far on Brava, São Thiago, and Cima islands.

REMARKS: The adult female is in freshly molted definitive basic plumage; the male collected on São Thiago April 22, 1924, was undergoing prebasic molt (primary 4 completing regrowth); and the young bird, collected on Brava, date unknown, was just beginning first prebasic molt (primary 5 lost, scattered first basic feathers on throat, upper breast and mantle).

The Cape Verde peregrine population continues a north to south cline of increasingly darker coloration from *calidus* through *peregrinus* to *brookei.* It shows in the rufous wash of the head and underparts an approach to the paler Canary Island and North African desert peregrine, *F. p. pelegrinoides.* A male identified as *pelegrinoides* (No. 537300 in the American Museum of Natural History) which had been kept at Tring, England for five years, but which was said to have come from Morocco (Hartert, 1915), is as dark as the male from the Cape Verde Islands, although the black on the mantle does not extend so far down the back. Below, this captive bird is even darker, providing a good example of the well-known tendency of individual peregrines to molt into darker or lighter plumage in response to altered diet and environment.

F. p. pelegrinoides and the desert peregrine of Asia, *F. p. babylonicus*, have recently been separated from the forest and tundra peregrines as a distinct species by Vaurie (1961) and Dementiew and Iljitschew (1961). The existence of populations intermediate in color, such as this from the Cape Verde Islands and another in North Africa ("*punicus*" see Kleinschmidt, 1912-1927, p. 95-96), and records of cross-mated pairs producing young in India (Dodsworth, 1913), however, induce us to retain all the peregrines in one cosmopolitan species. We shall discuss further the significance of intermediate specimens in another paper.

The long wing measurement of the Cape Verde Island population is unexpected, since there is a distinct north to south cline of decreasing wing length in the continental populations from northern Europe to Africa. It is possible, however, that a large predator nesting in the cliffs of a small oceanic island would need to forage at a distance so that a mutation for long wings would be at a selective advantage in a small population. Furthermore, the cold Canary Current from the north and local upwelling result in a climate remarkably temperate for the tropics, especially in summer (Murphy, 1924). If Bergmann's rule which appears to be valid in this species is related to temperature, the low summer temperature of the Cape Verde Islands may help account for the longer-winged peregrine.

The subspecific name is derived from the present participle of the Latin verb *madeo* and refers to the "saturated" plumage of the Cape Verde Island peregrine.

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ONTOGENY AND EVOLUTION IN THE MEGAPODES (AVES: GALLIFORMES)[1]

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INTRODUCTION

Unlike all other birds, megapodes of Australia and the Pacific Islands incubate their eggs in mounds or holes by heat from fermentation, sun, or volcanic activity. Furthermore, megapodes are unique among birds in being able to fly weakly on the day of hatching and in having no parental care for young.

These and other reptile-like aspects of megapode reproduction have been interpreted in two contradictory ways. Some authorities (e. g. Portmann, 1938, 1950, 1955) have maintained that megapodes are the most primitive of living birds, while others (e. g. Pycraft, 1910) have stated that the similarities of megapodes and certain reptiles are due to convergent evolution. A related and also unresolved problem has been the primitiveness of mound-building megapodes relative to those laying their eggs in holes (cf. Frith, 1962).

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[1] This study is based on a dissertation presented for the degree of Doctor of Philosophy at Yale University.

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Despite their anomalous nidification and precocity of young, megapodes as adults are structurally similar to other members of the Order Galliformes (e. g. pheasants) as exemplified by the overlap in adult osteological proportions (cf. data of Verheyen, 1956). Morever, the family Megapodiidae and the New World gallinaceous family Cracidae (chachalacas, guans, curassows) are particularly difficult to separate at the family level on a morphological basis (cf. Miller, 1924). Megapodes and cracids have been classified as the two most primitive gallinaceous families (Huxley, 1868; Peters, 1934).

Unlike the megapodes, most other species of Galliformes have a simple nest on the ground, but some pheasants, cracids, and the highly aberrant hoatzin (*Opisthocomus*) nest in trees. Since avian development often varies in accord with nidification, it was anticipated that the study of megapode embryos and juveniles would reveal clues pertinent to the analysis of megapode phylogeny.

Prior to this study, the only detailed accounts of structure of embryonic or juvenile megapodes were based on the genus *Megapodius* (cf. Pycraft, 1900; Friedmann, 1931; Becker, 1959). These previous investigations had led to contradictory conclusions on the homologies of the early plumages (cf. Nice, 1962) and on the phylogenetic origins of the family (cf. Frith, 1962). The object of the present study was to attempt to resolve the controversy over the phylogeny of megapodes through examining the morphology of embryos and juveniles representing several genera of megapodes.

MATERIALS AND METHODS

Specimens. Thirty embryos of the megapodes *Talegalla jobiensis* and *Leipoa ocellata* were studied (Tables 2, 3). The 11 *Talegalla* embryos were collected for this investigation in New Guinea during 1959-60 by E. T. Gilliard and S. D. Ripley in separate expeditions. The 19 *Leipoa* embryos were collected by me during 1960 in the mallee about 25 miles north of Griffith, New South Wales, Australia; the collecting area was favorable in having an unusually high density (Frith, 1959) of active *Leipoa* mounds which were as frequent as one per 50 acres in the limited suitable terrain. The eggs of *Leipoa* were marked as found and allowed to incubate in the mounds. Subsequent collections provided accurate ages for three embryos and minimal ages for certain others (Table 2). The temperature is ordinarily relatively uniform for *Leipoa* eggs together in a mound (Frith, 1959), and the time between egg layings by a hen is usually four or more days (Frith, 1959, and a few cases in this study). Thus when actual or minimal age of one embryo was known, minimal ages of progressively larger embryos in that mound were estimated by adding four more days for each. Since the first eggs were probably laid on September 4 or later, as judged from previous years (Frith, 1959), some specimens (Nos. 12, 16, 19, 1195, of Table 2) could be assigned presumed maximal ages; smaller embryos from the same mounds could also be assigned maximal ages, again using the hypothesis of four or more days between egg layings in a mound.

Eighty-two juvenile specimens (including 79 study skins) of megapodes were examined at the American Museum of Natural History and Yale Peabody Museum (YPM). Among these were the following species (with numbers of each): *Megapodius freycinet* (59), *M. laperouse* (5), *M. pritchardii* (1), *Macrocephalon maleo* (1), *Aepypodius arfakianus* (2), *Talegalla cuvieri* (2), *T. fuscirostris* (4), *T. jobiensis* (4), *Alectura lathami* (3), and *Leipoa ocellata* (1). More than 140 embryonic and juvenile specimens representing 22 genera of nonmegapode Galliformes were used for comparison.

Methods. Characters were chosen for interspecific morphological comparisons according to 1) potential accuracy of description or measurement, as determined by reproducibility in repeated examinations, and 2) potential phylogenetic significance demonstrated by the extent of intergeneric variation and its possible phylogenetic interpretations.

Measurements. Measurements, selected for their applicability over a wide range of sizes, were:

WING: folded and flattened, with a rule from the anterior edge of the wrist to the end of the manus, or, in feathered specimens, to the most distant tip of a remex. Due to the distal shriveling of the ensheathed remiges of embryonic megapodes, wing lengths over 20 mm (Tables 2, 3, 5) were rounded to the nearest 5 mm.

Tarsus: with Vernier calipers from the posterodorsal surface of the ankle along the tarsometatarsus to the level of the proximal surface of the base of the hallux.

Culmen: with calipers from the tip to the most posterior unfeathered point on the dorsal midline.

Humerus; radius: respective maximal lengths with calipers.

Third (middle) digit: straightened, with a rule from the tip to the most distal point of webbing connecting with an adjacent toe.

Megapode embryos Nos. 1, 20, and 21 (Tables 2, 3) were too immature to measure by these criteria.

Values in the Tables (2, 3, 5) are means of two measurements, each of which, unless otherwise noted, was rounded to the nearest millimeter. Estimated maximal ranges of variation in measuring were ± 1 mm for dimensions of 2 to 10 mm and up to ± 3 mm for dimensions of 150 mm; these maximal estimates were derived from the ranges in duplications of more than 500 measurements. Among the factors possibly affecting the accuracy in measuring were 1) unavoidable errors in aligning and reading calipers and rule, 2) structures changing in shape as well as length, 3) variations in the positions of parts of specimens at fixation, and 4) (for anatomical specimens) rate of fixation with 10 per cent formalin.

Weights (Tables 3, 5), recorded by collectors in the field, are given only for fresh specimens, as weights of preserved specimens would be unreliable. The weights and their cube roots were plotted on arithmetic and double logarithmic graphs against the various linear dimensions; if any one of the weights for *Talegalla* were grossly in error, this would have been seen as a point lying relatively far from the plot for the other points. Factors possibly influencing accuracy in weighing include uneven removal of the yolk sac of embryos before weighing, uneven drying of surface moisture on the feathers of embryos, and variations in the contents of the digestive tract of juveniles.

MORPHOLOGY OF EMBRYOS AND JUVENILES

Time in embryonic development. Young embryos of the megapode *Leipoa* developed slowly compared with embryos of phasianids (e. g. *Gallus, Phasianus, Coturnix*), as shown by the much later occurrence of the first gross appearance of egg tooth, feathers, labial groove, etc., in *Leipoa* (Table 1). Through the first 20 days, these *Leipoa* embryos attained a much smaller absolute size than did embryonic chickens (domestic *G. gallus*) as illustrated by comparing linear dimensions of *Leipoa* and chickens (Fig. 1; Tables 2 and 3). As an example, after 20 days of incubation the wing of an embryonic *Leipoa* was less than 50 per cent as long as that of a chicken (Fig. 1).

The normal incubation period of *Leipoa* is generally at least twice as long as that of known phasianids or turkeys (cf. Table 1; see also Frith, 1959, on *Leipoa*, and Romanoff, 1960, on phasianids). This lengthy incubation period of *Leipoa* is

TABLE 1. Time of certain gross morphological changes in embryos of the megapode *Leipoa* and of phasianids. Age in days after laying of the egg.

	Leipoa age	*Phasianus* age	*Coturnix* age	*Gallus* age
Egg tooth formed	21-22	9	5-6	6½-7
Labial groove formed ..	21-22	?	?	10
Feathers appear	11-21	9	5-6	6½-7
Toes are first separated	11-21	10-12	7-8	8-9
Scales appear on legs ..	29-54	13	8?-9	11-12
Eyelids come together ..	29-61	15	10-11	13
Labial groove lost	29-61	?	?	19
Hatching	60-73	23-24	16	20-21

Sources of data: *Leipoa ocellata*, specimens of this study; *Phasianus colchicus*, Fant, 1957, and Westerskov, 1957; *C. coturnix japonica*, Padgett and Ivey, 1960; domestic *G. gallus*, Hamilton, 1952.

related to both the slow early development and the large size at hatching (see p. 27 for discussion of the effects of incubation temperatures).

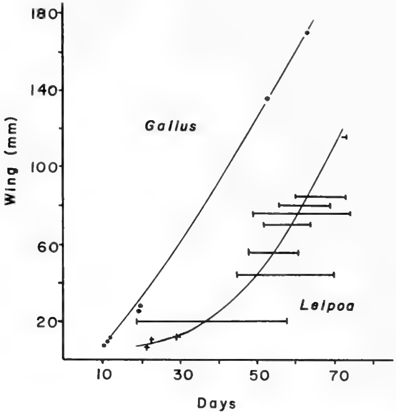

Figure 1. Chronological growth of the wing in *Leipoa ocellata* and domestic *G. gallus* (data from Tables 2 and 3). Curves showing length against time were fitted by inspection and should not be considered as quantitatively accurate.

Relative proportions and growth. At hatching *Talegalla* and *Leipoa* are about two to 15 times heavier than other newly hatched Galliformes of the genera *Coturnix*, *Colinus*, *Phasianus*, *Gallus*, and *Meleagris* (Lyon, 1962; Westerskov, 1957; Romanoff, 1960; see also Table 6). It is of interest that *Leipoa* and *Talegalla* at hatching have proportions and size like those of adult *C. coturnix japonica* (Table 5). The genus *Megapodius* is intermediate in hatching weight (Table 5) between *Talegalla* and phasianids or turkeys.

As a means of comparing changes in proportions during the growth of different species of the Order Galliformes, arithmetic and double logarithmic plots (e. g. Figs. 3, 4, 5) were prepared using the linear measurements of embryos and juveniles (data of Tables 2, 3, and 5). Such proportional growth was described approximately in certain cases by using the conventional allometric equation, $Y = AX^B$, or the equivalent form, $\log Y = \log A + B \log X$, where X and Y are the values of two dimensions. A and B (Table 4) were calculated using Bartlett's method as described by Simpson, Roe, and Lewontin (1960). B values for different species were compared using a modified t-test (Simpson *et al.*, 1960). Correlation coefficients for the sets of data expressed as B values in Table 4 were all significant at the 0.001 level.

To compare growth of linear dimensions relative to total body size in different species, the cube root of weight was used as one criterion for body size (see Amadon, 1943, for the

TABLE 2. Data for specimens of *Leipoa ocellata*. All are embryos except 1195. For procedures of measuring, see text. All lengths in millimeters. Estimated ages in days. Symbols: S, specimen number; W, wing length; T, tarsal length; C, culmen length; H, humerus length; R, radius length; Td, length of third digit; m, male; f, female;—, observation could not be made.

S	W	T	C	H	R	Td	Sex	Age
1	—	—	—	—	—	—	—	11-?
2	7	3	3	5	3	3	—	21-22
3	9	6	5	6	6	4	—	22
4	12	8	7	10	10	6	—	29
5	13	8	8	10	9	7	—	?-54
6	20	12	9	13	13	11	m	19-58
7	20	13	9	13	12	10	m	?-55
8	25	14	10	16	14	12	f	?-59
9	25	15	10	17	18	13	m	?
10	40	19	12	20	20	15	m	?
11	45	20	11	23	20	15	m	?-62
12	45	21	12	22	21	15	m	45-70
13	55	22	12	22	23	16	f	48-61
14	70	24	14	28	26	19	m	?-63
15	70	23	13	27	25	17	—	52-64
16	75	25	14	28	27	18	m	49-74
17	80	26	13	28	29	20	f	56-69
18	80	24	14	31	28	20	f	?-67
19	85	26	14	29	30	20	f	60-73
1195*	115	28	—	38	37	24	—	?-73

* This specimen, found dead in the field, was lacking its head.

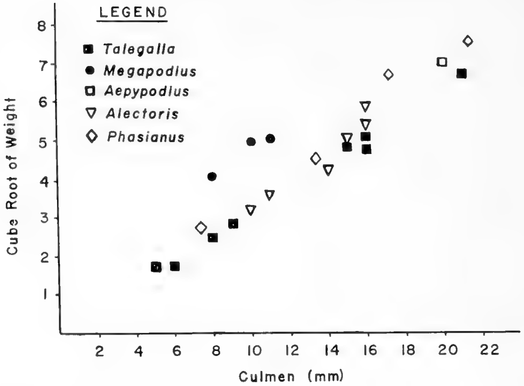

Figure 2. Relationships of the cube root of body weight in grams to the culmen length in the megapodes *Talegalla jobiensis, Aepypodius arfakianus, Megapodius freycinet* and the phasianids *Alectoris chukar* and *Phasianus colchicus.* All data from this study except that for *Phasianus,* for which mean values for males were taken from Westerskov, 1957. See text for discussion.

explanation of this procedure). Since weights were unknown for most specimens, a linear criterion for body size was also chosen. As the culmen length had a relatively direct relationship to the cube root of body weight over a fifty fold range of weights for eight specimens of embryonic and juvenile *Talegalla jobiensis* and for six juvenile specimens of the phasianid *Alectoris chukar* (Fig. 2), culmen was selected as a convenient linear measure for body size in these specimens. Moreover, similar analyses revealed that culmen is a relatively good measure for body size in embryonic chickens (10-21 days; matched lengths from figures of Hamilton, 1952, with weights from Romanoff, 1960) and in juvenile *Phasianus colchicus* from zero to nine weeks posthatching (Westerskov, 1957; see also Fig. 2 of this study). Since the culmen is a less sensitive and less accurate indicator of body size than is the cube root of body weight, certain interspecific differences have possibly gone undetected due to the use of culmen as a major standard for body size.

The scales for the cube root of weight in Figs. 3, 4, 5, are calculated from a mean value of 3.24 for the ratio of culmen length to the cube root of body weight in grams for the eight weighed specimens of *Talegalla jobiensis*. Due to the relative imprecision of culmen measurements (compared with weights)

TABLE 3. Data on specimens of *Talegalla jobiensis* and domestic *G. gallus*. Nos. 1196, A, B, C, S, T, U, V, W are posthatching specimens. For procedures of measuring, see text. All lengths are in millimeters. Weights in grams. Ages in parentheses are estimated from stages in Hamilton (1952). Symbols: S, specimen designation; W, wing length; T, tarsal length; C, culmen length; H, humerus length; R, radius length; Td, length of third digit; m, male; f, female; —, observation could not be made.

Talegalla:

S	W	T	C	H	R	Td	Sex	Weight
21	—	—	—	—	—	—	—	3.5
22	9	6	5	6	6	4	—	4.7
23	11	6	6	8	7	6	—	5
24	12	9	6	9	8	7	—	—
25	18	13	8	11	12	9	m	14.3
26	20	15	9	14	12	11	m	22
27	45	23	12	20	19	15	—	—
28	80	30	16	29	28	24	—	101
29	100	30	15	31	29	24	f	108
30	100	33	17	34	33	27	—	—
1196	115	38	16	38	35	28	—	—
A	115	35	16	—	—	—	f	125
B	160	47	21	—	—	—	m	292
C	164	49	18	—	—	—	—	—

Gallus:							*Age (days)*
N	8	5	5	5	4	4	(10-11)
O	10	8	7	7	6	6	(11-12)
P	11	9	6	8	7	7	(12)
Q	25	17	10	12	10	16	(19)
R	27	19	10	13	11	17	(19-20)
S	85	26	15	29	25	24	—
T	110	36	18	35	33	30	—
U	135	44	21	40	36	35	53
V	170	51	24	47	44	42	63
W	160	54	24	50	46	41	—

Note: Specimens A, B, C are study skins.

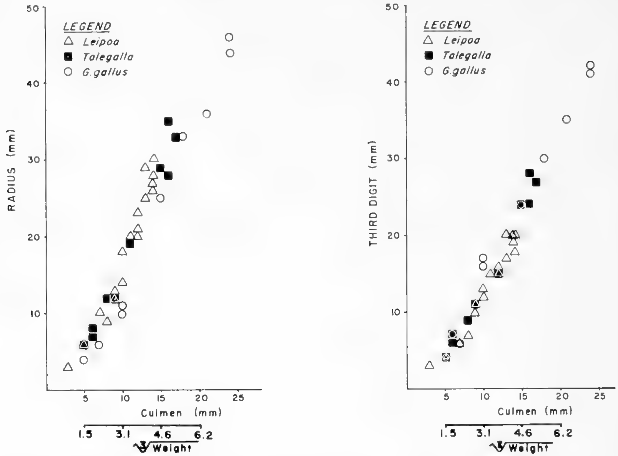

Figure 3A. (Left) Growth of the radius relative to the culmen in *Leipoa ocellata, Talegalla jobiensis* and domestic *G. gallus* (see also Fig. 4). B. (Right) Growth of the third digit relative to the culmen in these three species (see also Fig. 4).

Cube roots of weights in grams calculated by the method indicated in text (p. 9).

and probable interspecific variations in the mean ratio of culmen to the cube root of body weight, the cube root values in Figs. 3, 4, and 5, are probably not precise for individual specimens shown on the graphs; nevertheless, these cube roots of weights help to indicate, in an approximate way, the relative growth of the different species.

As shown by either arithmetic (e. g. Figs. 3, 5A) or logarithmic plots (Fig. 4), growth of linear dimensions relative to culmen in the two species of megapodes is generally similar to that of *Gallus* (see also Table 4). It should be emphasized, however, in view of the necessarily small sample sizes and inherent limits of accuracy in measurement, that these analyses tend to mask certain differences in relative growth. For example, in embryonic chickens the radius (Fig. 4A) and humerus temporarily have lower rates of relative growth followed again by higher rates (this study); the data of Romanoff (1960: 1146) show that the slow growth of these structures in chickens occurs about 14-17 days of incubation. As a consequence, the radius and humerus of chickens near hatching are a few millimeters shorter than those of similar-sized embryos of *Talegalla* or *Leipoa* (data in Tables 2, 3). In addition, measurements of three juveniles of the phasianid *C. coturnix japonica* revealed for this form also a slow mean rate of embryonic growth of radius and humerus relative to other dimensions followed by increased relative rates after hatching. The relatively short radius and humerus of *Gallus* and *Coturnix* in older embryos and at hatching are possibly adaptive in preventing premature flying of the young birds; such an adaptation would be analogous to the retarded development of remiges in juveniles of forms such as petrels and hawks. No trace of a relatively slow embryonic growth of radius and humerus was found in the megapodes.

Culmen measurement in the utilized samples covers a relatively small range (less than 20 mm), but this handicap is offset somewhat by the utility of this measurement for study skins. The culmen is measured linearly over a curved surface but nevertheless is empirically useful. In measuring the culmen of

Table 4. Interspecific comparison of allometric growth of dimensions relative to culmen. None of the interspecific differences in exponent is statistically significant. See text for details.

Dimension	Species	Exponent (B) with 95 per cent confidence interval	Coefficient (A)	Size of sample
Tarsus	*Leipoa*	1.6 ± 0.2	0.24	18
"	*Talegalla*	1.5 ± 0.3	0.20	13
"	*Gallus*	1.4 ± 0.2	0.18	10
Humerus	*Leipoa*	1.5 ± 0.4	0.19	18
"	*Talegalla*	1.4 ± 0.2	0.15	10
"	*Gallus*	1.4 ± 0.2	0.19	10
Radius	*Leipoa*	1.6 ± 0.2	0.26	18
"	*Talegalla*	1.4 ± 0.2	0.17	10
"	*Gallus*	1.5 ± 0.2	0.27	10
Third digit	*Leipoa*	1.5 ± 0.3	0.24	18
" "	*Talegalla*	1.5 ± 0.2	0.23	10
" "	*Gallus*	1.5 ± 0.2	0.20	10

late embryonic and juvenile chickens (*Gallus;* Table 3), the presence of the comb necessitated estimating culmen lengths in eight specimens through the projection of lines from the postero-lateral margins of the horny bill dorsally to the midline; however, this approximation did not alter the interpretations as shown by using other combinations of dimensions. At hatching in *Gallus*, *Leipoa*, and *Talegalla*, the culmen may lose up to 1 mm in length through loss of periderm, but this small change does not affect the interpretations of relative growth.

Analogous to the shorter culmen after hatching are reductions (about 5 mm) in wing length of juveniles of these species through loss of natal downs and also the decrease (less than 1 mm) in length of the third digit through loss of the claw pad at hatching. Here again the interpretations of relative growth were not affected.

Relative and proportional growth of gallinaceous wings was too complex to permit adequate representation in a simple equation, but, as shown by graphs (e. g. Fig. 5), relative growth of the wing in *Talegalla*, *Leipoa*, and other Galliformes was similar within the size range considered. The proportional growth illustrated in Fig. 5B suggests possible interspecific differences which, however, are not especially striking. Data for the Jungle Fowl (*G. gallus*) were used in Fig. 5 to provide a larger sample, but data for chickens (domestic *G. gallus;* Table 3) gave similar results.

Juvenile *Megapodius* have an unusually short culmen contrasted with those of juveniles of other megapodes or other Galliformes; the mean ratio of culmen length to the cube root of body weight for three *Megapodius freycinet* (Fig. 2; Table 5) was 2.1, compared with 3.24 for eight *Talegalla jobiensis.* Young juvenile *Megapodius* (Table 5) also differ from young juveniles of *Talegalla* in having a longer wing relative to the cube root of body weight.

Measurements of wing, tarsus and culmen of more than 110 other juvenile specimens representing 22 genera of non-megapode Galliformes (cf. Table 5) were plotted on graphs and compared. These species generally appear to have proportional growths similar to those of *Talegalla*, *Leipoa*, and *Gallus.* However, a juvenile *Crax rubra* of the cracids (Table 5) was exceptional in having a relatively short wing (shown also by figures of young *Crax globicera* (= *rubra*) in Heinroth, 1931). The shorter wing at hatching in *Crax* is apparently associated with the generally less well-developed feathers (p. 24). Forms such as ducks (e. g. *Anas*) which have delayed formation of juvenal remiges show plots of alar growth quite unlike those of Galliformes.

These analyses, although necessarily based on small samples, indicate that embryonic megapodes undergo proportional and relative growth analogous to that occurring up to several weeks posthatching in phasianids. Certain forms such as *Megapodius* and *Crax* show interesting deviations from the general gallinaceous conditions. Larger samples might reveal additional interspecific differences and possibly intraspecific variations according to individuals, sex or locality.

Some qualitative comparisons of embryos and juveniles. Embryos of *Leipoa* (e. g. Nos. 2 and 19) and of chickens shortly prehatching behaved similarly when taken from the shell, i. e. the embryos gaped and kicked. Even *Leipoa* embryos

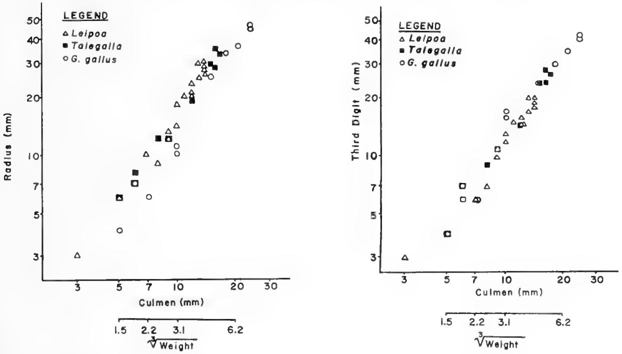

Figure 4A. (Left) Double logarithmic plot of growth of the radius relative to the culmen in *Leipoa ocellata, Talegalla jobiensis* and domestic *G. gallus*. B. (Right) Double logarithmic plot of growth of the third digit relative to the culmen in these three species.

Cube roots of weights in grams calculated by the method indicated in text (p. 9).

Table 5. Comparison of dimensions of some juvenile Galliformes. Specimens arranged by increasing tarsal length. For procedures of measuring, see text. Lengths in millimeters. Symbols: W, wing; T, tarsus; C, culmen; m, male; f, female; g, grams.

	W	T	C		W	T	C
Numida meleagris (f)	20	17	10	*Penelope purpurascens*	105	27	12
Chrysolophus pictus	20	18	7	*Megapodius pritchardii*	85	28	6
Phasianus colchicus	30	19	8	*Gennaeus leucomelanos*	105	28	15
Opisthocomus hoazin	40	19	12	*Chrysolophus pictus*	115	30	14
Gennaeus leucomelanos	50	19	10	*Alectoris chukar* (f; 154 g)	120	30	16
Syrmaticus mikado	30	20	8	*Tragopan temmincki*	130	30	14
Chrysolophus pictus	26	20	7	*Ortalis wagleri*	110	31	15
Phasianus colchicus	35	21	10	*Alectoris chukar* (f; 198 g)	130	31	16
C. coturnix japonica	90	22	12	*Mitu tomentosa*	85	32	14
Alectoris chukar (m; 73 g)	95	22	14	*Talegalla fuscirostris*	120	32	15
Phasianus colchicus	85	23	13	*Alectura lathami*	105	33	15
Meleagris gallopavo	45	24	10	*Phasianus colchicus* (f)	110	33	18
Ortalis wagleri	45	24	10	*Francolinus gularis*	120	33	15
Ortalis vetula	70	24	12	*Megapodius freycinet* (f; 117 g)	125	33	10
Megapodius freycinet (f; 63.6 g)	100	24	8	*Megapodius freycinet* (123.5 g)	130	33	11
Numida meleagris (m)	110	24	14	*Opisthocomus hoazin*	165	34	19
Megapodius laperouse	95	25	8	*Macrocephalon maleo*	140	35	15
Alectoris chukar (m; 121 g)	115	26	15	*Crax rubra* (m)	75	36	15
Meleagris gallopavo	55	27	9	*Dendragapus obscurus* (f)	175	36	18
C. coturnix japonica (adult)	100+	27	13				

considerably larger than chickens at hatching show this characteristic embryonic behavior.

Meyer (in Meyer and Stresemann, 1928) noted the large fat deposits in late embryonic *Megapodius;* both *Talegalla* and *Leipoa* embryos (this study) also have subcutaneous fat bodies distributed similarly to those of chicken embryos but covering a wider area in embryos near hatching. These deposits in older *Talegalla* and *Leipoa* embryos are especially well developed laterally along the neck and beneath portions of the ventral feather tract.

The genus *Megapodius* (Miller, 1924; confirmed in this study) is unusual among Galliformes in having a small web

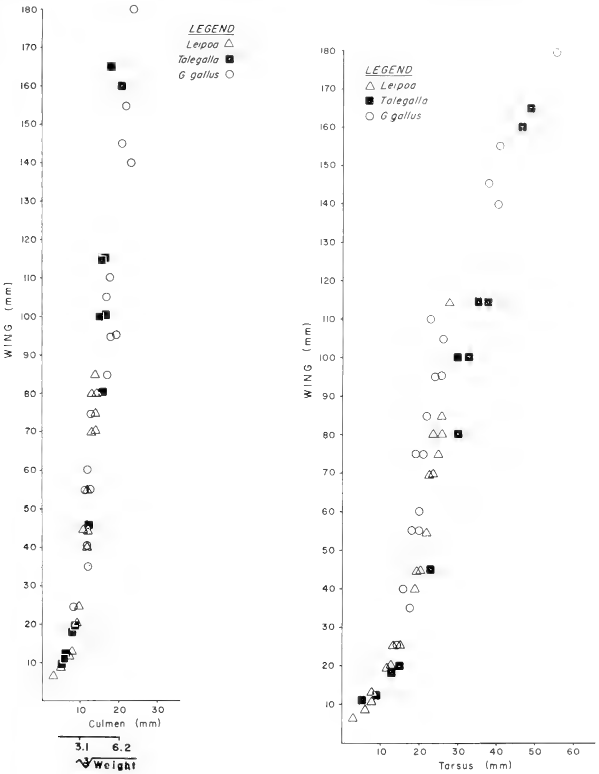

Figure 5A. (Left) Growth of the wing relative to the culmen in *Leipoa ocellata, Talegalla jobiensis* and *G. gallus.* Cube roots of weights in grams calculated by the method indicated in the text (p. 9). B. (Right) Proportional growth of the wing versus the tarsus in these three species.

between the second and third toes but, unlike forms such as *Leipoa*, *Talegalla* and *Gallus*, none between the third and fourth toes.

A few qualitative gross morphological changes appear at a greater absolute weight, and, for larger embryos, at a detectably greater linear size, in the megapodes (*Leipoa* and *Talegalla*; this study) than in *Phasianus* (Westerskov, 1957) or *Gallus* (structures from Hamilton, 1952, matched with weights from Romanoff, 1960). Examples of these phenomena in *Talegalla* versus phasianids (Table 6) include first appearance of feathers, egg tooth, labial groove, and coming together of the eyelids.

TABLE 6. Comparison of weights at times of certain qualitative morphological changes in *Talegalla jobiensis, Phasianus colchicus,* and domestic *G. gallus.* Weights in grams. *Talegalla* weights in parentheses were estimated from culmen lengths using the relationship reported in the text (p. 9).

Macroscopic character	*Talegalla* weight	*Phasianus* weight	*Gallus* weight
First appearance, feathers	3.5 - 4.7	0.7-1.7	0.4- 1.2
First appearance, egg tooth	4.7 - 5.0	0.7-1.7	0.4- 1.2
Formation of separate toes	3.5 - 4.7	1.4-4.8	0.7- 2.3
Formation of scales on legs	(5.5)-14.3	3.2-5.8	2.3- 7.3
Eyelids coming together	22-(40)	4.7-8.5	5.2-11.0
Hatching	110+	23	33

Sources of data: *Talegalla* from this study; *Phasianus* from Westerskov (1957); *Gallus* morphology from Hamilton (1952) combined with *Gallus* weights from Romanoff (1960: 1147).

Tarsal scutellation. My observations on the tarsal scutellation of megapodes support the findings of Ogilvie-Grant (1893). *Megapodius*, *Aepypodius*, and *Talegalla* are alike in having a single row of large scutes down most of the foresurface of the tarsus (tarsometatarsus), but *Aepypodius* has two rows distally. *Alectura* and *Leipoa* have two rows of large scutes down the foresurface, while *Macrocephalon* has many small scutes. Tarsal scutellation is similar in juveniles and adults within a species of megapode.

Turkeys, many phasianids and some cracids have two rows of large scutes on the foresurface, while many cracids possess only one row; *Opisthocomus* has many small scutes.

Feathering of the oil gland. *Talegalla jobiensis* has a naked oil gland (no feathers on the tip; Fig. 6, this study) and thus

Figure 6. Oil glands of domestic *G. gallus* (19 day embryo; ca. 5.5×), *Magapodius laperouse* (YPM 89; juvenile; ca. 3×), and *Talegalla jobiensis* (No. 29, embryo; ca. 1.5×), from left to right. Dorsal view.

is like *Alectura* and *Leipoa* (Miller, 1924; confirmed in this study). In contrast, *Megapodius laperouse* (Fig. 6, this study) has a tufted oil gland as was reported by Miller (1924) for other species of *Megapodius* and for *Macrocephalon*. Most *Galliformes*, excluding megapodes, have tufted oil glands (Fig. 6 of this study; Miller, 1924; see also Table 7 for a summary of this character in other birds).

Eutaxy. Unlike other gallinaceous families, megapodes have variation in eutaxy (presence of the fifth secondary; Steiner, 1918; Miller, 1924). As anticipated from reports on allied species (i. e. *Alectura* and *Leipoa;* Miller, 1924), *Talegalla jobiensis* is eutaxic (this study). Both *Talegalla* and *Leipoa* are eutaxic at the first embryonic appearance of the secondaries. *Megapodius laperouse* (YPM 89) is also eutaxic, but *M. pritchardii* (Pycraft, 1900) and some (but not all) members of *M. freycinet* (Steiner, 1918; Miller, 1924) are diastataxic (lacking the fifth secondary). *Macrocephalon* is also diastataxic (Miller, 1924). In contrast, all other Galliformes, including chickens, are eutaxic (Miller, 1924; see also Table 7 for a summary of diastataxy and eutaxy in other birds).

Carotid arteries. In agreement with the data reviewed by Glenny (1955) for *Megapodius freycinet*, *M. pritchardii*, *Macrocephalon*, and *Alectura*, the megapodes dissected in this study (e. g. *Leipoa* No. 17, *Talegalla* No. 29, *Megapodius laperouse* YPM 89) had a left dorsal carotid artery but none on the right side; in contrast, chicken embryos possessed both right and left dorsal carotids. Glenny (1955) has reported that all Galliformes except megapodes are bicarotid (see Table 7 for a summary of this feature in other birds).

Early plumages. Studer (1878) and Pycraft (1900) believed that megapodes molt natal downs before hatching, but Portmann (1955) and Becker (1959) have contended

TABLE 7. Status of dorsal carotid arteries, disastataxy versus eutaxy, and oil gland feathering in nongallinaceous birds. Symbols: 2, bicarotid; 1, unicarotid; E, eutaxy; D, diastataxy; T, tufted oil gland; N, naked oil gland; O, no oil gland.

Taxonomic group	Carotid arteries	Fifth secondary	Oil gland
Tinamidae	2	E	T
"Ratites"	1,2	D,E	O, ?
Gaviidae	2	D	T
Podicipediformes	1	D	T
Procellariiformes	2 (1)	D	T
Spheniscidae	2	D	T
Pelecaniformes	1, 2	D, E	T
Ciconiiformes	1, 2	D	T, N
Anhimidae	2	D	T
Anatidae	2	D	T
Falconiformes	2	D	T, N
Gruiformes	1, 2	D, E	T, N, O
Charadriiformes	2 (1)	D, E	T
Columbiformes	2	D, E	N, O
Psittaciformes	1, 2	D	T, O
Musophagidae	2	E	T
Cuculidae	2	E	N
Strigiformes	2	D	T, N
Caprimulgiformes	1, 2	D	N, O
Apodiformes	1, 2	D, E	N
Coliiformes	1	E	N
Trogoniformes	1	E	N
Coraciiformes	1, 2	D, E	T, N
Piciformes	1, 2	E	T, N, O
Passeriformes	1	E	N

Sources of data: arteries, Glenny, 1955; eutaxy and diastataxy, Steiner, 1956; oil gland, Beddard, 1898, and Miller, 1924.

that megapodes lack natal downs and that their first feathers represent the phylogenetic precursors of natal downs. In contrast, Friedmann (1931) stated that megapodes at hatching bear juvenal feathers in opposition to several authors (e. g. Ogilvie-Grant, 1893), who referred to the downy young. In order to determine which, if any, of these conflicting views is correct, it was necessary to analyze many features of pterylosis, feather growth, and molt.

In the embryonic early growth of the megapode feathers, those of the tail are longest. For example, on one *Leipoa* (No. 5) the caudal sheaths (10 mm long) were 5 mm longer than the next longest ones on the cervical region and femoral tract. Similarly, a *Talegalla* embryo (No. 24) with tail feathers of 10 mm had the next longest sheaths (3 mm) on the cervical region. Precocious embryonic early growth of caudal natal downs occurs in chickens (Hamilton, 1952) and Coturnix Quail (Padgett and Ivey, 1960) and is apparently a gallinaceous trait.

Although a row of 9 or 10 relatively large papillae initially were formed on the posterior surface of the manus (e. g. on Nos. 3, 22, 23), of these only primaries 1 through 8 were large on older embryos and newly hatched *Talegalla* and *Leipoa* (see also Pycraft, 1900, for *Megapodius*). Such embryonic repression of the juvenal outer primaries (9 and 10) is characteristic for many Galliformes.

Embryonic megapodes do not molt, contrary to the report of Studer (1878), who was misled partly by the ease with which immature sheaths are dislodged from the skin. Indeed, feather maturation, manifested by hardening, does not occur on the body in *Talegalla* and *Leipoa* until the last quarter of incubation as determined by dissection of sheaths from eight tracts. At hatching, as in other Galliformes, the feathers on the body are fully grown or nearly so, but the vanes of the remiges continue growing.

Feather sheaths at hatching are longer on *Talegalla* and *Leipoa* than on chickens. To illustrate this condition, the mean lengths (M) and coefficients of variation (CV) were calculated for six sheaths from each of three embryos near hatching. The six sheaths were taken from corresponding positions on six

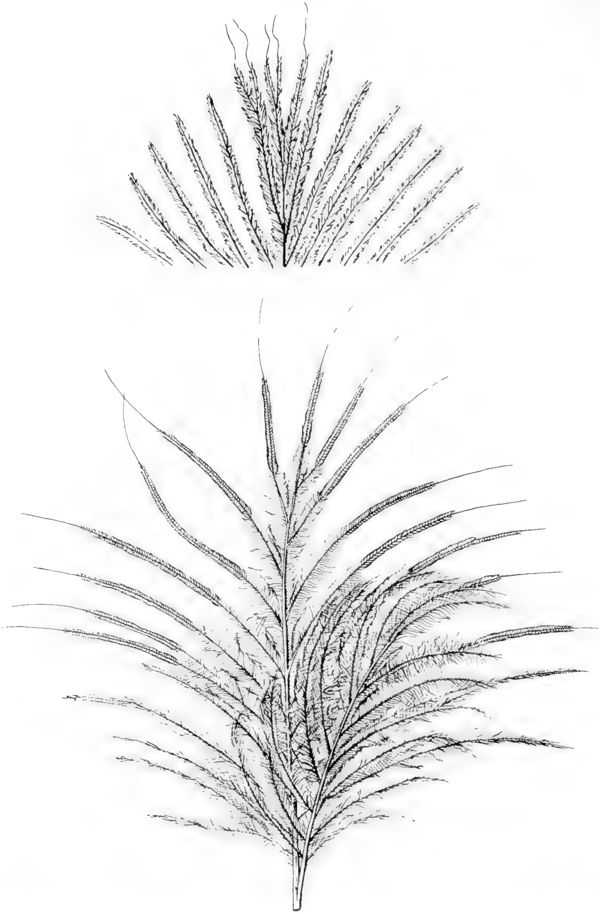

Figure 7. Comparison of the tip of secondary No. 9 of the right wing (top; ca. 4×) with a natal down from the body (bottom; ca. 3×). *Leipoa ocellata* No. 19; 60-73 days of incubation.

tracts on the body of each of the embryos. The values were: *Gallus* (19 day) M 13.8 mm (CV 37.6); *Leipoa* (No. 19) M 28.6 (CV 39.9); and *Talegalla* (No. 30) M 36.5 mm (CV 38.8). In view of the great variation in lengths of sheaths within a tract, these values are useful only to indicate the great difference between megapodes and chickens.

Sheaths on the body of *Talegalla* and *Leipoa* embryos appeared conventional, having opaque and unshriveled tips, but sheaths of remiges, alula quills, and certain alar upper coverts of the older *Talegalla* and *Leipoa* embryos had unusual translucent and shriveled tips as noted by Pycraft (1900) for remiges of embryonic *Megapodius.* Pycraft (1900) figured a constriction of the sheath of the *Megapodius* remex in the region of transition from opaque to translucent portions. This constriction does not occur in *Leipoa* and *Talegalla* (this study); due to lack of a suitable specimen of *Megapodius,* it was not possible to check Pycraft's report of a constriction in that genus.

Within the translucent tips of the sheaths of remiges on older *Talegalla* and *Leipoa* embryos are weak filaments which are distal portions of the central barbs of the tip of the remex (Fig. 7). These distal filaments are easily dislodged in removing remiges from the sheaths so that some or all filaments are missing from the expanded remiges of embryos (as in Fig. 7) and juveniles. Unlike the correspondingly placed natal downs on the tips of juvenal remiges of phasianids or cracids, these filaments on the tips of remiges of embryonic megapodes are weakly developed and lack barbules.

On juveniles of six megapode genera (this study), the feathers at hatching have 1) barbule-free distal ends of central barbs of body feathers (Fig. 7); 2) a central rhachis; 3) a large aftershaft on the body feathers (Fig. 7); 4) a well-formed vane in the remiges; these features in common demonstrate that megapodes had common ancestors possessing such features at hatching. In contrast, the feathers of chickens at hatching have 1) barbule-free distal ends of central barbs; 2) a distinct rhachis only in the short and growing juvenal remiges; 3) no aftershaft; 4) a well formed vane only in the growing remiges.

Hall (1901), Blasyzk (1935), and Frith (1962) have reported for juvenile *Leipoa* and *Alectura* that the feathers on the body at hatching are later carried out on the tips of the growing second feathers. The finding of these connections (this study) on *Leipoa ocellata* (Fig. 8), *Alectura lathami*, *Talegalla jobiensis*, and *Megapodius freycinet*, demonstrates that this is another general feature of megapodes. As the first feathers are easily dislodged from the tips of the second ones, the rarity of observations of these junctions on preserved specimens is to be expected. These connections resemble those between natal downs and juvenal feathers in other Galliformes.

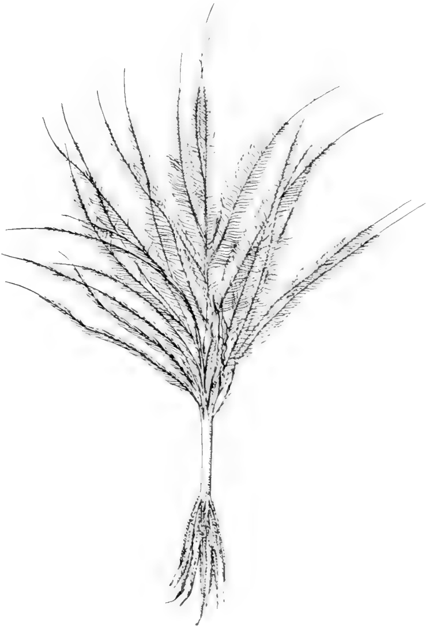

Figure 8. A natal down attached to the tip of a juvenal rectrix from juvenile *Leipoa ocellata*. (YPM 1195) ca. 3×.

However, since similar connections occur between other generations of feathers in Galliformes (Watson, 1963), these attachments, considered alone, do not demonstrate conclusively that the first feathers on the body of megapodes are natal downs.

Nevertheless, the homology of megapode feathers on the body at hatching with the natal downs of other Galliformes is shown by the following features in common: 1) the precocious early growth of embryonic tail feathers; 2) the plumulaceous structure of the feathers on the body at hatching relative to the more pennaceous structure of later generations of feathers and of the first remiges; 3) attachment of the first feathers to the tips of growing feathers of the second generation; 4) barbule-free distal ends of central barbs; 5) start of the first body molt within two weeks posthatching (data on *Leipoa* timing from Hall, 1901, and Frith, cited in Nice, 1962).

The following group of characters demonstrates that the megapode first remiges are juvenal like those of other Galliformes: 1) only eight primaries at hatching but ten on older juveniles and adults; 2) similar lengths of growing primaries Nos. 1(first basic = postjuvenal) and 10 (juvenal) on juvenile *Megapodius* (YPM 89) as in certain juvenile phasianids (cf. Heinroths, 1928); 3) remiges more pennaceous than other feathers at hatching; 4) similar location of the distal filaments on the embryonic remiges of megapodes and of the corresponding natal downs on other Galliformes; 5) time of initial loss of a first remex (two weeks posthatching in *Leipoa;* Hall, 1901); synchrony of molt of natal downs on the body and juvenal remiges is characteristic for Galliformes.

The lengths of rhachises in the natal downs of Galliformes can be partly correlated with the size of the newly hatched birds. For example, the young of small phasianids, e. g. *Coturnix*, lack rhachises in their natal downs, while turkeys (*Meleagris;* Pycraft, 1900, and confirmed in this study; and *Agriocharis;* this study) and tragopan pheasants (this study), both of which are larger at hatching than are the small phasianids, have short rhachises in their natal downs. Megapodes, still larger at hatching, have longer rhachises (Fig.7). Certain cracids, e. g. *Crax*, are exceptional in being large at hatching (over 100 grams; Heinroth, 1931), while lacking or having only short rhachises in their natal downs (this study).

As might be expected from the data thus far presented, many phasianids molt the last of their natal downs at a body size smaller than that of juvenile megapodes at the time of loss of the last natal downs. For example, *Phasianus colchicus* at 160 grams has lost nearly all the natal downs (Westerskov, 1957), while *Talegalla* (e. g. B of Table 3) at this weight retains many natal downs on the breast, back and head.

Thus the hatching plumages of megapodes and other Galliformes are homologous but differ structurally.

Structures associated with hatching. Several authors (e. g. Frith, 1959) have reported megapodes at hatching kicking their way out of the shell, and some observers (e. g. Elvery in Campbell, 1901) have emphasized the difference from hatching in chickens. A relatively detailed description of megapodes at hatching is that of Bergmann (1961), who observed that, in *Talegalla cuvieri,* at the time of breaking open of the shell, the only parts of the body to break through the shell membrane were the legs and feet. Thus *Talegalla* is unlike both chickens (Hamilton, 1952) and Coturnix Quail (Clark, 1960) which use the egg tooth of the beak conspicuously in breaking open the shell.

Although Friedmann (1931) could not find an egg tooth on one *Megapodius pritchardii* embryo, and Bergmann (1961) could not find an egg tooth on *Talegalla cuvieri* at hatching, I (1960, 1961) have found egg teeth on both *Talegalla jobiensis* and *Leipoa ocellata* embryos (latter observation made independently by Frith, 1962). Frith has kindly shown me one specimen of prematurely hatched *Leipoa* bearing an egg tooth, which, together with my finding that many other specimens of newly hatched megapodes lack egg teeth, suggests that egg teeth are usually lost about the time of hatching in megapodes. The egg teeth of chickens near hatching are approximately two times larger in linear dimensions than the fully grown egg tooth of *Leipoa* (Fig. 9) or *Talegalla.* Especially when considered relative to body size at hatching, the megapode egg tooth is quite small. I (1961) have reviewed the occurrence of egg teeth in birds as a whole; egg teeth probably occur on most, if not all, birds. Megapodes are the only birds for which egg teeth are thought to be nonfunctional at hatching.

In *Talegalla* and *Leipoa* the Musculus complexus or "hatching muscle" is located dorsally on the neck immediately under the skin (and under fat deposits in larger embryos), attached anteriorly to the parietal of the skull, and posteriorly connected to the third, fourth, and fifth cervical vertebrae and the muscular complex overlying these vertebrae. The two complexus muscles were separated in the dorsal midline in the 20 examined anatomical specimens of megapodes: in *Leipoa* by minimal distances of 1.5 (No. 4) to 3 mm (No. 19) and in *Talegalla* by 2.5 (No. 26) to 5 mm (No. 30). In contrast, in chicken embryos near hatching, the two complexus muscles met in the dorsal midline (Fig. 10). The anterior insertions meet in the dorsal midline long before hatching and after hatching move laterally, separating in the dorsal midline (Fisher, 1958; this study). The M. complexus of megapodes and chickens also differed in the apparent lack of a temporary enlargement about the time of hatching in megapodes. In chickens near hatching this muscle appears swollen, protruding above the level of adjacent cervical muscles and reaching a thickness of at least 2.5 mm, whereas in megapodes no swelling was observed and maximal thickness was always less than 1 mm. Similarly, although maximal width of the complexus muscle in each of four chickens near hatching was 7 mm, in none of the megapodes did this width exceed 5-7 mm, which was reached only in the largest specimens (e. g. Nos. 19, 30).

Figure 9. Egg tooth of an embryonic *Leipoa ocellata*. (No. 9) Overlying periderm removed. Ca. 7 ×.

Length measurements of the M. complexus were unreliable due to the lack of a clear posterior boundary of the muscle. When measurements of width and midline separation were analyzed relative to body size by plotting on arithmetic and double logarithmic graphs, no indications of prehatching variations other than growth and individual variations were detected for the megapodes, but the precision of these measurements (about ± 0.5 mm) is not very great relative to the dimensions measured. These observations do not eliminate the possibility of a transient enlargement of the M. complexus at hatching in megapodes, but they provide no support for such a view. The separation in the dorsal midline and apparent lack of special enlargement of the complexus muscle at hatching in megapodes are very likely correlated with the larger size of megapodes at hatching.

Figure 10. The Musculus complexus of domestic *G. gallus* (19 day embryo; ca. 1.2×) and of *Talegalla jobiensis* (No. 30; ca. 1.4×). *Talegalla* on the right.

The small egg tooth and unusual features of development of the M. complexus of megapodes appear to be associated with the different methods of hatching in megapodes and phasianids.

DISCUSSION AND CONCLUSIONS

Gallinaceous growth and maturation. The embryonic megapodes *Leipoa* after the first 20 days were relatively immature compared with chickens of similar age. Although slow early embryonic development is a reptile-like character, not too much phylogenetic significance can be attributed to this condition in *Leipoa,* since the slow developmental rate is associated with the methods of incubation including relatively low incubating temperatures. It is possibly phylogenetically significant that *Leipoa* can hatch successfully (Frith, 1959) at incubating temperatures so low (below 95°F) as to be lethal for chicken embryos (Romanoff, 1960); however, data on the normal range of egg temperatures of wild birds in general (Huggins, 1941) indicate that megapodes are perhaps not unusual among birds with respect to tolerated incubating temperatures.

Interpretation of the chronology of embryonic megapodes is complicated by great individual variation. For example, normal prehatching periods in *Leipoa* from different mounds range from 50 to 90 days in association with intermound variations from 96° down to 80°F in incubating temperatures (Frith, 1959). Since incubating temperatures of the megapode *Talegalla jobiensis* (Ripley, 1964) are within the range for *Leipoa* (Frith, 1959), it is possible, though unproven, that *Talegalla* has an embryonic chronology similar to that of *Leipoa.* Analysis of differences in embryonic chronology between megapodes and phasianids is further complicated by the great interspecific variation among phasianids incubated at 100°F. For example, *Colinus* weighing 6 grams (egg weight, 9 g) and *Phasianus* weighing 18 grams (egg weight, 32 g) are both hatched in 24 days, while chickens of 31 grams (egg weight, 60 g) are hatched in only 21 days (Romanoff, 1960: 1143). Data are not available for a quantitative comparison of the effects of varied incubation temperatures on the development of chickens versus megapodes.

Both the phasianid *Phasianus colchicus* (Westerskov, 1957) with an adult (male) weight of 1400 grams and the megapode *Alectura lathami* (Coles, 1937) with a slightly higher adult weight (Heinroth, 1922) reach full size about 25-30 weeks after laying of the egg, indicating that the posthatching growth of *Alectura* is neither unusually fast nor slow compared with that of phasianids.

The data of this study show that *Leipoa* and *Talegalla* before hatching undergo proportional and relative growth analogous to that occurring up to several weeks posthatching in other Galliformes. The similarity of relative growth in young Galliformes is in agreement with the morphological homogeneity of adults (cf. data of Verheyen, 1956). The relative growth appears, in this case, to be phylogenetically generally more conservative than chronological growth. The differences in relative growth of radius and humerus between megapodes and phasianids do not indicate that either group is more primitive than the other.

The noted interspecific variations in the size of embryos at the first macroscopic appearance of certain structures may represent interspecific differences in the growth of anlage of these structures, for, as Schmalhausen (1926) and others have pointed out, relative growth itself can produce qualitative changes in form.

Although the weight of a bird at hatching is relatively directly correlated with the weight of the egg (Heinroth, 1922), the ratio of the size of the egg relative to that of adults often shows considerable intergeneric variation (Heinroth, 1922). Megapodes and certain small phasianids (e. g. *Coturnix*) have eggs generally in the range from 8 to 18 per cent of adult body weight in contrast to other phasianids and turkeys with eggs weighing less than 5 per cent of adult body weight (Heinroth, 1922).

The precocity of megapodes at hatching is associated with 1) the large absolute egg size and correspondingly large size of young at hatching together with 2) an embryonic relative growth of the wing analogous to that occurring up to several weeks posthatching in phasianids. No birds other than megapodes have large eggs plus extensive embryonic growth of the wings.

Megapodes and reptiles. Portmann (1938) listed the following as primitive (reptile-like) traits of megapodes: lack of natal downs, possible lack of an egg tooth at hatching, absence of parental care for young, eggs incubated in sand by solar heat, long incubation period, large clutch size, slow growth to adult size, and precocity of young at hatching. However, as shown by my study, megapodes do have natal downs, and at least some species have egg teeth. Furthermore, there is no good evidence for an especially slow posthatching growth of megapodes.

Moreover, the many adaptive interrelationships (coadaptations) of the reptile-like characters of megapodes should be considered. For example, the long incubation period is correlated with the methods of incubation and the large size and precocity of young at hatching. The precocity of young is also correlated with the lack of parental care which in turn is associated with the incubating methods and clutch size. The reptile-like traits of megapodes all belong to one, or perhaps two, group(s) of coadapted characters. Considered in this way, the evidence for special affinities of megapodes and reptiles is unconvincing, since the points of similarity are all related to common reproductive adaptations.

The case for special reptilian affinities of megapodes would be greatly strengthened if there were reptile-like characters relatively independent of the central adaptation in megapodes: however, no such characters have yet been found. As one example, there is reported to be a significant difference in the caloric values of reptilian and avian egg yolks (Slobodkin, 1962), yet samples of yolk collected during this study from relatively fresh eggs of *Leipoa* and *Gallus* had values agreeing with those of other avian species (Slobodkin, 1962).

Furthermore, advocates of the primitiveness of the megapodes among birds as a whole have generally failed to analyze the possibility of convergent evolution. In short, evidence for the primitiveness of megapodes among birds as a whole is unacceptable.

Evolution of the megapode family. Megapodes are basically similar in morphological development to phasianids. Differences in the structure of natal downs, in absolute and relative sizes of eggs, in sizes of subcutaneous fat bodies, in development of the hatching apparatus, etc., are all directly or indirectly correlated with the sizes of the young at hatching.

Huxley (1868) emphasized that, in contrast to other Galliformes, megapodes and cracids are alike in depth of the sternal notches and in position of the hallux. From this anatomical basis, he postulated that these forms, isolated respectively in the Australian and Neotropical regions, are remnants of an ancestral gallinaceous stock which has been replaced through most of the Old World and Nearctic region by more modern Galliformes.

However, the differences at hatching in feather structure between cracids and megapodes support the generalization that megapodes and cracids are not especially closely related in evolution, contrary to some current classifications (e. g. Peters, 1934).

The contemporary megapodes are characterized by 1) rhachidial natal downs on the body, 2) long juvenal remiges and large body size at hatching, 3) a relatively high ratio of egg to adult weights compared with other Galliformes, and 4) the unicarotid condition; it is likely that these distinctive traits were present in a population ancestral to all living megapodes. Megapodes are apparently unique among birds in having such long and weak natal downs preceding the embryonic juvenal remiges. These weak natal downs are clearly vestiges rather than preadaptations and indicate the evolution of megapodes from unknown gallinaceous ancestors possessing a natal plumage and less precocious chicks resembling those of extant phasianids.

This phylogenetic interpretation is also supported by the finding of a vestigial egg tooth and the apparent lack of special enlargement of the complexus muscle at hatching; these features strongly indicate an evolutionary origin of megapodes from forms less precocious at hatching. One aspect of the evolution of megapodes has been the transition from the use of the egg tooth in hatching to kicking open the shell.

The variation in the number of carotid arteries in birds as a whole (Table 7) appears to be due to much convergent evolution. The most readily conceived sequence is a loss of one carotid artery (Glenny, 1955), but a possible evolutionary increase cannot be excluded. The occurrence of only one carotid in megapodes in contrast to two in all other known Galliformes suggests that megapodes are specialized in this respect.

My conclusions, based on morphology, are compatible with the concept of Mainardi and Taibel (1962: Fig. 4), based largely on erythrocyte antigens, that megapodes, cracids, and phasianids have evolved as three separate lines from unknown gallinaceous ancestors.

It is pertinent that there are living forms intermediate in structure of feathers at hatching and in precocity of young between megapodes and phasianids such as *Phasianus* or *Gallus*. For example, the phasianid genus *Tragopan* has natal downs with short rhachises (this study), relatively long juvenal remiges at hatching (Beebe, 1918), and initial flight on the third day posthatching (Nice, 1962; after the Heinroths). Although *Tragopan* probably does not represent the phylogenetic ancestors of megapodes, certain aspects of its structure and behavior of young aid in visualizing the evolutionary origin of the megapodes.

Evolution within the megapodes. *Megapodius* and *Macrocephalon* lay their eggs in holes (*Megapodius* also uses mounds) and are known to lay their eggs communally, while the four other genera use mounds exclusively as far as known. (In accord with the study of Ripley (1964) the form *Eulipoa wallacei* is here included in the genus *Megapodius*.)

The specialized *Macrocephalon* is somewhat intermediate in adult proportions of wing, tarsus, and tail between other large megapodes (4 genera) and the smaller *Megapodius* (data in Ogilvie-Grant, 1893). The relatively uniform color of *Megapodius* and its relative simplicity of nesting habits have led some authors (e. g. Becker, 1959) to consider *Megapodius* primitive among the megapodes. The uniform color pattern of *Megapodius* resembles that of *Aepypodius* or *Talegalla* and may indeed be a primitive trait among living megapodes. But simplicity of nesting site (e. g. the incubation of eggs in holes in the ground) does not necessarily imply primitiveness as illustrated by the specialized brood-parasitic avian species which also build no nests.

Since one trait of the megapodes is the relatively high ratio of egg weight to adult weight, and since megapodes have evolved from apparently more conventional gallinaceous ancestors, it is likely that, during megapode evolution, sizes of eggs increased relative to adult size. Although megapode evolution has very likely also involved an increase in the absolute size of eggs and chicks at hatching, the absolute sizes of newly hatched young do not necessarily indicate the relative primitiveness of the contemporary megapodes. Indeed, if, as seems likely, the evolution of megapodes has involved an increase in the absolute size of eggs and hence of young at hatching, then a large ancestral adult would have been better preadapted, in terms of size, than a small ancestral adult for the evolution of larger absolute sizes of eggs.

More critical features suggesting the direction of evolution within the megapodes are the proportions at hatching. In this respect *Megapodius* is more remote than *Talegalla* or *Leipoa* from the conditions in non-megapode Galliformes. In view of the relatively shorter bill and longer wing at hatching and the unusual webbing of the toes in *Megapodius*, the simplest hypothesis is that *Megapodius* has secondarily evolved from a form like *Talegalla* or *Aepypodius*. Thus *Megapodius*, perhaps most reptile-like of the megapodes in certain respects, is structurally specialized.

The small size (and relatively short culmen) of adult *Megapodius* appear to be adaptive in reducing potential ecological competition where *Megapodius* and other megapode genera occur sympatrically (Ripley, 1960). From the present study it is apparent that a shorter culmen and smaller body size at hatching also characterize *Megapodius* when compared with other megapodes.

Megapodius and *Macrocephalon* have possibly primitive characters in the occurrence of diastataxy (variable in *Megapodius*) and the tufted oil gland. Distribution of these characters in birds as a whole (Table 7) indicates that there is no necessary correlation in the presence of these features and that they have been subject to considerable convergent evolution. Despite the contention of Steiner (1918, 1956) that diastataxy is primitive because it occurs in "primitive" birds, there is no convincing evidence against the possibility that diastataxy might evolve from eutaxy (see Humphrey and Clark, 1961, for a review of the various hypotheses on the origin of diastataxy). Similarly, there is no reason to assume that a tufted oil gland is necessarily primitive.

In view of the intraspecific constancy of tarsal scutellation and its intergeneric variation in the megapodes, it appears useful in dividing the megapodes into subgroups; however, in view of the range of variation within the megapode family, it would probably be unwise to emphasize this feature in attempting to determine the affinity of megapodes with other gallinaceous families.

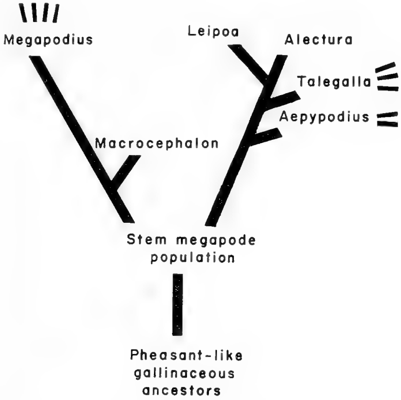

Figure 11. Provisional phylogeny of the family Megapodiidae. The smaller branches leading from the genera represent speciation.

From these considerations, the first phylogeny to cover intergeneric relationships within the megapodes has been developed (Fig. 11). The ancestral stem population (Fig. 11) would have possessed large adult and chick sizes, like *Talegalla,* rhachidial natal downs, a relatively long culmen at hatching, and egg laying in mounds. If this phylogeny is correct, then current classifications (e. g. Peters, 1934) are misleading in placing *Megapodius* first in the sequence of megapode genera.

In examining megapode development, I have found no characters indicating that megapodes are especially primitive birds; indeed, the evidence demonstrates the specialized nature of megapode ontogeny which has probably evolved from a phasianid-like condition.

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SUMMARY

Many differences found in development between megapodes and phasianids are associated with megapodes having before hatching proportional and relative growth equivalent to that occurring up to several weeks posthatching in phasianids.

Contrary to published reports, megapodes at hatching bear juvenal remiges and natal downs on the body and are thus like other Galliformes, although there are structural differences in the natal downs. Vestigial natal downs preceding the embryonic juvenal remiges indicate that megapodes evolved from forms with more conventional gallinaceous feathering at hatching and less precocious young.

This interpretation of megapodes as evolutionarily specialized is also upheld by their vestigial egg teeth and apparent lack of a special enlargement of the complexus muscle which aids in the hatching of other Galliformes.

Compared with other megapode genera and other Galliformes, young juvenile *Megapodius* have a long wing and unusually short bill. It is therefore concluded, contrary to published reports, that, despite its apparent simplicity in color pattern and egg laying habits, *Megapodius* is specialized among megapodes.

A phylogeny of the megapode genera is proposed on the basis of proportions at hatching, tarsal scutellation, foot webbing, eutaxy, oil gland feathering, and other characters.

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Postilla

YALE PEABODY MUSEUM

OF NATURAL HISTORY

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NOTEWORTHY AMPHIPODA (CRUSTACEA) IN THE COLLECTION OF THE YALE PEABODY MUSEUM

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During the last half of the nineteenth century the Peabody Museum of Natural History, Yale University, was the focus of much marine biological research. A. E. Verrill and S. I. Smith amassed a considerable collection of North American invertebrates and exchanged specimens with European biologists. In the course of my curatorial work on the amphipod crustaceans in this collection a number of interesting locality records and type specimens have come to light.

The type specimens are primarily those of S. I. Smith and B. W. Kunkel. Smith apparently based his descriptions on several specimens of each species and designated no types, so I have chosen lectotypes where this was warranted by the condition and locality data of the collections. The type terminology used follows the recommendations of the International Code of Zoological Nomenclature (Stoll et al., 1961). Four of Smith's species are redescribed here from lectotype specimens. They are *Melita nitida*, *Ampithoe longimana*, *A. valida* and *Cymadusa compta*. These are common New England or Middle Atlantic Coast species, so these redescriptions should be helpful for comparative purposes. A generic diagnosis has been included for each redescribed species.

I have examined some probable type specimens of Bermuda amphipods described by Kunkel (1910), including those of *Pariphinotus tuckeri*, *Ceradocus colei*, *C. parkeri*, *Elasmopus magnispinatus*, *Eusiroides verrilli* and *Ampithoe pollex*. The poor condition of the specimens makes designation of lectotypes inadvisable for all species except *Eusiroides verrilli*.

Paratypes of the recently described species *Ampelisca vadorum* and specimens of *Listriella clymenellae* from the type locality are also present in the Peabody Museum collections and are listed here. Interesting locality records for a number of other species are also included in this paper.

Professor W. D. Hartman encouraged the curatorial and systematic work on these collections. I am grateful for his support and for the stimulus of conversations on systematic zoology. Dr. Fenner A. Chace, Jr., of the United States National Museum, helped me with problems of type nomenclature. This work was supported financially under NSF grants G-10772 and GB-583 to Yale University.

Abbreviations used in the species discussions are: YPM–Yale Peabody Museum catalogue number; USFC –United States Fish Commission; USNM—United States National Museum accession number.

Family AMPELISCIDAE G.O. Sars

Ampelisca vadorum Mills

Ampelisca vadorum Mills, 1963, p. 971-989, figs. 1-3.

Material: YPM 5642–Sta. 1, Long Island Sound, Conn., 41°11.1′N, 73°08.8′W. Coarse sand, depth 10-12 meters. Dredge with stramin liner. 24 May 1962. S. W. Richards, collector. 2 adult ♂♂ 10 adult ♀♀, paratypes. YPM 5643–same data 10 juv. ♂♂, 10 juv. ♀♀, paratypes.

Ampelisca spinimana Chevreux

Ampelisca spinimana Chevreux, Chevreux and Fage, p. 81-82, fig. 73.

Material: YPM 4698–USNM 37152. Sta. 36B, (Steamer "Bache") 42°18′N, 69°49′W, 23 ½ mi. ENE ¼ N from Race Pt., 142 fm. (260 meters). Soft blue mud. Sept. 1873. 1 specimen.

This species has been recorded only recently from North America and appears to be widespread on the continental slope (Mills, 1963).

Ampelisca eschrichti Krøyer

Ampelisca eschrichti Krøyer, Gurjanova, 1951, p. 307-308, fig. 170.

Material: YPM 5008–45 fm. (82 meters). Georges Bank, 41°25′N, 66°45′W, 16 Sept. 1872. S. I. Smith and Oscar Harger. 1 juv. ♂.

Seven lots of this species are present in the Yale collections. Six are from boreal and subarctic waters of Labrador and the Gulf of St. Lawrence. However, one collection, described above, is a southern record for the species on the East Coast of North America. Smith and Harger (1874) record "*Ampelisca* sp." in this haul on the east side of Georges Bank. *Ampelisca macrocephala* is known to be common on Georges Bank (Roland L. Wigley, personal communication), but the present species must be rare or absent now, with the recent warming of New England waters. (Taylor, Bigelow and Graham, 1957).

Family PHLIANTIDAE Stebbing

Pariphinotus tuckeri Kunkel

Pariphinotus tuckeri Kunkel, 1910, p. 19-21, fig. 6.

Material: YPM 5613–Bermuda, 1901, W. G. Van Name. 1 broken ♂; 1 ♀, 5.5 mm.

Kunkel's (1910) description was undoubtedly based on these two specimens. Since the specimens were dessicated and the male now lacks head and urosome Kunkel's description must stand.

Family LILJEBORGIIDAE Stebbing

Listriella clymenellae Mills

Listriella clymenellae Mills, 1962, p. 158-162, figs. 1, 2.

Material: YPM 4492–Sta. F (Sanders), Barnstable Harbor, Mass., sand flats in Clymenella tubes, August, 1960, H. L. Sanders. 5 specimens. YPM 4493–Sta. A (Sanders), Barnstable Harbor, Mass., in tube of *Clymenella torquata*, 5 August 1959, Eric L. Mills. 1 specimen.

These specimens were collected at the type locality (Mills, 1962.)

Family GAMMARIDAE Leach

Crangonyx pseudogracilis Bousfield

Crangonyx pseudogracilis Bousfield, 1958, p. 102-105, fig. 16.

Material: YPM 5473–Axelshop Pond, Mount Carmel, Conn., weedy area, 15 Oct. 1961, Eric L. Mills. 9 juveniles.

This is apparently the first record under this name for Connecticut. Bousfield (1958) suggested that the species would be present in Atlantic state watersheds. Kunkel's (1918) records of *Crangonyx gracilis* Smith from New Haven, Conn., and Providence, R. I. (as *Eucrangonyx gracilis*), are partially referable to *C. pseudogracilis* (Bousfield, 1958). Bousfield has shown that *Crangonyx gracilis* has been authentically recorded only from the Great Lakes basin, while *C. pseudogracilis* is a widespread species of warm, shallow fresh waters.

Genus *Melita* Leach 1813/1814 (cited by Stebbing, 1906.)

Stebbing (1906, p. 421) defines the genus as follows:

"Body slender, peraeon smooth, pleon with one or more of the segments dorsally dentate and armed with bristles. Head not rostrate, lateral corners rounded. Side-plate 4 the largest, emarginate behind. Eyes usually distinct, rather small. Antenna 1 slender, longer than antenna 2, 1st and 2nd joints rather long, 3rd not short, with accessory flagellum. Mouth-parts, so far as known, normal. Upper lip with small central emargination. Lower lip, inner lobes tolerably distinct. Mandibular palp rather slender. Maxilla 1, inner plate with several setae, outer with 11 spines. Maxilla 2, inner plate sometimes with setae on inner margin. Maxillipeds, outer plates with teeth on inner margin, passing into slender spines on apex. Gnathopod 2 larger, often unequal, and one in the male sometimes larger than the other, sometimes approximately chelate. Peraeopods 3-5, 2nd joint well-expanded. Peraeopods 4 and 5 subequal, longer than others. Branchial vesicles simple. Marsupial plates narrow. Uropod 2 the shortest. Uropod 3 projecting much beyond the others, outer ramus long, 2nd joint wanting or rudimentary, inner ramus very short. Telson small, deeply cleft. Some characters subject to much variation within the species."

Melita nitida Smith

(Fig. 1)

Melita nitida Smith, (in: Verrill and Smith, 1873, p. 560-561). Della Valle, 1893, p. 716. Holmes, 1905, p. 505-506, figs. Kunkel, 1918, p. 99-100, fig. 22. Shoemaker, 1935a, p. 70-71, fig. 2.

Diagnosis: 1) Gnathopod 1 propodus oblong, palm transverse, with projection defining lower corner. 2) Gnathopod 2 propodus, palm and lower margin forming a single even curve. 3) Hind margins of peraeopod 3-5 bases finely serrated and setose. 4) Pleon and urosome not dentate, with only a few spines on each side of the midline of urosome segment 2.

Description: MALE (8.7 mm) LECTOTYPE. Fig. 1 (a-p). Head only as long as first two body segments combined; interantennal lobe large, rounded above, rather square below. First antenna stout, a little longer than second; peduncle about equal in length to flagellum; flagellum with 20 articles; accessory flagellum of 3 articles. Second antenna stout; 4th peduncle segment with a few small ventral setae; 5th peduncle segment with several groups of long curved setae on ventral margin; flagellum of 12 articles, about half again as long as 5th peduncle segment.

Epistome finely setose and slightly angular below, but not medially notched or emarginate. Mandible, incisor process with 3 teeth, lacinia mobilis finely dentate, molar process strong, projecting outwards; palp, second segment with 3 groups of marginal setae, 3rd segment inner margin lined with long setae. Lower lip inner plates not fully distinct from outer plates; both plates finely setose on the mediodistal margins. Maxilla 1, inner plate distal margin oblique, with several setae; outer plate with 9 pectinate spines; palp, second segment with 5 spines and several setae. Maxilla 2, inner and outer plates equal in length, inner with distal margin oblique and heavily setose, outer with distal margin transverse and setose. Maxilliped, inner plate slightly emarginate distally with an oblique row of setae; outer plate inner margin evenly set with 11 small spines which grade distally into 3 long stout spine setae; palp curved distally, second segment setose medially, 3rd segment sparingly setose.

Coxal plates rather shallow, first 3 deeper than wide, oblong, rounded distally; fourth with a posterodistal lobe rounding evenly into the distal margin; fifth and sixth small, with rounded anterior and posterior lobes; seventh small, rounded below.

Gnathopod 1, basis flattened and slightly expanded; carpus longer than propodus, lower margin with several groups of long, strong setae; propodus oblong, slightly curved, dactyl arising in middle of almost transverse palmar margin; propodus palmar margin defined by finely setose prominence at corner; dactyl very short, stout. Gnathopod 2, propodus greatly expanded, thick, palmar margin set with spinules, rounding evenly into an almost straight lower margin; dactyl long, stout, when closed fitting into a long oblique groove lined with setae on inner side of propodus.

Peraeopods 1 and 2 almost equal in size, short, rather slender. Peraeopods 3, 4 and 5 very similar, highly spinose, bases with groups of spines on anterior margin, posterior margins finely serrated and setose; peraeopod 3 the shortest; peraeopods 4 and 5 about equal in length.

Epimeral plate posterior margins setose, first two slightly rounded posteriorly, with a small tooth at the posterodistal corner; third with square or slightly toothed posterodistal corner. Pleopod peduncles and rami slender; coupling spines 2, hook-shaped. Dorsal pleonal and urosomal teeth absent.

Urosome short, second segment with 3 to 5 articulated spines on either side of the dorsal mid-line. Uropod 1 extending slightly beyond uropod 2, peduncle margins with strong spines, rami with apical spine groups; outer ramus outer margin with 4 spines, inner margin 2 spines; inner ramus outer margin with 3 spines, inner margin with 5 spines. Uropod 2, peduncle margins spinose, rami with apical spine groups, outer ramus outer margin with 4 spines, inner margin with 2 spines; inner ramus outer margin with one spine, inner margin with 3 spines. Uropod 3 peduncle stout; outer ramus very long, margin and apex with groups of strong setae; inner ramus very small, with 2 apical spines, set in a sinus of the peduncle. Telson short, deeply cleft and spread, lobes with 2 to several spines apically.

FEMALE (9.3 mm) PARALECTOTYPE. Fig. 1 (u-z, aa). Very similar to male in most features. Antennae slightly shorter, but flagellum articles same in number as in male. Gnathopod 1 smaller than in male, propodus shape similar. Gnathopod 2 smaller than in male, carpus lower margin longer and with more groups of stout setae; propodus similar in shape to that of male, but palmar margin minutely serrated and with a stout spine at the lower corner; propodus lacking setose groove into which dactyl of male fits; dactyl with a tooth near the tip. Peraeopod 4 coxa projected into a curved, finger-like lobe anteriorly, rather than the short, rounded lobe of the male.

Type locality: Great Egg Harbor, New Jersey.

Material: YPM 1247–Great Egg Harbor, New Jersey. A. E. Verrill and S. I. Smith. April 1871. "*Melita polita.*" 1 lectotype ♂, 8.7 mm, 8 paralectotype ♂♂ (one dissected by Kunkel, 1918), 5 paralectotype ♀♀. YPM 4897–New Haven, Connecticut, S. I. Smith. 11 ♂♂, 8 ♀♀, 5 juv. YPM 4899–probably New Jersey or Long Island Sound. S. I. Smith. No data. "*Melita polita.*" 1 ♂, 4 juv.

Discussion: Shoemaker (1935a) figured specimens of this graceful species from Sinaloa, Mexico. The type specimens described here have been refigured for comparative purposes, although Shoemaker's figures characterize the species well. At the time of Shoemaker's paper the species was known from Cocos Island, Ecuador, Panama, the west coast of Mexico. and from Louisiana to Cape Cod (see Pearse, 1913, and Kunkel, 1918). E. L. Bousfield (personal communication) has collected the species as far north as Pugwash, Nova Scotia.

Ceradocus colei Kunkel

Ceradocus colei Kunkel, 1910, p. 41-43, fig. 15

Material: YPM 4532–no data. Specimen dry, examined 1961. Probably Bermuda (no locality label with specimen.) 1 ♀, about 5 mm.

This was probably the "single female specimen" mentioned in Kunkel's description. Over the course of the years the specimen dried out and has broken into three pieces. New figures of the species are essential to replace Kunkel's meagre drawings, but they could not possibly be made from this material.

Ceradocus parkeri Kunkel

Ceradocus parkeri Kunkel, 1910, p. 39-41, fig. 14.

Material: YPM 4534–no data. Specimen dried out. Bermuda? (No locality label with specimen.) 1 ♂, 6 mm.

This specimen lacks most of the head appendages [apparently lost since Kunkel's (1910) description] and is not satisfactory for a redescription.

Elasmopus magnispinatus Kunkel

Elasmopus magnispinatus Kunkel, 1910, p. 54-56, fig. 20.

Material: YPM 4543–no data. Probably Bermuda, 1901, A. E. Verrill. 2 ♀ ♀; 8 juv. ♂ ♂.

Kunkel's description and figures must stand, since his original specimens are in poor condition.

Gammarus (Gammarus) fasciatus Say

Gammarus (Gammarus) fasciatus Say, Bousfield, 1958, p. 69-72, fig. 4.

Material: YPM 4506–Mashpee River, near Route 28, Cape Cod, Mass. Weed, cool stream. 16 July 1961. Eric L. Mills, collector. 1 ovig. ♀, 12 juvs. YPM 4529–Mill River below Axelshop Pond, Mount Carmel, Hamden, Conn. Roots and weeds, edge of river. 15 Oct. 1961. Eric. L. Mills, collector. 28 juvs. YPM 4628–Woodbridge, Conn. A. E. Verrill, 5 specimens.

These three collections help to fill in the range and occurrences listed by Bousfield (1958). The Woodbridge, Conn. collection is undoubtedly that mentioned by Kunkel (1918, p. 107). Smith (1874a) first documented the occurrence of the species in Connecticut.

Gammarus (Rivulogammarus) lacustris lacustris G. O. Sars.

Gammarus robustus Smith, 1874b, p. 610, pl. 2, fig. 7-12; Barnard, 1958, p. 55.

Gammarus limnaeus Smith (in part), Shoemaker, 1920, p. 16.

Gammarus lacustris lacustris, Bousfield, 1958, p. 80-81, fig. 8.

Material: YPM 4876–"*Gammarus robustus*," Wasatch Mountains (Utah). L. E. Ricksecker, collector. 3 broken ♀♀.

The status of Smith's *Gammarus robustus* has remained a mystery since its description, although Shoemaker (1920) placed it with *G. limnaeus* (= *G. lacustris*) and Bousfield (1958) suspected that this move was correct. Smith's original specimens have now come to light in the Yale collections, and, after examining them, Dr. Bousfield has informed me that they are females of *G. l. lacustris*. The above synonymy establishes the status of Smith's species with certainty.

Family PLEUSTIDAE Stebbing

Neopleustes pulchellus (Krøyer)

Neopleustes pulchellus (Krøyer), Gurjanova, 1951, p. 643-645, figs. 439, 440.

Material: YPM 1301–USFC, (B1), 50 fm. (92 meters), 1872. USNM 35646. Georges Bank, 41°25′N, 66°25′W. S. I. Smith and O. Harger. 1 ♀.

This is apparently the southernmost record in New England. Holmes (1905) recorded the species (as *Paramphithoe pulchella*) from Grand Manan, New Brunswick, and Shoemaker (1930) includes Casco Bay, Maine, in his distribution records. As mentioned in the case of *Ampelisca eschrichti* Krøyer, warming trends in New England waters may make Georges Bank unsuitable at present for some arctic and subarctic species, perhaps including *Neopleustes pulchellus.*

Family ATYLIDAE G. O. Sars

Atylus swammerdami (H. Milne-Edwards)

Paratylus swammerdami (H. Milne-Edwards), G. O. Sars, 1895, p. 463-465, pl. 163.
Atylus swammerdami, Barnard, 1958, p. 31.

Material: YPM 5632–Sta. 1231. "Fish Hawk." Vineyard Sound Lightship, W by N ½ N; Cuttyhunk N by W ¾ W; Gay Head SE ¾ E. 16 fm. (29 meters). Sand. 29 Aug. 1887. 1 juv., 6 mm.

There are apparently no other records of *Atylus swammerdami* from North America. This specimen agrees well with specimens from the west of Ireland collected by Canon A. M. Norman about 1866 (YPM 5620), but differs slightly from Sars' (1895) figures in having a more convex hind margin of the peraeopod 5 basis and a setose hind margin of the peraeopod 4 basis which is not projected at the posterodistal corner.

Other species of the genus are apparently not common on the East Coast of North America, although *A. carinatus* (Fabricius) occurs as far south as the St. Lawrence estuary (Brunel, 1961b), and Shoemaker (1932) summarizes occurrences of *Nototropis* (now *Atylus*) *minikoi* Walker from Chesapeake Bay to Brazil.

Family EUSIRIDAE Stebbing

Eusiroides verrilli (Kunkel)

Pontogeneia verrilli, Kunkel, 1910, p. 29-31 fig. 10.
Eusiroides verrilli, Schellenberg, 1929, p. 273-282.

Material: YPM 5338–#11. Castle Harbor. Bermuda? A. E. Verrill. 1 lectotype ♀, 9 mm, (figured by Kunkel); 2 paralectotype adult ♂♂, 8 and 10 mm; 32 paralectotype ♀♀; 3 paralectotype juveniles.

A dissected adult female, 9 mm, is apparently the specimen used by Kunkel (1910, fig. 10) for his description of the species (as *Pontogeneia verrilli*). It is designated a lectotype. Kunkel's description and figure seem adequate, so the species has not been redescribed.

Family PODOCERIDAE Stebbing

Dulichia spinosissima Krøyer

Dulichia spinosissima Krøyer, Gurjanova, 1951, p. 990-991, fig. 688.

Material: YPM 5618–Sta. 81. West Harbor, Fisher's Is., N.Y. Fisher's Is. Sound. Sand and shells. 3½ fm. (6.4 meters). 10 Aug. 1874. USFC. 1 broken juv. ♂.

Brunel (1961a) records this species from the Gulf of St. Lawrence. The present specimen is apparently the southernmost record of the species.

Family AMPITHOIDAE Stebbing

Genus *Ampithoe* Leach 1813/1814 (cited by Stebbing, 1906.)

Stebbing (1906, p. 631) defines the genus as follows:

"Head without rostrum. Side-plates 1-5 well developed, 5th as wide as 4th, with a very small hind lobe. Antenna 1 without accessory flagellum, usually longer than antenna 2, though with shorter peduncle. Mouthparts prominent below the head. Upper lip distally rounded. Lower lip ... inner lobes well developed; outer lobes bifid; mandibular processes prominent. Mandible normal, principle and secondary plate multidentate, spines in spine row numerous, molar of moderate size; 3rd joint of palp sometimes widened distally and crowded with setae, at others not widened and slightly armed. Maxilla 1, inner plate very small, usually with 1-3 setae, outer plate with 10 spines; 2nd joint of palp with several spical spines. Maxilla 2, outer plate the larger, inner distally-narrowed, inner margin not very elongate. Gnathopod 1 subchelate, usually the smaller. Gnathopod 2 usually subchelate, stronger in ♂ than in

♀ and generally of a different shape. Peraeopods 1 and 2, 2nd joint expanded, sometimes greatly, for the cement glands, the secretion from which issues through the apex of the finger to supply fibres for constructive purposes. Peraeopods 4 and 5 longer than the others. Uropod 3, outer ramus carrying 2 reverted spines. Telson short, usually or always having the angles of the apex minutely hooked."

Ampithoe longimana Smith

(Figs. 2, 3)

Amphithoe longimana Smith, (in: Verrill and Smith, 1873, p. 563). Holmes, 1905, p. 509, figs. Kunkel, 1910, p. 87, fig. 34. Kunkel, 1918, p. 147-149, fig. 43.

Ampithoe longimana Smith, Stebbing, 1906, p. 634, 738. Pearse, 1913, p. 376. Barnard and Reish, 1959, p. 36-37, pl. 12.

Diagnosis: 1) Antenna 2 peduncle segments 4 and 5 of ♂ long. 2) Gnathopod 1 propodus of ♂ long, even in width. 3) Uropod 3 rami very short, rounded. 4) Peraeopod 5 basis convex, spine at posterodistal angle.

Description: Male (10.1 mm) LECTOTYPE Fig. 2 (a-t), 3 (u). Head short, length less than first two body segments combined; interantennal lobe with rounded margins, rather prominent; inferior antennal sinus with oblique, gently-rounded posterior margin; eye yellowish-brown in alcohol, with about 50 facets.

Antenna 1 as long as body; peduncle extending a little beyond 4th peduncle segment of antenna 2, 1st peduncle segment with a few setae and one short spine distally, 2nd segment longer than 1st, lightly setose; 3rd segment about ½ length of second; flagellum 1½ to 2 times length of peduncle, of 29 articles. Antenna 2 stout; peduncle long, 4th segment about equal to first two segments of antenna 1 peduncle in length, 5th segment slightly longer than 4th; flagellum equal in length to 5th peduncle segment, of 23 articles.

Mouthparts projecting below head. Upper lip rounded and finely setose below. Mandible, palp slender, third segment lightly expanded distally, armed with several long plumose setae; incisor process strongly toothed; lacinia mobilis large, associated with a few slender spines; molar process with ridged triturating surface. First maxilla, palp apical segment curved, outer plate armed with 10 strong dentate spines. Second maxilla inner plate short, outer margin short, oblique, inner margin setose along its entire length; outer plate projecting over inner distally. Lower lip outer plates with marked lateral projections; medial margins with deep rounded incisions. Maxilliped, outer plate armed with rather small spines; inner plate inner margin partially oblique, set with plumose setae.

Gnathopod 1, coxa projected anterodistally; basis with an anterodistal rounded lobe armed with a few spines; carpus elongated; propodus long, even in width, palmar margin short and transverse, armed with a blunt spine near the dactyl and several setae, lower margin of segment slightly concave and heavily set with groups of setae; dactyl long, inner margin dentate. Gnathopod 2 basis with an anterodistal rounded lobe; carpus wide, about 3/4 length of propodus; propodus only slightly shorter than that of gnathopod 1 but much wider, lower margin slightly concave, palm oblique, concavity defined by a ventral projection, with a quadrate setose lobe near base of dactyl, palm and lower margin set with groups of long setae; dactyl dentate on inner margin, extending length of palm.

Peraeopods 1 and 2 short, very similar; basis expanded medially; propodus narrow, with a few setae ventrally; dactyl short, 1/3 length of propodus.

Peraeopod 3, coxa with a large anterior lobe and small posterior lobe; basis expanded, rounded anteriorly and posteriorly; dactyl stout, curved.

Peraeopods 4 and 5 very similar in form, but 4 shorter than 5, extending at most to the middle of peraeopod 5 propodus. Peraeopod 4, coxa slightly lobed anteriorly; basis rounded posteriorly, with a small posterodistal concavity marked by a single spine; merus, carpus and propodus about equal in length. Peraeopod 5 coxa rather narrow, slightly concave distally; propodus longer than carpus, about equal in length to merus.

Gills all simple, short and broad.

Epimeral plates; first very short, rounded anteriorly, slightly concave posteriorly; second strongly rounded anteriorly, posterior margin convex proximally, becoming slightly concave near posterodistal corner; third strongly rounded anteriorly, posterior margin convex above posterodistal corner. Pleopod rami about half again as long as peduncles; coupling spines short, apex with one hook on one side, 2 on the other.

Uropods all extending to same point. Uropod 1 stout, peduncle with 7 spines on outer margin, 10 on inner margin; outer ramus shorter than inner, outer margin evenly set with 8 spines, inner margin with 2 spines only; inner ramus outer margin with two spines, inner margin with 3 spines. Uropod 2 stout; peduncle margins each with 4 to 5 spines; outer ramus slightly shorter than inner, outer margin with 6 spines, inner margin with 4 spines; inner ramus outer margin with 3 spines, inner margin with 5 spines. Uropod 3 short; rami very short, rounded, outer ramus with 2 lateral hooks, inner ramus with an apical spine, 2 lateral spines and a tuft of apical setae; distal margin of peduncle with 6 spines.

Telson short, narrowed, quadrate, and with 4 setae distally.

Female (9.7 mm) PARALECTOTYPE Fig. 3 (v-y). Antenna 1 peduncle more slender than in male but proportions about the same; flagellum of 25 segments, extending 3/4 length of body. Antenna 2 less robust than that of male, peduncle segments 4 and 5 slender, almost equal in length; flagellum of 17 articles.

Gnathopod 1 carpus shorter and smaller than male, almost straight ventrally; propodus about equal to carpus in length, palmar margin rounded, oblique, dactyl long, dentate, half its length beyond palm. Gnathopod 2 propodus shorter and smaller than in male, palmar margin convex near dactyl, gradually becoming concave ventrally, palm with quadrate lower corner.

Oostegites present on gnathopod 2 and peraeopods 1-3, lobate, broad, fringed on most margins with long curved setae. Uropod 3 with 1-3 spines on inner ramus inner margin.

Other features as in male.

Type locality: Vineyard Sound, Mass.

Material: YPM 5214–Vineyard Sound, Mass. U. S. Fish Commission, 1871. 1 lectotype ♂, 8 paralectotype ♂ ♂. YPM 5215–Vineyard Sound, Mass. U. S. Fish Commission, 1871. 8 paralectotype ♀ ♀ (1 figured). YPM 4631–Great Egg Harbor, N.J. (?) A. E. Verrill and S. I. Smith, 1872, 1 juv. ♀. YPM 5238–no data. Several dessicated specimens. YPM 5239–Provincetown, Cape Cod, low water, USFC. Aug. 22, 1879. USNM 35662. 2 adult ♂ ♂, 1 juv. ♂, 1 ovig. ♀ YPM 5240–Long Island Sound, USFC, 1874. USNM 35619. 1 adult ♂. YPM 5241–Long Island Sound, USFC, 1874. USNM 35618.

Discussion. The material here described and figured was almost certainly that used by Smith for his original description of the species (in: Verrill and Smith, 1873). Smith did not mention the numbers of animals in his original collection. Among the specimens in this series is one which Kunkel (1918) apparently used for his figure 43. However, since this specimen was incomplete and no trace could be found of missing appendages, the lectotype chosen was a male in better condition.

One difference was noted between Smith's description and the material at hand. All specimens examined had yellow-brown eyes, while Smith stated their color was black. Fresh specimens of the species from Sengekontacket Pond, Martha's Vineyard, Mass., in my personal collection, have dark brown eyes in alcohol. Thus it seems that eye pigment gradually leaches out after years in preservative.

Barnard (in: Barnard and Reish, 1959) outlines the range of *A. longimana* as including the United States East Coast, Bermuda (see Kunkel, 1910), and parts of southern and lower California. Barnard's figures show that the California populations are virtually identical with those on the East Coast. Table 1 outlines the main morphological differences between females of the present species and females of *Ampithoe rubricata* (Montagu).

Ampithoe pollex Kunkel

Amphithoe pollex Kunkel, 1910, p. 93, fig. 36.

Grubia indentata Stout, 1913, p. 656-657. Shoemaker, 1941, p. 188.

Ampithoe pollex, J. L. Barnard, 1954, p. 29-31, figs. 27-28.

Material: YPM 5291–probably Bermuda, A. E. Verrill, 2 ♂♂, 5.5 mm and 3.8 mm.

Kunkel's type material consists of two damaged males which agree well with his figures (1910) and with the description and figures of Barnard (1954). Since the species is so well characterized no attempt has been made to figure the poor specimens at hand.

TABLE 1. Main morphological differences between females of *Ampithoe longimana* and *Ampithoe rubricata.*

	A. longimana ♀	*A. rubricata* ♀
Eye	Round, large.	Slightly oval, small.
Antenna 1	Peduncle slender.	Peduncle stout.
Antenna 2	Peduncle segment 4 and 5 slender.	Peduncle segment 4 and 5 more stout.
Mandible	Palp segment 3 almost linear.	Palp segment 3 flattened, inflated distally.
Gnathopod 1	Propodus narrow, palm short; dactyl longer than palm.	Palm longer, dactyl equals palm length.
	Carpus lower margin long, shallowly rounded.	Carpus lower margin short, more sharply rounded.
Gnathopod 2	Very similar in both	
Peraeopod 5	Basis hind margin widest proximally, convex. *Spine at posterior angle.*	Basis even width throughout, hind margin linear. *No spine at posterior angle.*
Uropod 1	Outer ramus inner margin with 2 spines.	Outer ramus inner margin spineless.
Uropod 2	Outer ramus inner margin and inner ramus outer margin with spines.	Outer ramus inner margin and inner ramus outer margin lacking spines.
Uropod 3	Rami very short, rounded.	Rami ½ length of peduncle or more, less rounded.
	Inner ramus with a few spines and few apical setae.	Inner ramus with several spines, large clump of apical setae.
	Outer ramus with no lateral setae.	Outer ramus with clumps of lateral setae.
Telson	Few apical setae.	Several apical setae (3/side)

Ampithoe valida Smith

(Fig. 4)

Amphithoe valida Smith (in: Verrill and Smith, 1873, p. 563).
Amphithoe rubricata (in part), Della Valle, 1893, p. 459. Holmes, 1905, p. 510. Kunkel, 1918, p. 149-151.
Ampithoe valida, Stebbing, 1906, p. 635. J. L. Barnard, 1954, p. 34-35, pl. 31. Alderman, 1936, p. 68.
Amphithoe shimizuensis Stephensen, 1944, p. 77-80, figs. 28, 29.

Diagnosis: 1) Gnathopod 1 carpus and propodus broadly expanded, carpus with broad lobe on lower margin. 2) Gnathopod 2 propodus massive, palm almost transverse, with a blunt, square tooth medially. 3) Uropod 3 rami half length of peduncle, outer ramus with 2 stout out-curved spines. 4) Antenna 2 only slightly shorter than antenna 1.

Description: Male (12.7 mm) LECTOTYPE. Fig. 4 (a-q). Head slightly shorter than first two body segments combined; interantennal lobe large, slightly truncated, corners rounded.

Antenna 1 about half as long as body, peduncle segments 1 and 2 equal in length; flagellum of 35 articles. Antenna 2 slightly shorter than antenna 1, peduncle segment 5 slimmer than 4, about equal to it in length; flagellum with 20 articles.

Epistome slightly rounded and finely setose below.

Mandible, incisor process with 6 sharp teeth; lacinia mobilis large and toothed; 6 pectinate spines between incisor and molar processes; molar process well-developed, ridged and sclerotized; palp 3rd segment broad, with several setae on the curved distal margin. Maxilla 1, last segment of palp rounded distally, bearing 8 spines and a seta; outer plate with 10 stout spines; inner plate small, unarmed. Maxilla 2, inner plate setose along entire inner margin; outer plate projecting over inner plate distally. Maxilliped, palp segments short; outer plate with 11 small short spines on inner margin, grading into longer spines distally; inner plate broadly rounded distally and set with marginal setae.

Gnathopod 1, coxa projected anterodistally; basis with an anterodistal rounded lobe laterally; carpus broad, with a lateral fringe of long setae on the upper margin, lower margin broadly lobed, extending partly over the base of the propodus; propodus almost as broad as carpus, palmar margin rounding evenly into lower margin, defined by a spine at the lower corner; dactyl stout and short. Gnathopod 2, basis stout, with a large anterodistal lateral lobe; merus projecting slightly below carpus; carpus short, with a few setae on a lower lobe; propodus massive, slightly expanded distally, palm almost transverse, with a small square median tooth and a rounded prominence at the lower corner; dactyl stout, tip fitting behind prominence at lower corner of palm.

Peraeopods 1 and 2 very similar; basis expanded, setose on the hind margin; carpus and propodus slender. Peraeopod 3 basis rounded, with a few spines on the anterior margin; propodus with 5 spines on anterior margin; dactyl pointed outward or forward. Peraeopods 4 and 5 quite similar, peraeopod 4 short, extending to about middle of peraeopod 5 propodus, its basis with a sharp notch posterodistally.

Epimeral plate 1 rounded anteriorly, with a slight posterodistal tooth and a squarish projection posteriorly; epimeral plate 2 rounded posteriorly, with a slight tooth at the posterodistal corner; epimeral plate 3 larger than 2, quite similar in shape. Pleopod peduncles stout, coupling spines 9, mushroom-shaped; rami about half again as long as peduncles, of 16-18 segments.

Urosome short, flattened. Uropods all extending to same point. Uropod 1 long; outer ramus slightly over half as long as peduncle, shorter than inner ramus, outer margin with 6 spines, inner margin spineless; inner ramus outer margin spineless, inner margin with 4 spines. Uropod 2, outer ramus outer margin with 5 spines, inner margin spineless, inner ramus outer margin spineless, inner margin with 3 spines. Uropod 3 short, peduncle about twice length of rami, dorsal surface with 3 spines at base of outer ramus and 2 at base of inner ramus; outer ramus with 2 out-curved spines distally; inner ramus with 4 short spines and a tuft of setae distally and a small spine on the outer margin.

Telson short, distal corners slightly notched, apex slightly acute (rounded in some specimens), dorsal surface with setae near margins and at distal corners.

FEMALE. The collections contain a number of juvenile females, all previously identified as *A. valida.* All, however, are indistinguishable from females of *A. longimana.* It appears that Smith's original collection contained both species and that he or a subsequent viewer of the material mistook the female of *A. longimana* for that of *A. valida.* Smith (in: Verrill and Smith, 1873, p. 563) says of the female of *A. valida*: "The female differs in having the hands of the first pair of legs slightly more elongated, and those of the second pair more elongated than in the male, and the palmar margin slightly oblique."

This description fits the gnathopod condition of a paralectotype juvenile male exactly, and presumably the female of the species is very similar. It is possible that Smith's description was based on this paralectotype male.

Alderman (1936) undoubtedly saw a female of *A. valida,* since his description is based on a mating pair. Of the female gnathopod characters he says only (p. 68): "First gnathopod somewhat more slender in female than in male . . . . Fifth joint of second gnathopod in female produced as in male, shorter than sixth joint. Palm smooth, convex. Second joint as in male."

Further collections are necessary to clarify the morphology of the female.

Type locality: Beesley's Point, New Jersey.

Material: YPM 1230–Beesley's Point, New Jersey. A. E. Verrill and S. I. Smith, April 1871. 1 lectotype ♂ (12.7 mm), 5 paralectotype adult ♂ ♂, 1 paralectotype juv. ♂.

Discussion. Uncertainties about the identification and description of females have been discussed previously.

Smith's description (in: Verrill and Smith, 1873) fits the specimens at hand very closely, except that the specimens have pale brown eyes, rather than black. This is certainly attributable to leaching of color in alcohol, as discussed for *A. longimana.*

On the United States East Coast *A. valida* is apparently known only from the type locality, although Smith (in: Verrill and Smith, 1873) noted its presence in Long Island Sound. Alderman (1936) and Barnard (1954) both record the species from the United States West Coast (California and Oregon, respectively). Alderman's description differs from Smith's specimens in a few points, all probably attributable to size difference.

These differences are:

	Alderman's description	*Smith's specimens*
Size	9-11 mm	10-13 mm
Antenna 1 flagellum	50 articles	35 articles
Antenna 2 flagellum	25 articles	20 articles
Antenna 2 peduncle segment 4	Half again as long as 5	Equal to 5 in length
Maxilla 1 inner plate	9 spines	10 spines

Barnard's figures indicate that his specimen may have been slightly subadult, since the limbs are less spinose than the New Jersey material figured here and the male gnathopod 1 is slightly less developed. However, agreement is very close.

Holmes (1905) first placed *A. valida* in the synonymy of *A. rubricata*, and his action was followed by Kunkel (1918). Holmes stated (p. 510): "Specimens sent to the U. S. National Museum by Professor Smith under the name *Amphithoe valida*, and which I have examined, agree well with Professor Smith's description of that species, which is certainly identical with *A. rubricata*." Holmes' mistake could have been due to the examination of immature specimens of *A. valida*. Mature males are quite distinct in the character of both pairs of gnathopods.

Genus *Cymadusa* Savigny 1816.

Ruffo (1947, p. 168) defines this genus as follows: "Characters of the genus *Amphithoe* Leach. . . , but first pair of antennae provided with an accessory flagellum of 1-6 articles. The genus is particularly distinguished by the following combination of characters; mandible furnished with a well-developed palp, first pair of antennae provided with an accessory flagellum."

Cymadusa compta (Smith) new combination
(Figs. 5, 6)

Amphithoe compta Smith, 1873 (in: Verrill and Smith, 1873, p. 564.)

Grubia compta, Holmes, 1905, p. 510-511, figs. Kunkel, 1918, p. 151-153, fig. 45. ?Shoemaker, 1921, p. 102.

Amphithoides comptus, Stebbing, 1906, p. 645.

?*Grubia* sp., Pearse, 1913, p. 376.

Not *Grubia compta*, Pearse, 1913, p. 376, fig. 6.

Grubia hirsuta Chevreux (in part), Schellenberg, 1925, p. 186-187.

Cymadusa filosa Savigny (in part), Pirlot, 1939, p. 64-67.

Diagnosis: 1) Coxae of gnathopods 1 and 2 sparingly setose. 2) Gnathopod 1 propodus palmar margin slightly concave. 3) Gnathopod 2 carpus of ♂ long, without distinctly projecting ventral lobe. In ♀, gnathopod 2 carpus with a large, round-margined ventral lobe. 4) Gnathopod 2 propodus equal in width to carpus, dactyl longer than palmar margin. 5) Antenna 1 flagellum with about 33 articles; antenna 2 flagellum with 20-28 articles.

Description: Male (8.6 mm). LECTOTYPE. Fig. 5 (a-p). Head slightly shorter than the first two body segments combined; inter-antennal lobe square and projecting; hind margin oblique; inferior margin slightly concave. Eye slightly ovate, straw-colored in specimens in alcohol.

Antenna 1, first segment of peduncle as long as head; second segment equal in length to first, third segment about 1/3 length of second; accessory flagellum of one main article and a small setose apical article; flagellum slender, long, extending almost to end of body, of about 33 articles.

Antenna 2 slightly shorter than antenna 1, peduncle stout, segments 4 and 5 about equal, each armed ventrally with 8-9 groups of long setae; flagellum of 20-28 articles.

Epistome rounded ventrally and finely setose.

Mandible, incisor process large, curved, with 6 sharp teeth; lacinia mobilis stout, armed with several small teeth; 8 setae between incisor and molar processes; molar process ridged and heavily sclerotized;

palp slightly curved, 3rd segment expanded distally and set with several long pectinate setae.

Hypopharynx with well-developed, finely setose, inner lobes, outer lobes bilobed medially.

Maxilla 1, inner plate small, acute apically, with 7 setae on the medial margin; outer plate with 10 stout toothed spines; palp segment 3 expanded distally, bearing 7 short stout spines and one or two setae. Maxilla 2, outer plate large, distal margin oblique, set with long setae; inner plate small, narrowed distally, with an oblique row of setae joining setae found along the entire medial margin.

Maxilliped, inner plate narrow, with 2 or 3 stout spines and several long setae distally and a row of long plumose setae along the medial margin; outer plate set with several long, curved setae distally and with a series of 13 stout spines along the medial margin; palp segments 3 and 4 with groups of long setae medially.

Gnathopod 1, coxal plate small, projecting anteriorly; basis stout, with several groups of long plumose setae near the hind margin; merus with a long anteroventral projection extending nearly halfway along the carpus, set with groups of long plumose setae; carpus long, broad, anterior margin almost straight and square, ventral margin set with thick groups of long plumose setae; propodus shorter than carpus, with thick groups of plumose setae on upper margin, palmar margin oblique, set off by a stout spine at the lower angle, and a slight hump near the attachment of the dactyl, lower margin rounded, receding into a narrow connection with the propodus, with groups of long setae; dactyl stout, curved, inner margin serrated.

Gnathopod 2, coxal plate deeper than wide, corners rounded; basis heavily set with long plumose setae; merus small, with a rounded anteroventral projection armed with groups of long setae; carpus long and broad, upper and lower margins heavily set with long plumose setae; propodus almost as long as carpus and about as wide, with groups of long plumose setae on the upper margin, palmar margin oblique and slightly concave, with a small hump near the base of the dactyl and a small acute projection at the ventral corner; dactyl stout, inner margin serrated.

Peraeopod 1, coxal plate deeper than wide, lower anterior corner rounded, posterior corner almost square; basis stout, glandular (glandular material also present in ischium and merus); carpus and propodus about equal in length, both with several groups of setae on ventral margin; dactyl short, stout, curved. Peraeopod 2 very similar.

Peraeopod 3, coxa with a posterior rounded lobe, lower corners rounded; basis ovate, armed with 6 spines on the anterior margin; merus and carpus about equal, short, stout, with one and two spines on the posterior margin respectively; propodus about half again as long as carpus, with 4 stout spines on the posterior margin and 5 groups of setae on the anterior margin; dactyl short, stout, turned posteriorly.

Peraeopod 4 shorter than peraeopod 5; coxa small, with a rounded anterior lobe; basis narrow, posterior margin concave distally and with 1-2 short spines; merus with 2 spines on posterior margin; carpus slightly shorter than merus, with one spine on the posterior margin; propodus slightly expanded distally, with 5 spines on anterior margin; dactyl stout, turned anteriorly. Peraeopod 5 similar to peraeopod 4, but more stout and longer; coxa not lobed, slightly narrowed distally; basis with a posterior proximal lobe, 3 spines on the posterior margin; propodus more heavily setose than that of peraeopod 4.

Gills short, slightly longer than wide, simple.

Pleon slightly compressed dorsoventrally. Pleopod rami about half again as long as peduncles, with about 13-14 segments. Pleopod coupling hooks anchor-shaped. Epimeral plate 1 small, posterior margin convex, lower posterior corner acute, with a small spine. Epimeral plate 2 with a rounded projection anteriorly, posterior angle acute, posterior margin concave distally, convex proximally. Epimeral plate 3 larger than 2, acute posteriorly, posterior margin gently convex.

Urosome slightly flattened dorsoventrally. Uropods all extending to same point. Uropod 1 stout, peduncle with 5 spines on inner margin, 6 spines on outer, produced into a long ventral spine-like process which extends between the rami; both rami with distal spine groups, inner ramus longer than outer; outer ramus outer margin with 4 spines, inner margin with two spines; inner ramus outer margin with one spine, inner margin with 4 spines. Uropod 2 shorter than 1, peduncle inner margin with 3 spines, outer margin with 4 spines; both rami with distal spine groups; inner ramus longer than outer, inner margin with 4 spines, outer margin with 2; outer ramus, inner margin with 3 spines, outer margin with 4. Uropod 3 short, peduncle with 4 spines on inner margin, 2 spines and 2 groups of ventral setae on outer margin, and 3 short spines at the base of the outer ramus; inner ramus straight, armed with 3 spines on the inner margin, an apical spine and tuft of setae, and one spine on the outer margin; outer ramus curved, with 2 distal spines which curve outward.

Telson short, broad, corners acute, with setae set in notches; 3 groups of lateral setae on each side; dorsal surface with 4 groups of setae.

Female (14.4 mm) PARALECTOTYPE. Fig. 6 (v-z). Quite similar to the male, but antennae a little shorter and more slender and gnathopods considerably smaller.

Antenna 1 flagellum with 37 articles; antenna 2 flagellum with 27 articles.

Gnathopod 1 with only a few long simple setae proximally on the hind margin of the basis; merus with a short, acute anteroventral projection set with a few simple setae extending about 1/3 the length of the carpus; carpus broad, with a broad ventral oblique lobe set with simple setae ventrally; propodus about as long as carpus, with only a few long setae on upper margin, palmar margin oblique, but not as much as in male and shorter, defined by a stout spine at the lower corner and a slight hump near the attachment of the dactyl, lower margin slightly rounded, set with groups of setae, receding into narrow connection with the propodus; dactyl stout, inner edge serrated.

Gnathopod 2, basis with several groups of long setae, merus small, with a rounded anteroventral projection armed with groups of long setae; carpus short and broad, with a ventral lobe thickly set with groups of long setae, upper margin almost bare of setae; propodus as long as carpus and about as wide, with a few groups of setae on the upper margin, palmar margin oblique and almost straight, defined by a stout spine at the lower corner; dactyl stout and serrated on the inner margin.

Oostegites long, ovoid, margins with many close-set long setae.

Type locality: Vineyard Sound, Mass.

Material: YPM 5209–Vineyard Sound, Mass., USFC, 1871. 1 Lectotype ♂ (8.6 mm); 3 paralectotype adult ♂ ♂ (1 dissected by Kunkel, 1918); 3 paralectotype juv. ♂ ♂. YPM 5210–Vineyard Sound, Mass., USFC, 1871. 8 ovig. ♀ ♀, 4 juv. ♀ ♀, paralectotypes. YPM 5211–Long Island Sound, USFC, 1874. 1 juv. ♂, 1 ovig. ♀. YPM 5212–Long Island Sound, USFC, 1 ovig. ♀, 5 juvs. YPM 5242–Long Island Sound, USFC, 1874. 1 juv. ♂.

Discussion. This species, described by Smith (in: Verrill and Smith, 1873) as *Amphithoe compta*, has a complicated nomenclatural history. Stebbing (1906) transferred the species to the genus *Amphitoides* Kossman, believing it to have only one hook on the outer ramus of uropod 3. Smith's description makes no mention of uropod 3. Holmes (1905) placed the species in the genus *Grubia*. Kunkel (1918) pointed out Stebbing's mistake and retained the genus *Grubia*. Schellenberg (1925) stated "Ich halte nach allem die Arten von Chevreux, Kunkel und Pearse für identisch" and placed *Grubia compta* in *G. hirsuta* Chevreux. With Pirlot's (1938, 1939) resurrection of the genus *Cymadusa* Savigny to replace *Grubia*, *G. compta* and its several synonyms were listed with *Cymadusa filosa* Savigny, as was Schellenberg's "*Grubia hirsuta*." Ruffo (1947) suggested that Smith's species was erroneously included in Pirlot's list. This has proved to be the case, since *C. compta* differs greatly from *C. filosa* and other *Cymadusa* species in its gnathopod characters and seems to have a disparate range.

The known range includes New England (present material), south to North Carolina (Kunkel, 1918, on Smith's authority). Pearse's (1913) record of the species from Florida is *C. filosa*, as Barnard (1955) pointed out, judging by Pearse's figures, in which gnathopods 1 and 2 have been reversed. Pearse also records "*Grubia sp.?*" from Key West, Florida; this may be *C. compta*. Shoemaker's (1921) record of "*Grubia compta*" from Barbados may be *C. filosa*. The latter species seems never to have been taken north of Florida and is undoubtedly tropical.

Kunkel describes the preference of *C. compta* for eelgrass. The species was very common in eelgrass with *Ampithoe longimana* Smith at Sengekontacket Pond, Martha's Vineyard, Mass., in August, 1962.

Cymadusa filosa Savigny

(For synonymy see Barnard, 1955, and Ruffo, 1947.)

Material: YPM 5208–no data. Bermuda (?). 2 ♂♂, 2 ♀♀, 2 juv. Probably Kunkel's types of *Grubia coei*. YPM 5213–Bermuda. "*Grubia crassicornis*." 2 ♀♀, 2 juv.

Kunkel (1910, p. 97 and fig. 38) dissected and figured a subadult male of YPM 5208 as *Grubia coei*. These figures and the specimens are in close agreement with Shoemaker's (1935b) and Ruffo's (1947) figures of *Cymadusa filosa* Savigny and support Pirlot's (1939) and Ruffo's views of the status of *Grubia coei* as synonymous with *C. filosa.*

Although YPM 5213 was labelled "*Grubia crassicornis,*" the specimens do not agree with Kunkel's figures (1910, fig. 37) of *G. crassicornis* Costa and so cannot be the specimens on which the figure was based. They are clearly specimens of *Cymadusa filosa.*

The confusion of *C. compta* (Smith) with *C. filosa* Savigny has been discussed earlier in this paper.

C. filosa has been recorded from widely separated localities, including Bermuda (Kunkel, 1910), Florida and Puerto Rico (Shoemaker, 1935b), Mediterranean Sea, Red Sea, Canary Islands (Ruffo, 1947), Hawaii, Indian Ocean, Australia and West Africa (summary in Barnard, 1955).

Family COROPHIIDAE Stebbing

Erichthonius difformis H. Milne-Edwards

Erichthonius difformis H. Milne-Edwards, Gurjanova, 1951, p. 950-951, fig. 661.

Material: YPM 5633–USFC. No other data. 2 adult ♂♂, 2 juv. YPM 5665–Bay of Fundy, USFC, 1872. 20 adults, 4 juv.

Eleven collections of species of the genus *Erichthonius* occur in the Yale collection. Based on male gnathopod 2 characters primarily, nine are *E. rubricornis* (Stimpson), and all were collected in the region from Georges Bank to Halifax Harbour, Nova Scotia. Two collections, listed above, contain *E. difformis.* Most specimens in these two collections agree quite well with Sars' (1895) figures. However, some variability in the form of the male second gnathopod occasionally makes specific identification difficult. Taxonomic problems have been noted in other combinations of species in this genus. Dahl (1946) maintained that *E. difformis* and *E. hunteri* were specifically distinct, while Enequist (1950) suspected that the two forms could be the same species, the variability in form being caused by the effect of environment on growth rates.

It is noteworthy that the form of the male second gnathopod in *E. rubricornis* is closer to that of *E. hunteri* (as illustrated by Sars) than Holmes' (1905) figures would indicate. For this reason, as well as to clarify the problems outlined above, a critical morphological study of the common North Atlantic species would be of great value.

The distribution of *E. difformis* on the East Coast of North America is not clear. Brunel (1961a) records only *E. rubricornis* and *E. tolli* from the Gulf of St. Lawrence region. Some of S. I. Smith's references to *E. difformis* in New England refer to *E. rubricornis,* since some of his specimens in the Yale collection, labelled *E. difformis,* are actually *E. rubricornis.* Holmes (1905) seems to have recognized this fact. The present specimens indicate only that *E. difformis* occurs south at least to the Bay of Fundy.

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Figure 1.

Melita nitida Smith. Great Egg Harbor, New Jersey.

LECTOTYPE ♂ (8.7 mm). a, head and antennae. b, upper lip. c, mandible. d, lower lip. e, maxilla 1. f, maxilla 2. g, maxilliped (outer plate separated). h, gnathopod 1. i, gnathopod 1 propodus and dactyl, inner. j, gnathopod 2. k, gnathopod 2 propodus and dactyl, inner. l, peraeopod 1. m, peraeopod 2. n, uropod 1. o, uropod 2. p, epimeral plates 1-3 and 3rd pleopod.

PARALECTOTYPE ♂ (8.9 mm). q, uropod 3.

PARALECTOTYPE ♂ (7.1 mm). r, peraeopod 3. s, peraeopod 4. t, peraeopod 5.

PARALECTOTYPE ♀ (9.3 mm). u, antenna 1. v, antenna 2. w, telson. x, gnathopod 1. y, gnathopod 1 propodus and dactyl, inner. z, gnathopod 2. aa, gnathopod 2 propodus and dactyl, inner.

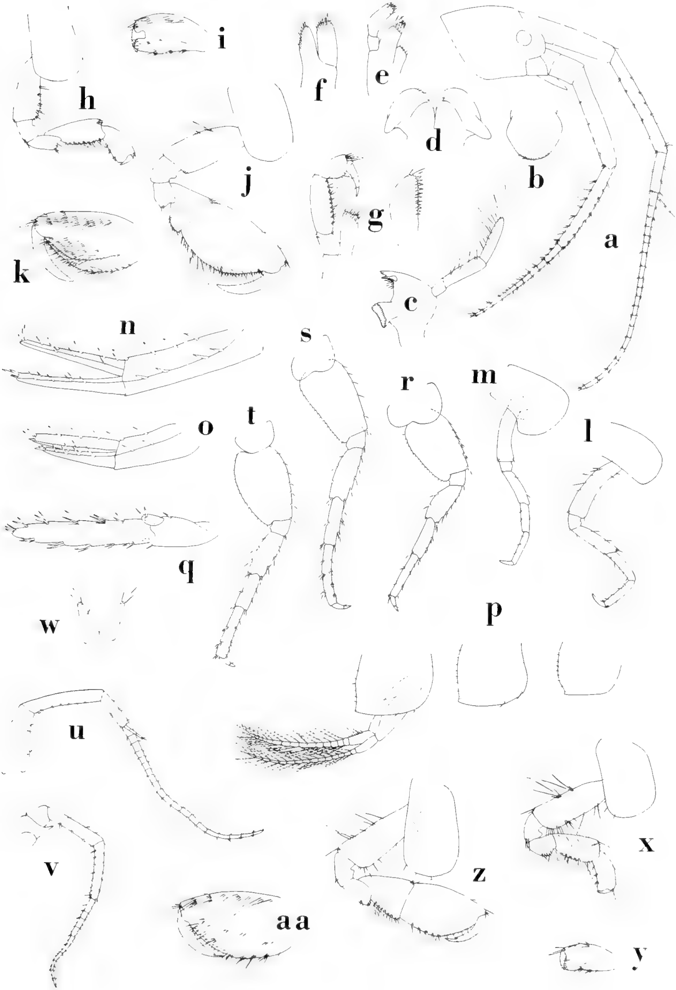
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Figure 2.

Ampithoe longimana Smith. Vineyard Sound, Massachusetts.

LECTOTYPE ♂ (10.1 mm). a, head. b, antenna 1. c, antenna 2. d, upper lip. e, mandible (with lateral view of palp terminal segment). f, lower lip. g, maxilla 1. h, maxilla 2. i, maxilliped (outer plate separated). j, gnathopod 1, inner. k, gnathopod 2, inner. l, peraeopod 1. m, peraeopod 2. n, peraeopod 3. o, peraeopod 4. p, peraeopod 5. q, uropod 1. r, uropod 2. s, uropod 3. t, telson.

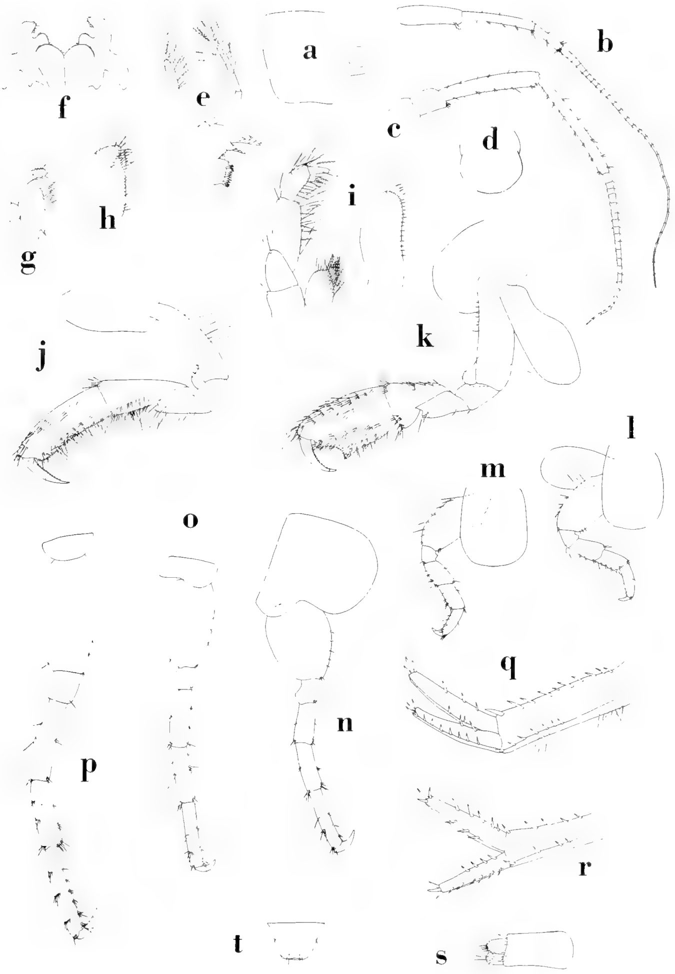
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Figure 3.

Ampithoe longimana Smith. Vineyard Sound, Massachusetts.

LECTOTYPE ♂ (10.1 mm). u, epimeral plates 1-3 with pleopods.

PARALECTOTYPE ♀ (9.7 mm). v, antenna 1. w, antenna 2. x, gnathopod 1, inner. y, gnathopod 2, inner.

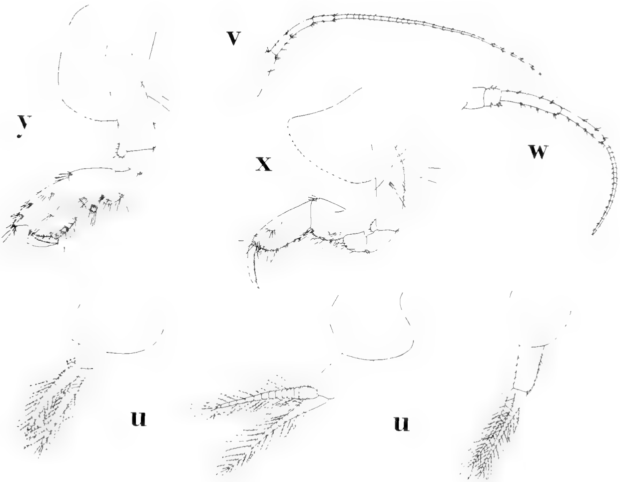
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Figure 4.

Ampithoe valida Smith. Beesley's Point, New Jersey.

LECTOTYPE ♂ (12.7 mm). a, antenna 1. b, antenna 2. c, upper lip. d, mandible (lacinia mobilis and incisor in detail). e, lower lip. f, maxilla 1. g, maxilla 2. h, maxilliped (outer plate separated). i, gnathopod 1. j, gnathopod 2. k, epimeral plate 1. l, epimeral plate 2. m, epimeral plate 3 and pleopod 3. n, uropod 1. o, uropod 2. p, uropod 3. q, telson.

PARALECTOTYPE ♂ (7.9 mm). r, peraeopod 1. s, peraeopod 2. t, peraeopod 3. u, peraeopod 4. v, peraeopod 5. w, head.

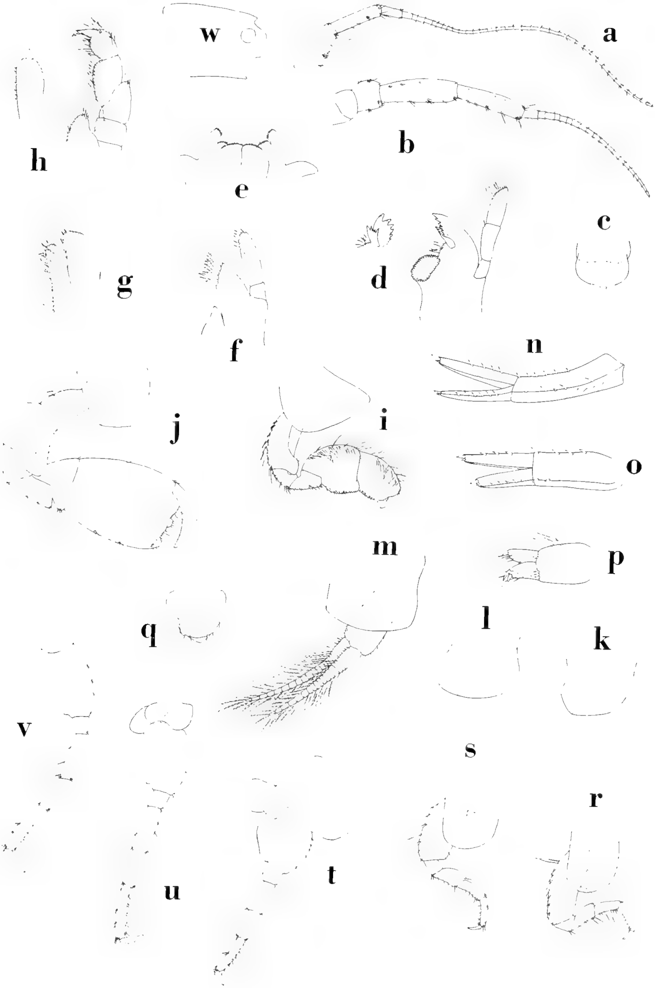
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Figure 5.

Cymadusa compta (Smith). Vineyard Sound, Massachusetts.

LECTOTYPE ♂ (8.6 mm). a, head, b, upper lip. c, mandible. d, lower lip. e, maxilla 1. f, maxilla 2. g, maxilliped (outer plate separate). h, gnathopod 1 (inner). i, gnathopod 2 (inner). j, peraeopod 2. k, epimeral plates 1-3 (right to left), with pleopod 3. l, pleopod 1 coupling hooks. m, uropod 1 (side view of ventral spine below). n, uropod 2. o, uropod 3. p, telson.

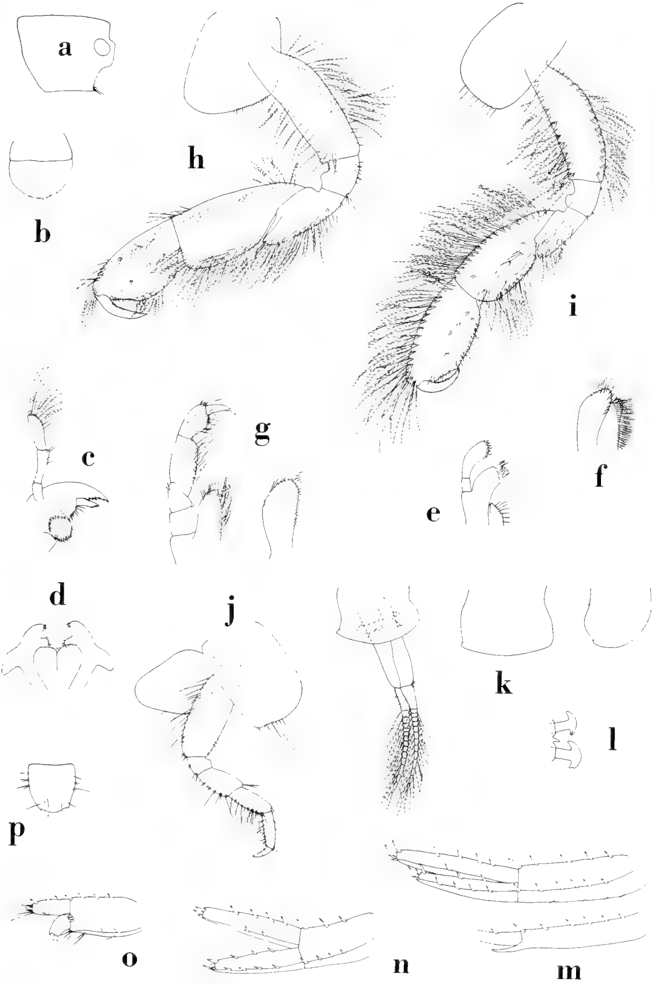
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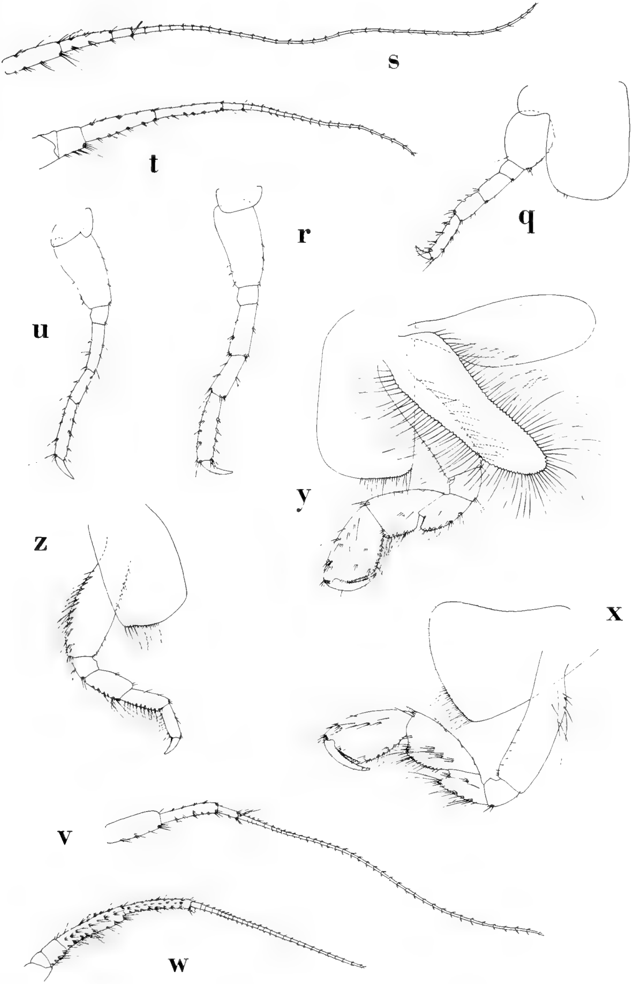
Figure 6.

Cymadusa compta (Smith). Vineyard Sound, Massachusetts.

PARALECTOTYPE ♂ (7.5 mm). q, peraeopod 3. r, peraeopod 5.

PARALECTOTYPE ♂ (12 mm). s, antenna 1. t, antenna 2. u, peraeopod 4.

PARALECTOTYPE ♀ (14.4 mm). v, antenna 1. w, antenna 2. x, gnathopod 1 (inner). y, gnathopod 2 (inner). z, peraeopod 1.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PEABODY MUSEUM OF NATURAL HISTORY
YALE UNIVERSITY

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CYPRIA PETENENSIS, A NEW NAME FOR THE OSTRACOD *CYPRIA PELAGICA* BREHM 1932

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Recently during the preparation of a comprehensive account of the lake plankton (Hutchinson, *in press*) a rather unfortunate case of homonymy was discovered in the genus *Cypria*.

In 1932 Brehm brought forward the name *Cypria pelagica* for a planktonic species from Laguna de Petén, Guatemala. Brehm mentioned several characters of the species and commented that they suggest "Beziehungen zu der südamerikanischen *Cypria pellucida* Sars." Since his remarks merely indicate apparent *affinities* with *pellucida* but unhappily contain no "statement that purports to give characters differentiating the taxon," the name *pelagica* Brehm (1932) appears to be, under Article 13a of the International Code, invalid and must be treated as a *nomen nudum*.

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[1] Research supported by National Science Foundation Grant GB-1534.

In the next year Klie (1933) published a description of *Cypria javana* subspec. *pelagica* from lakes in Java and Bali, which is apparently identical with a pelagic species from the Lake of Colombo erroneously identified by Apstein (1907) as *Cypris purpurascens* Brady. Whatever the status of Klie's form may be, the name *pelagica* was validly proposed as subspecific, and in view of the invalidity of Brehm's use of *pelagica* in the previous year, cannot be used for any other subsequently described *Cypria*.

Brehm (1939) returned to the problem and gave an illustrated description of *Cypria pelagica*, presumably based on the material to which he had referred in 1932. Recently we have had the opportunity to examine specimens of what is doubtless the same species, collected in the Laguna de Petén by Drs. Georgiana B. and Edward S. Deevey. In view of the history of the species a new specific name is clearly required.

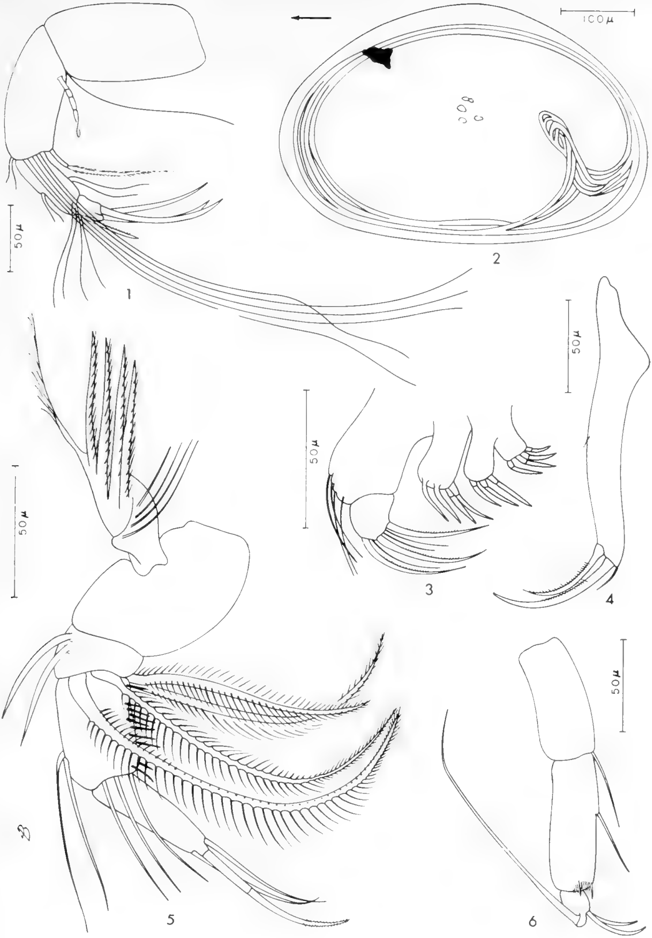
Family CYPRIDAE Baird 1845

Genus *CYPRIA* Zenker 1845

Cypria petenensis n. sp.

Figs. 1-6

Specific characters: Female—Eye prominent. Valves translucent, surface with scattered hairs and without other ornamentation. anterior and posterior margins with sparsely placed hairs; shell seen from the side boldly arched, greatest height near middle, anterior and posterior margins broadly rounded, ventral margin of right valve convex, that of left slightly concave; length of valves 0.52 mm—0.53 mm, height 0.31 mm—0.32 mm. Natatory setae of second antennae reaching beyond tips of end-claws by more than twice the length of the claws; distal end of antepenultimate podomere bearing a short seta with an elongate plumose terminal portion; olfactory club apparently with four segments. Mandibular palp is a very striking structure, respiratory plate with five prominent setae; antepenultimate and penultimate podomeres with long, plumose setae on ventral margins; ultimate podomere with two smooth spines and a longer two-segmented spine bearing two lateral rows of short setae at tip. Proximal podomere of maxillary palp very wide and bearing four long setae on laterodistal margin; width of distal podomere equal to length with three pectinated spines; spines of



Cypria petenensis n. sp.—Drawings of figures 1, 3, 4, 5, and 6 were made from the female holotype stained with lignin pink and mounted in polyvinyl lactophenol. The drawing of figure 2 was made from the androtype stained in a 1% alcoholic solution of eosin Y and mounted in Canada balsam. 1. Second antenna of female holotype. 2. Lateral view of right valve of androtype. 3. Maxilla and maxillary palp of female holotype. 4. Furcal ramus of female holotype. 5. Mandibular palp of female holotype. 6. Third thoracic appendage of female holotype.

all three masticatory processes two-segmented and smooth. Ultimate podomere of third thoracic appendage with two short setae of unequal lengths and a long, reflexed seta equal to the combined lengths of the antepenultimate, penultimate and ultimate podomeres; terminal margin of penultimate podomere with a patch of setae. Furcal ramus strongly developed, stout, length approximately 10× least width; dorsal seta short, occasionally inconspicuous and removed from the subterminal spine by the length of spine; terminal and subterminal spines pectinated; length of subterminal spine about eight-tenths that of terminal; terminal seta one-third length of subterminal spine.

MALE—Valves similar to those of female. Testes extend as circuitous bands along margins of valve. Prehensile palps of first thoracic appendages dissimilar; penis triangular. Males appear in numbers equal to females.

Type locality: The type specimens were collected on March 10, 1961 by Drs. Georgiana and Edward S. Deevey from the Laguna de Petén, Guatemala.

Type specimens: Microscopic mounts of the holotype and androtype are deposited in the Yale Peabody Museum (YPM 5670, 5671). Paratype male and females have been deposited in the British Museum (Natural History) and the Zoologisches Museum, Hamburg, Germany.

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