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RESULTS OF THE LATHROP CENTRAL AFRICAN REPUBLIC  
EXPEDITION 1976, ORNITHOLOGY



By HERBERT FRIEDMANN

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# RESULTS OF THE LATHROP CENTRAL AFRICAN REPUBLIC EXPEDITION 1976, ORNITHOLOGY<sup>1</sup>

By HERBERT FRIEDMANN<sup>2</sup>

**ABSTRACT:** Some 400 specimens of 94 species of birds were collected in the vicinity of the Ouossi River, in the southern, forested part of the Central African Republic, by the Lathrop Expedition in June 1976. Forty-three of these species are here recorded for the first time from that country. Others, known from there from one or a few earlier specimens, constitute sizeable extensions of previously known ranges. Aside from these distributional data, weights of all the birds are recorded as well as the gonadal condition of each specimen, information of a sort lacking until now for the birds of that portion of central Africa.

## INTRODUCTION

This paper presents the results of the Lathrop Central African Republic Expedition in ornithology carried out in 1976. All the bird collecting was done from one base camp, near the Ouossi River, about 11 k west of Baroua, elevation 680 m, roughly 5°20' N-24°20' E. This is a forested area in the extreme southern part of what Chapin (1932:90) termed the Ubangi-Shari Savanna District in his map of the faunal areas of Africa. The collecting was done by Andrew Williams and his two African assistants and skinners, Julius Kyongo and Philip Imbayi, between 31 May and 22 June 1976. In his report to the museum, Williams wrote that the forests near the camp site proved to be of three separate types which he found had small differences in their bird life: 1) the mature riverine forest along the Ouossi River, with the largest trees of the three, and, for the most part, dense, lush undergrowth; 2) an area of mature, but more open forest away from the river north of the camp, somewhat drier, and with no little streams running through it; 3) a still more open type of woodland bordering on open grassland. The forests visited were fairly small and restricted and were some distance west of the larger supposedly isolated, lowland forest shown in Map B in Hall and Moreau's Atlas of African Ornithology (1970), but, judging from the birds obtained in them, they were similar to, but

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<sup>1</sup>REVIEW COMMITTEE FOR THIS CONTRIBUTION  
CHARLES T. COLLINS  
RALPH W. SCHREIBER  
KENNETH E. STAGER

<sup>2</sup>Director Emeritus, Natural History Museum of Los Angeles County, 900 Exposition Boulevard, Los Angeles, California 90007.

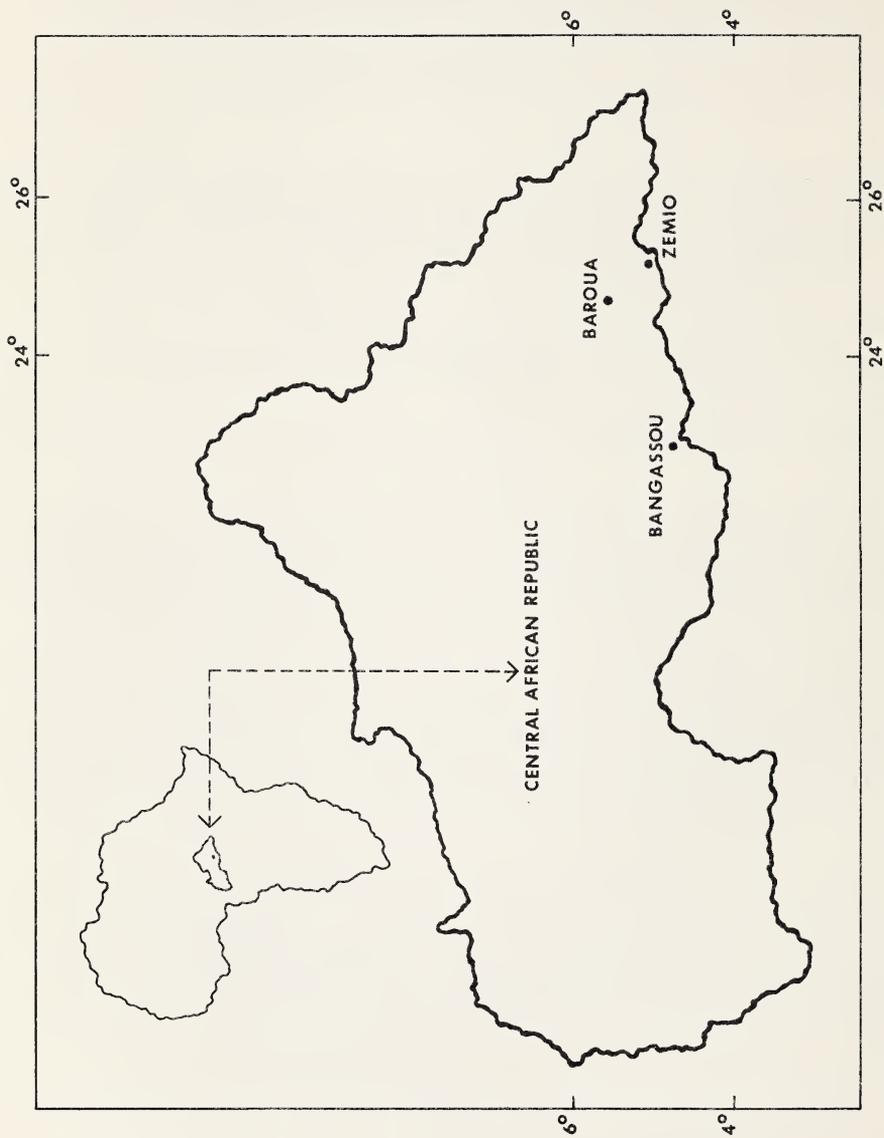


FIGURE 1. Map of Africa showing the Central Africa Republic and the locality of the present collection near Baroua.

somewhat less humid than the northern parts of the great Congo forest of Zaire to the south. During his collecting, involving both mist nets and shotgun, Williams became aware of the absence of starlings and of akalats (*Sheppardia*) in all three of these forested areas. It is not conclusive that these birds do not occur there, as at least 6 species of *Lamprotornis* and 1 of *Sheppardia* have been reported earlier from the Central African Republic, but they cannot be abundant near the Ouossi River, or they would have been noted.

A collection of 400 specimens of 94 species, made during a little over 3 weeks in the field, cannot be looked upon as a complete representation of a local, tropical forest bird fauna. However, it is significant in filling gaps in our knowledge of the distribution of central African birds. The collecting was confined almost wholly to the forested areas, but a few birds were taken in the open grasslands immediately adjacent to them. The collector carefully and conscientiously recorded in detail the colors of the soft parts (eye, bill, bare skin areas and feet), as well as the weight, the state of the gonads (unmeasured) and the contents of the stomach of every specimen. The weights and gonadal condition reported here are the first for their area. The colors of the soft parts and the stomach contents are included only for species of which Chapin (1932-1954) had little material, and only for some species of special interest has systematic discussion been thought useful.

In evaluating the extensions of known ranges of a large number of the included species, the maps of each of the passerines in Hall and Moreau's atlas are of the first importance. The maps in Mackworth-Praed and Grant's two volumes on the birds of west-central and western Africa show mere black swatches to indicate ranges, and these are not precise in the sense that are those of Hall and Moreau, which attempt to show every locality of record. In all such species maps, where the swatches suggest distributional limits beyond those given by Hall and Moreau, and where there are no published records in the earlier literature, I have assumed they were not based on actual specimens or on definite observations, and have been guided basically by the corresponding maps in Hall and Moreau. Assuming a period of three years from the completion to the publication of these maps, I have gone back to 1967 in my search of the literature for possible unmapped records from the Central African Republic.

Table 1 lists birds in the Lathrop Expedition's collection which are the first records in print for their species from the Central African Republic. A number of others fill sizeable gaps in the specimen records mapped by Hall and Moreau, but are not new for that political area.

The systematic order and the nomenclature used in this paper is that of Mackworth-Praed and Grant (1970-1973), the most recent complete work on the birds of western and central Africa. In a few species it has been deemed better not to follow their treatment. Further, the generic and specific names and sequence have been changed, where needed, to conform with the Reference List of the Birds of the World, by Morony, Bock and Farrand (1975).

TABLE 1

Species of birds hitherto unreported from the Central African Republic.

<i>Pachyoccyx audeberti</i>	<i>Erythropygia leucosticta collisi</i>
<i>Cuculus clamosus clamosus</i>	<i>Cossypha natalensis intensa</i>
<i>Cuculus clamosus gabonensis</i>	<i>Alethe diademata woosnami</i>
<i>Cercococcyx mechowi</i>	<i>Alethe poliocephala carruthersi</i>
<i>Alcedo leucogaster leopoldi</i>	<i>Trichastoma albipectus albipectus</i>
<i>Halcyon badia</i>	<i>Trichastoma rufipenne rufipenne</i>
<i>Halcyon malimbica malimbica</i>	<i>Ptyrticus turdinus</i>
<i>Tockus hartlaubi granti</i>	<i>Camaroptera superciliaris flavigularis</i>
<i>Pogoniulus scolopaceus flavisquamatus</i>	<i>Camaroptera chloronota toroensis</i>
<i>Pogoniulus bilineatus leucolaema</i>	<i>Macrosphenus flavicans hypochondriacus</i>
<i>Pogoniulus subsulphureus flavimentum</i>	<i>Platysteira castanea castanea</i>
<i>Pogoniulus atroflavus</i>	<i>Trochocercus nigromitratus</i>
<i>Trachyphonus purpuratus purpuratus</i>	<i>Anthreptes rectirostris tephrolaema</i>
<i>Melignomon zenkeri</i>	<i>Nectarinia seimundi traylori</i>
<i>Indicator maculatus stictithorax</i>	<i>Nectarinia cyanolaema octaviae</i>
<i>Indicator exilis exilis</i>	<i>Nigrita bicolor brunnescens</i>
<i>Melichneutes robustus</i>	<i>Nigrita canicapilla canicapilla</i>
<i>Campethera nivosa herberti</i>	<i>Mandingoa nitidula schlegeli</i>
<i>Smithornis capensis camarunensis</i>	<i>Spermophaga ruficapilla ruficapilla</i>
<i>Pitta angolensis longipennis</i>	<i>Malimbus nitens microrhynchus</i>
<i>Pycnonotus gracilirostris chagwensis</i>	<i>Dicrurus atripennis</i>
<i>Baeopogon indicator indicator</i>	

### SPECIES ACCOUNTS

Species here reported for the first time from the Central African Republic are marked with an asterisk.

#### FAMILY ACCIPITRIDAE

*Accipiter tachiro canescens* (Chapin). — Two adult males and one young, but fully grown female of this hawk were collected 2, 13 and 16 June. The subspecies must be commoner in the Ouossi River area than might have been expected, as it has been a seldom collected bird in most parts of its range. The female was in worn plumage with a few adult feathers coming in on the upper wing coverts, and also had a very few pale chestnut feathers showing on the sides of the otherwise white breast and abdomen. The two males weighed 194 and 205 g, the female 325 g; both adults had enlarged gonads. One of the specimens was taken in swampy riverine forest; one in open forest undergrowth, and one in dense undergrowth of mature forest.

## FAMILY COLUMBIDAE

*Turtur tympanistria tympanistria* (Temminck and Knip). — One male, testes enlarged, 5 June, weight 67 g.

*Turtur brehmeri brehmeri* (Hartlaub). — The Blue-headed Dove must be fairly common in the dense forest around the Ouossi River as 4 examples were obtained on four different days, 1, 2, 10 and 16 June. Two of them had enlarged gonads, the other two had small, inactive ones; 1 male weighed 120 g; the 3 females 105, 107 and 130 g respectively.

## FAMILY CUCULIDAE

*Clamator levaillantii* Swainson. — This crested cuckoo is not a bird of the true forest, but does come into the margins of such areas. One adult male was captured in a mist net in the undergrowth of mature forest 8 June; testes somewhat enlarged; weight 110 g.

\**Pachyococyx audeberti* (Schlegel). — Because of the still limited number of records of this scarce cuckoo, it may be noted that Andrew Williams saw, but was unable to collect, one just outside the forest.

*Cuculus solitarius solitarius* Stephens. — One adult male, testes not enlarged, was taken in open forest, bordering grassland, 7 June; weight 83 g.

\**Cuculus clamosus gabonensis* Lafresnaye. — One adult female, ovary enlarged, was taken in open forest 8 June; weight 78 g. This specimen, together with one of *C. solitarius*, collected the day before, raise again the old doubts as to the nature of the relationship of the two species. Furthermore, Williams wrote that he also saw, but did not obtain, one pure black *clamosus*. Were it not for the fact that in their vocalisms, the coloration of their egg shells, and their different choice of hosts, *clamosus* and *solitarius*, at least in southern and eastern Africa, are quite distinct, one might be tempted to regard them as variables within a single broadly phenotypic species. This is, however, negated by these considerations and the only possible conclusion is that the two species may have had a common origin in the forested regions of central Africa where the persistent, present population still reveals the phenotypic spectrum of the ancestral stock (including such variables as *jacksoni*, *gabonensis* and *mabirae*). It is known to occur, not far to the south, in the forests of Zaïre. The all black individual seen by Williams must have been *C. clamosus clamosus* of southern Africa, a race known to migrate north after the southern breeding season to the Congo forests and even as far north as southern Ethiopia. It too, is a first record for the Central African Republic.

\**Cercococyx mechowi* Cabanis. — The Dusky Long-tailed Cuckoo is generally thought of as an uncommon, or, at least, elusive bird, “. . . more easily heard than seen” (Mackworth-Praed and Grant, 1970:369), of the central African forests, but it must be anything but scarce in the Ouossi River area, as five examples, all females, were obtained there, 1, 10, 12 and 17 June. One of these was an immature bird, the others were adult; some were shot from as high as 40

feet up in trees while others were taken in mist nets set in the undergrowth. The weights of the adults were 54, 55, 59 and 61 g; the young bird 61 g. One bird had the ovary enlarged; the others had small ovaries.

#### FAMILY CAPRIMULGIDAE

*Scotornis climacurus sclateri* Bates. — One adult male, testes enlarged, 5 June, weight 44 g, taken in open country near the forest edge.

#### FAMILY TROGONIDAE

*Apaloderma narina brachyurum* Chapin. — One adult male, testes slightly enlarged, weight 63 g, 10 June, was collected in mature riverine forest with open undergrowth.

#### FAMILY ALCEDINIDAE

*Alcedo quadibrachys guentheri* Sharpe. — Four specimens, 10 to 18 June, were taken in mist nets over a small stream in riverine forest; all had small, inactive gonads; 2 males weighed 33 and 36 g, 2 females 32 g each.

\**Alcedo leucogaster leopoldi* (Dubois). — Between 6 and 16 June, 4 males and 3 females were taken in mist nets set in swampy riverine forest. The birds had gonads ranging from not enlarged to slightly so; weights were 12, 12, 12 and 14.5 g for the males; 14, 14 and 16 for the females. The present specimens agree in coloration and in size with a series from western Uganda, but show less diversity in the purplish or greenish-blue bars on the coronal feathers. In the birds from two forests in Uganda, the Bwamba in extreme western Uganda, and the Malabigambo near the western shore of Lake Victoria, it was found (Friedmann 1969:4) that there were almost two color phases in this character and that there were no intermediates. This is not the case with the Ouossi River birds, some of which actually have both purplish and greenish-blue bars on different feathers.

*Myioceyx lecontei* (Cassin). — Between 6 and 15 June, 6 specimens of the Dwarf Kingfisher were netted in dense riverine forest undergrowth. None were in breeding condition; weights 10 to 10.5 g (4 males), 10 and 12 g (2 females). Comparison of these specimens with a long series in the Los Angeles County Museum from western Uganda, including a number from the Budongo Forest (type locality of van Someren's proposed race *M. I. ugandae*) show no differences in dimensions or in coloration. The small blue coronal spots that were the basis of *ugandae* are by no means constant in Uganda birds, and are present in 2 of our 5 adults from Ouossi River. I conclude that this species has no recognizable races.

*Ispidina picta picta* (Boddaert). — The Pigmy Kingfisher is represented by 2 males and 1 female taken 16 and 19 June in mist nets set in swampy riverine forest; all in non-breeding state, or, at most, with slight gonadal enlargement; weights 12 and 12.5 g (males); 11 g (female).

\**Halcyon badia* Verreaux. — One female, ovary not enlarged, was netted in the forest undergrowth 18 June. Comparison with a dozen west Uganda specimens in the Los Angeles County Museum, including a series of topotypes of *budongoensis* from the Budongo Forest, shows no reason for recognizing that subspecies. It is sufficient to note a general clinal increase in size toward the eastern parts of the range of the species. Our specimen weighed 47 g. This specimen was caught in mist nets which suggest that Mackworth-Praed and Grant (1970:431) were in error when they wrote that this species usually “. . . keeps twenty or thirty feet from the ground.”

\**Halcyon malimbica malimbica* (Shaw). — Four specimens, 2 of each sex were taken (3 in mist nets) in the riverine forest undergrowth, 1 to 15 June, all with slightly enlarged gonads; weights 83 and 90 g (males); 83 (both females).

## FAMILY BUCEROTIDAE

\**Tockus hartlaubi granti* (Hartert). — A breeding male, one of two birds seen about 60 feet up in a tree, catching insects on the wing, was taken 3 June in lush forest; weight 135 g. This specimen agrees in coloration with another male in the Los Angeles County Museum from Bwamba Forest, western Uganda, but has a much longer bill (culmen to base 74 mm; 63 in the Bwamba bird). There is some difference in the wing and tail lengths of the two, but the Uganda bird is in very abraded plumage, especially in its remiges and rectrices, which naturally affects its dimensions.

## FAMILY CAPITONIDAE

\**Pogoniulus scolopaceus flavisquamatus* (Verreaux). — One female, ovary not enlarged, weight 13 g, was netted in dense undergrowth in degraded forest, 5 June.

*Pogoniulus chrysoconus chrysoconus* (Temminck). — Three male examples of the Yellow-fronted Tinker-bird were collected, 17 and 19 June, in mist nets set at a fruiting tree at the forest edge; weights 10, 11 and 11.5 g; one of them had large testes, the others small ones. They agree in size and coloration with other specimens in the Los Angeles County Museum from the Ivory Coast, Uganda and western Kenya.

\**Pogoniulus bilineatus leucolaema* (Verreaux). — Four males, 2 with large, 2 with small gonads, were collected 8 to 18 June in the forest edge; weights 10.5 to 12 g (average 11.1). These specimens are slightly paler below than a long series of *P. b. mfumbiri*, less yellowish below than *P. b. sharpei* from the Ivory Coast.

\**Pogoniulus subsulphureus flavimentum* (Verreaux). — The Yellow-throated Tinker-bird was common in the Ouossi River area, where 3 females in non-breeding state, and 2 males with enlarged testes, were collected 15 to 17 June; weights 9 and 10.5 g (males); 10 g (females). All were collected while feeding in fruiting forest trees. These specimens agree in size and coloration with a long series in the Los Angeles County Museum from western Uganda.

\**Pogoniulus atroflavus* (Sparrman). — The Red-rumped Tinker-bird was found to be very common in the Ouossi River area, and some 13 specimens were collected 12 to 19 June; 6 males, 7 females, gonads enlarged in 4 individuals, small in the others; weights 17 to 21.5 g (average 18.1) in males, 14 to 20 g (average 17.5) in females. Three of the birds were caught in mist nets, but the majority (10) were shot as they were feeding well up in fruiting trees.

\**Trachyphonus purpuratus purpuratus* Verreaux. — The Yellow-billed Barbet was met with twice, 9 and 16 June, in the riverine forest; 1 male with slight testicular enlargement and 1 female with a small ovary; weights 87 g (male), 89 g (female). These examples are placed with the nominate race of the species, but it is not clear that *T. p. elgonensis* is constantly different. That eastern subspecies is said to have the whitish edges of the feathers of the throat and foreneck less well marked, but a very long series in the Los Angeles County Museum from the forests of western Uganda suggests that this character is one that appears as the feathers become abraded. Some of the Uganda birds have these edges as well developed as in our Ouossi birds, while others have no sign of them. Unfortunately, we have insufficient west African material for comparison, but it would seem that only specimens in fresh plumage of the two can be expected to demonstrate the racial difference. The distributional maps in Mackworth-Praed and Grant (1970:553) suggest that they had no records from the area we are concerned with in this report, but their range for *T. p. purpuratus* comes nearer to it than that of *T. p. elgonensis*. White (1965:271) writes that the nominate race intergrades in the upper Congo with *elgonensis*, and it would seem that this is true as well in the Central African Republic.

#### FAMILY INDICATORIDAE

\**Melignomon zenkeri* Reichenow. — One specimen of this rarely collected species was caught in a mist net 1 m above the ground in dense forest undergrowth by a small stream along the Ouossi River, 2 June; a female in breeding condition, the largest ovarian follicle 2.5 mm; bill dark horn brown, the lower base yellowish; iris dark brown; feet pale olivaceous yellow; eye skin dark gray; weight 24 g. The specimen agrees in coloration with another breeding female from Bwamba (Los Angeles County Museum #66898), extreme western Uganda (July 9), but is smaller, this being especially noticeable in the bill and tail. The Ouossi bird measures: wing 76, tail 47.6, culmen from the base 10.1 mm; the Bwamba one: wing 77.6, tail 53.7, culmen from base 11.8 mm, weight 25 g.

The stomach of the present specimen contained a sizeable quantity of finely ground or comminuted grayish waxy material mixed with tiny black bits of insect fragments, very similar to that reported in detail from the earlier Bwamba specimen (Friedmann 1968:281-282), which was determined to be scale insect wax, not the paler, more yellowish beeswax usually present in the stomachs of honey-guides of the genus *Indicator*.

The fact that the genus *Melignomon* is intermediate in its characters between *Indicator* and *Prodotiscus*, but somewhat more like the latter, makes it of interest to note that while taking the present specimen out of the mist net, Andrew Williams found it to have a very "hard" body like that of an *Indicator*, not like the softer, "delicate" body of a *Prodotiscus*.

\**Indicator maculatus stictithorax* Reichenow. — The Spotted Honey-guide was found to be very common in the forests along the Ouossi River, and 16 males, 17 females, and 1 unsexed specimen were collected, 31 May to 19 June. While most of the birds had no, or only little, gonadal enlargement, 2 taken on 31 May were marked as breeding and 1 other, collected 3 June, had an enlarged ovary. Most of the specimens were caught in mist nets placed near wild bees' nests, baited with bits of becomb. The weights of the birds varied from 43 to 51 g (average 50.6) in males; 40 to 50.5 g (average 40.6) in females. Almost all the birds had beeswax in their stomachs, many also had insect fragments, and one had 2 small seeds as well as insect parts. The condition of the plumage varies from extremely worn to fresh, but no correlation between gonadal state and feather wear could be discerned.

The above series presented an opportunity to compare central African with western Ugandan (Bwamba) birds. The more eastern population averages slightly larger, but the limits of size variation are about the same in our Bwamba and Ouossi River birds (no topotypical *stictithorax*, described from Cameroon, have been available for direct comparison). Thus, males have wing lengths of from 95.5 to 106.5 mm (average 101.5) in 12 Bwamba specimens, 95.0 to 104 mm average (99.9) in 17 Ouossi River birds; females have wing lengths of 95 to 98.8 mm (average 96.4) in 11 Bwamba birds, 92.1 to 100.3 mm (average 90.4) in 16 Ouossi River examples.

A general clinal increase in size occurs in the species as a whole from west to east. Mackworth-Praed and Grant (1970:558) write that nominate *maculatus* (Gambia to Nigeria) have wing lengths of 97 to 103 mm, *stictithorax* 100 to 107 mm. I have found no specimen with wings as long as 110 mm, the maximum for *stictithorax* given by Malbrandt and Maclatchy (1949:275).

According to Chapin (1939:548) typical *maculatus* differs from *stictithorax* in being a little darker on the crown, the cheeks and malar region unstreaked, dark olive, and the abdomen less yellowish. Judging from our large series of *stictithorax* it would seem that the abdominal coloration is too variable to be of much diagnostic value, but all of our 59 birds have streaks on the cheeks and malar region.

*Indicator indicator* (Sparrrman). — The Greater Honey-guide is represented by 4 adult males, 1 adult female, 3 immature birds of both sexes, taken 1 to 15 June, all with little or no gonadal enlargement, weights 45 to 50 g (average 48) in the adult males, 52 g in the adult female; 45 and 46 g in 2 immature females, 54 g in an immature male. The specimens were taken at the edge of the forest, some of them in mist nets near wild bees' nests; they were in remarkably fresh, unfaded plumage.

Clancey (1970:378) described a race of this honey-guide from southern Mozambique, *I. indicator inquisitor*, said to be characterized by smaller size; wing length of males 105 to 110.5 mm, as against 113 to 120 in males of the nominate subspecies. While the validity of a southeast African race may seem tangential to a study of a series from the Central African Republic, it does affect the present use of a binomial for our specimens. Our males from Ouossi River have wing lengths of from 104 to 107.8 mm (average 106.4), and our comparative material from Kenya have wings 103 to 109.8 mm; in other words all are within the size range given for the race *inquisitor*; one male from the Ivory Coast has a measurement of only 102.5 mm. The wide geographic spread of small *I. indicator* makes one ask whether typical *indicator* may be a large race confined to the Cape Province, an area from which no material has been available for comparison. However, Clancey stated that coastal Kenya birds are equally large and must be considered *I. i. indicator*. Our coastal Kenya adult males (Lamu, Tana River and Sokoke) have wing lengths of from 104.5 to 107.0 mm. The mensural data given by Irwin and Benson (1966:16) for birds from various parts of Zambia are similarly difficult to account for in terms of geographic subspeciation, although in a later paper Clancey (1972:181-182) extended the range of *inquisitor* to include “. . . the valley of Luangwa, Zambia, and that of the lower Shire R., Malawi, and, perhaps, on the coast of Tanzania and the off-shore islands of Mafia, Zanzibar and Pemba.” However, it seems unlikely that this supposed race could also extend to the Central African Republic and even to the Ivory Coast, and until further clarification, it seems better to consider the species monotypic.

*Indicator minor riggenbachi* Zedlitz. — The Lesser Honey-guide was found to be very common along the Ouossi River in open areas at the edges of the forest; 12 males and 3 females were collected 3 to 18 June; all with little or no gonadal enlargement; weights 27.5 to 34 g (average 30.4) in the males, 27 to 30 g (average 28.3) in the females. Many of the specimens were caught in mist nets near wild bees' nests, and most (11) of them had beeswax as well as insect fragments in their stomachs. This series agrees very closely with many others from extreme western Uganda, and does not show any trend toward the ventral pallor of *I. minor alexanderi*, the race that occurs to the northwest of their area, and still less to the still paler *I. minor senegalensis* with which White (1965:275) has united *alexanderi*.

\**Indicator exilis exilis* (Cassin). — The Least Honey-guide must be a very common bird in the forest along the Ouossi River, as in 17 days, 2 to 19 June, the expedition obtained a series of 29 specimens (17 males, 12 adult, 5 immature; and 10 females, 6 adult, 4 immature; and 2 birds of unrecorded sex). As might be expected from the geographic location of the area, the birds are somewhat intermediate between nominate *exilis* and the slightly larger, more eastern, *pachyrhynchus* (Bahr-el-Ghazal province of the Sudan to eastern Zaïre, Uganda and western Kenya), but seem better placed with the former subspecies. Thus, the wing lengths of our 12 adult males vary from 68 to 80.5 mm (average 75.9); 6 adult females 66.2 to 71.2 mm (average 68). Chapin

(1962:41-42) noted wing lengths of 72 to 79.5 mm for male *exilis*, 65 to 70 for females; while for *pachyrhynchus* he gave wing lengths of 75.5 to 84 mm for males, 68 to 76 mm for females. In the Itombwe area of eastern Zaire, Prigogine (1971:101-102) found the two races to be altitudinally distinct. *I. e. exilis* below 1200 m, and *I. e. pachyrhynchus* above 1800 m, a conclusion difficult to accept. In this connection I have reviewed and measured all the specimens in the Los Angeles County Museum collections from the Impenetrable Forest, southwest Uganda, and find them all to be *pachyrhynchus*; they were collected at altitudes of from 4000 to 7500 feet. In the report on the birds of the Impenetrable Forest (Keith, Twomey, Friedmann, and Williams 1969:14) only *I. exilis exilis* is listed and only from 4000 feet. Some of our specimen records from higher elevations were collected too late for inclusion in that paper, and at that time *pachyrhynchus* was considered not different enough from *exilis* to recognize by name. The two races are based, it is true, on only average differences; Mackworth-Praed and Grant (1970:566) also consider them as one subspecies. However, in view of Chapin's long experience with these birds in the field and museum, I am inclined to follow him in keeping the two apart.

The 10 immature examples of our present series are noticeably dusker below than the adults, and lack the black malar stripe and the white loreal streak of the older birds. Identical differences between young and adult birds are also present in a still larger series of specimens from Bwamba and other forests of extreme western Uganda. The young birds average slightly smaller than the adults; their wing length averages 72.5 mm in the males, 67 mm in the females. Of the 12 adult males in our Ouossi River series, none had testes more than slightly enlarged; of the 6 adult females, all but 1 had enlarged ovaries, an anomalous situation.

Many of our specimens were collected in mist nets near wild bees' nests at the edge of the forest, but a few were shot while feeding on fruits well up in small trees. Most of them had beeswax and insect fragments in their stomachs, but 2 of them, both immature, had small fruits as well. This is the first time this Honey-guide (or any of its congeners) has been found to eat small fruits, an unexpected diet for a Honey-guide. In my earlier (1955:227) survey of the feeding habits of this species, I noted that a seed of unknown kind had been found in the gizzard of one specimen, but otherwise the stomach contents were invariably insects and beeswax (and probably honey). The 12 adult males weighed from 16 to 20.5 g (average 18.2), the adult females 12 to 17.5 g (average 15.9); immature males 16 to 18 g (average 17.5); immature female 17 g.

The use of mist nets placed near bees' nests as a method of obtaining specimens of this Honey-guide was well documented by Archer and Glen (1969:1-2) in their work in the Malabigambo Forest, Uganda. They concluded that their success was due to the fact that the birds made periodic visits to all the wild bees' nests known to them. Despite there being a total of over 2500 yards of mist nets used in the month's work in that forest, not a single Honey-guide was netted except in the immediate vicinity of the bees' nests, although

in the Namalala Forest they did catch one in a net "set at random" (but possibly not very far from a bees' nest unknown to the collectors).

The receipt of this fine series, added to the great number of specimens from western Uganda, now in the Los Angeles collections, has caused me to restudy the variation of *I. exilis*. This leaves me with serious doubt as to the identification of one example (LACM #66903) from Ntandi, Bwamba Forest, Uganda, previously published (Friedmann and Williams 1968:18;1971:33) as *I. pumilio*. It now seems that minimal specimens of *exilis* are just as small as *pumilio*, and indeed, can hardly be distinguished from the latter, without careful study. Thus, the Ntandi bird has a bill slightly larger than in *pumilio*, more like *exilis*, to which species it is now identified even though it is actually exceeded by some examples of *pumilio* in its wing length, tail length and body weight. The minute bill of the latter species seems to be its most reliable diagnostic character; to be appreciated, the bills of *exilis* and *pumilio* should be examined with a hand lens, preferably from the underside. Although the specimen from Kakamega Forest, western Kenya, that Williams and I previously (1965:21-22) decided was *I. pumilio*, is not available for restudy, I began to wonder if it too might be a minimal *I. exilis*. However, Prigogine writes me (25 July 1977) that he recently examined it and one other Kakamega specimen in the Nairobi museum, and found them to be *I. pumilio*, of an undescribed subspecies, which, I hope, he will elucidate in his next paper. Zimmerman's report of *pumilio* from the Kakamega Forest (1972:295) was based solely on a sight record.

While collecting the present series, Williams had in mind the possibility of some of them being *I. willcocksii*, as I also had when studying them, but all are *I. exilis*.

\**Melichneutes robustus* (Bates). — The Lyre-tailed Honey-guide is still so scarce a bird in museum collections (not, apparently, in nature) that additional specimens are examined with much interest. Two adults, one of each sex, were caught in mist nets set in open forest near a wild bees' nest, and baited with beecomb, 6 and 9 June. The male showed some gonadal enlargement, testes 4 × 3 mm, the female had a small, inactive ovary. The female was in much worn and faded plumage; the male was not in fresh, but in less abraded, feathering, and was darker above; weight 61.5 g in the male, 49.5 in the female; stomach contents of male "entirely beeswax—weighed 3 g"; of female "insect fragments"; soft parts were recorded as follows: bill dark horn brown, lower base paler; iris orange-brown (male) to dark brown (female); feet dark brownish gray to blackish gray; bare eye skin pinkish brown (male), olive gray (female); wing length 95.8 mm (male), 94 mm (female).

Inasmuch as so little is still known of this Honey-guide it may be well to call attention to a specimen taken more than 12 years ago, in a snare baited with beecomb, in the Mongomo region, Rio Muni (now Spanish Continental Guinea), a record published anonymously (probably by J. Sabater Pi) in a little-consulted popular journal of the Barcelona Zoological Park (Anon. 1963:43). This record has been overlooked by all the ornithological journals, and is the first, and so far, the only, record from that country. The specimen is

now in the American Museum of Natural History (AMNH #802455). While this record did not increase the known range of *Melichneutes*, which was previously reported from Gabon to the south, and from Cameroon to the north, the almost simultaneous report by Beatty (1963:100-101) suddenly extended its range westward by about 1000 miles to Mt. Nimba, at the point where Liberia, Ivory Coast and Guinea come together. The previous westernmost record was in southern Nigeria, but it is probable that the range is not that discontinuous; the species may be expected to "turn up" in the upper Guinean forests of the Ivory Coast, Ghana and Dahomey.

## FAMILY PICIDAE

\**Campethera nivosa herberti* (Alexander). — The Buff-spotted Woodpecker was found to be common along the Ouossi River and 4 males and 3 females were collected 1 to 18 June, all with little or no gonadal enlargement; weights males 34 to 38 g (average 37); females 34.5 to 38 g (average 36.1).

*Campethera caroli* (Malherbe). — One male, 4 females, all with small gonads, taken 6 to 17 June; weights: male 60 g; females 53 to 68 g (average 58.6). These specimens agree with a long series from western Uganda in the Los Angeles collections, and would have to be considered *budongoensis* if that race were upheld, as it is by Mackworth-Praed and Grant (1970:571), but the characters of that subspecies do not appear to be constant enough to warrant its recognition.

*Dendropicos xantholophus* Hargitt. — This woodpecker apparently is less common in the area than either of the *Campethera* species; only a single example was obtained 5 June, a male with small testes; weight 58 g. It was shot in the tree tops, whereas the *Campethera* were taken largely in the mist nets, which may account for their apparent greater numbers and relative abundance.

## FAMILY EURYLAEMIDAE

\**Smithornis capensis camarunensis* Sharpe. — Three specimens, 1 saved as a study skin and 2 as skeletons, were collected in mist nets in the forest undergrowth 2 to 13 June; the male preserved as a study skin and a female saved as a skeleton had enlarged gonads; a male (skeleton) showed only slight testicular swelling; weights 26 g in each male, 24 g in the female. The subspecific identification of the study skin is based on the conclusions of Mackworth-Praed and Grant (1970:609), but it agrees very well with a series of *meinertzhageni* from western Uganda, which Mackworth-Praed and Grant consider the same as *medianus*. More extensive series with more complete geographic coverage are needed to settle the matter of races of this bird.

## FAMILY PITTIDAE

\**Pitta angolensis longipennis* Reichenow. — One male, testes not enlarged, was taken in a mist net 3 feet up in dense undergrowth of mature forest,

5 June, wing 121.5 mm, weight 84 g. The fact that this bird, and also its other African congener, *P. reichenowi*, are captured so seldom, even in mist nets, suggests that they are really scarce and not merely difficult to see.

#### FAMILY ALAUDIDAE

*Mirafra rufocinnamomea tigrina* Oustalet. — The Flappet Lark is a bird of the open grasslands, not of the forest; 2 males, 1 with enlarged, the other with small testes, were taken just outside the forest edge 6 and 16 June; weights 27 and 28 g. This race of the Flappet Lark has been collected but seldom; no records from the Central African Republic for the species are indicated in Hall and Moreau (1970:map 6). Meyer de Schauensee (1949:8) listed a specimen of *M. r. zombae* from Oka, which may be referable to *tigrina*. White (1961:20) places *zombae* in the synonymy of *fischeri*, but it seems likely that the name *tigrina* could be applied to a specimen from the Ubangi-Shari region.

*Galerida modesta bucolica* (Hartlaub). — The Sun Lark was found in the open grasslands at the edge of the forest; 2 males and 1 female, all with small gonads, were taken 6 and 12 June; weights 21.5 and 22 g in the males, 18 g in the female; stomach contents, insect fragments and grass seeds.

#### FAMILY PYCNONOTIDAE

*Pycnonotus virens virens* (Cassin). — The Little Greenbul was common in the Ouossi River area; 5 specimens were netted in the forest undergrowth 31 May to 9 June, 3 males with enlarged testes, and 2 females, one with enlarged, the other with slightly enlarged ovary; weights males 23.5, 24 and 24 g; females 21 g.

*Pycnonotus curvirostris curvirostris* (Cassin). — Fairly common; 3 males and 1 female were netted in the riverine forest undergrowth 2 to 17 June; gonads enlarged in the 3 males, slightly so in the female; weight males 24, 25, 26 g; female 26 g. Only one record from the Central African Republic is indicated in Hall and Moreau (1970:map 68); none in Malbrandt and Maclatchy (1949).

*Pycnonotus latirostris latirostris* (Strickland). — Two females, 1 with small, 1 with enlarged ovary, were netted in the forest undergrowth 31 May and 10 June; weights 22 and 30 g. Because these birds are fairly small, wing length 72 and 76 mm, they are placed with the nominate race of this Greenbul, in accordance with Chapin's (1953:113) arrangement, although they are not smaller than some of a long series of *eugenia* from Uganda. Chapin admitted that it was "difficult to determine the limits" between the two. In the Central African Republic this species must be restricted to the forested areas in the south along its border with the Republic of the Congo.

\**Pycnonotus gracilirostris chagwensis* (van Someren). — One bird of each sex, both with gonads enlarged, shot in a fruiting tree at the forest edge 8 and 15 June; weight 32 g (male), 40 g (female). The map in Mackworth-Præd and Grant (1970:82) seems to anticipate its presence there, but as stated earlier, this is not a definite statement.

\**Baeopogon indicator indicator* (van Someren). — One male, testes slightly enlarged, June 19; weight 46 g.

*Phyllastrephus scandens orientalis* (Hartlaub). — Six specimens, 8 and 9 June, gonads enlarged in 1 male, not enlarged in 2 others and in 3 females; mostly netted in open forest undergrowth; weights males 48 and 50.5 g, females 38, 41, 45 g; all the specimens in worn plumage.

*Phyllastrephus albigularis albigularis* (Sharpe). — Common; 6 specimens were caught in mist nets in the forest undergrowth 31 May to 10 June; 3 with large, 3 with small gonads; weight males 26 and 28.5 g, females 20 to 24 g (average 22.2). These birds agree in size and coloration with a long series from western Uganda. Ouossi River provides a specimen record locality that fills a large gap in Hall and Moreau's map (1970:map 90).

*Bleda syndactyla woosnami* Ogilvie-Grant. — Five adults, taken in riverine forest undergrowth 31 May to 7 June; gonads varying from small to large; weights males 48, 49 g; females 41, 48 g. These specimens agree with a long series from western Uganda and do not show any intergradation with *B. syndactyla multicolor*, although the distribution maps in Mackworth-Praed and Grant (1970:57-58) suggest that the latter might be the race to be expected in the southern part of the Central African Republic. Hall and Moreau (1970:map 80) show only one record of this bird in the Central African Republic, where its range must be limited to the southern forests near the border of the Republic of the Congo.

*Bleda eximia ugandae* van Someren. — The Green-tailed Bristle-bill is represented by 5 adult males, testes large in 4, slightly enlarged in 1, and 1 adult female, ovary slightly enlarged; 31 May to 7 June; weights 42 to 48 g in males (average 44); 36 g in the female.

*Nicator chloris* (Valenciennes). — Although many recent authors place *Nicator* in the shrike family, I prefer to follow Chapin's arguments (1953:183-185) and keep it among the bulbuls, somewhat aberrant as it may be in that family. It must be common in the Ouossi River forests, where 7 adults were obtained, largely in mist nets in the undergrowth in both open and dense forest, 2 to 19 June; 3 males with enlarged testes, 4 females with small or slightly enlarged ovaries; weight males 50, 54, 58 g; females 40, 41, 43, 43g.

*Criniger calurus emini* Chapin. — Fairly common; 5 specimens, 3 males and 2 females were taken in mist nets in the riverine forest undergrowth, 3 to 16 June; gonads not enlarged in 3, enlarged in 2 of the birds; weights males 30.5 to 34 g (average 32.1); females 25 and 30 g.

#### FAMILY LANIIDAE

*Malaconotus cruentus adolfifriederici* Reichenow. — One male, testes slightly enlarged, was taken in dense forest undergrowth 31 May; weight 79.5 g. The races of this shrike are ill-defined and not too certainly identifiable. However, the small size of the present specimen, wing 107 mm, agrees with one from the Semliki River (Chapin 1954:40), and it is placed with *adolffriederici*. Hall and Moreau (1970:map 112) show no records for *M. cruentus*

from the Central African Republic east of Bangui, and Mackworth-Praed and Grant (1973:460) seem to restrict *adolfifriederici* to the eastern parts of Zaïre and western Uganda, so the present specimen extends the known range of that race a long distance to the northwest.

FAMILY MUSCICAPIDAE  
Subfamily Turdinae

\**Erythropygia leucosticta collsi* Alexander. — Three adult males, 1 breeding, 1 with enlarged and 1 with small testes; 1 female with an enlarged ovary, were taken in mist nets in heavy forest undergrowth 6 to 12 June; weights males 26, 27, 28 g, female 27 g; stomach contents beetles and a small snail.

*Erithacus erythrothorax mabirae* Jackson. — A common bird in the Ouossi River forest, but one that is seldom seen except when caught in mist nets; 5 males and 2 females were so captured in dense forest undergrowth 31 May to 4 June, gonads large in 1 male, small or only slightly enlarged in the others; weights males 16.5 to 19 g (average 17.5), females 16.5, 17 g. Judging from the absence of records in Hall and Moreau (1970:map 145) the above are the first specimens collected in the Central African Republic other than in the extreme southwest, near the Cameroon border.

\**Cossypha natalensis intensa* Mearns. — Two males, 1 female, all with gonads much enlarged, taken in forest undergrowth 8 to 10 June; weights males 37, 39 g, female 38 g. These extend the known range of this Robin-chat northward to the southern part of the Central African Republic.

\**Alethe diademata woosnami* Grant. — The Fire-crest Alethe was found to be common in the Ouossi River forests and its range in the Central African Republic is probably restricted to the forests near the Zaïre border. Between 31 May and 9 June 8 specimens were taken, 4 males with large testes, 1 female with an oviduct egg, 2 with slight ovarian enlargement, and 1 subadult female molting into adult plumage; weights males 32 to 34 g (average 32.6), female adults 32 to 39 g (average 34.7), subadult female 28 g.

\**Alethe poliocephala carruthersi* Grant. — Four adult Brown-chested Alethes, two of each sex, the males with large testes, the females varying from small to slightly enlarged ovaries, were netted in the dense forest undergrowth 31 May to 15 June; weights males 30, 32.5 g; females 26, 31 g respectively.

*Stizorhina fraseri vulpina* Reichenow. — Fairly common in the Ouossi River forests, 1 male and 4 females were taken there 1 to 11 June; gonads enlarged in most of the birds, one female marked "breeding"; weight of male 34 g, females 32, 33.5, 36 and 39.5 g; all had been feeding on small beetles.

*Neocossyphus poensis praepectoralis* Jackson. — Two males, 1 female, with gonads enlarged in 1, not in the others, were taken in riverine forest undergrowth 31 May to 10 June, and extend the known range of this bird a considerable distance north. In the Central African Republic the species was reported earlier only from the extreme southwest corner, close to the Cameroon border. The males weighed 52 and 53 g, the female 50.5 g.

Subfamily Timaliinae

\**Trichastoma albipectus albipectus* (Reichenow). — Common in the forest undergrowth; 4 males and 3 females were taken 1 to 19 June, gonads varying from small to large; weights males 31 to 38 g (average 35.2), females 30 to 36 g (average 32.3); stomach contents beetles and one lepidopteran larva. These specimens extend the known range of the species to the northwest of the records plotted by Hall and Moreau (1970:map 165).

\**Trichastoma rufipenne rufipenne* Sharpe. — Apparently less numerous than *T. fulvescens*; 3 males, all with enlarged testes, taken 2 to 5 June, weights 26 to 30 g (average 28), agree with a long series from western Uganda.

*Trichastoma fulvescens ugandae* (van Someren). — A common species in the forest, 4 adults of each sex were collected 1 to 17 June; gonads varying from not enlarged to large; weights 31 to 38 g (average 34.7) in males; 28 to 30.5 g (average 29) in females.

\**Ptyrticus turdinus turdinus* Hartlaub. — Two examples of the Thrush-babbler were taken in the dense undergrowth of the forest 11 and 12 June, one of each sex, both with small gonads; weight male 72.5 g, female 59 g. The male is considerably larger than the female, wing 107.4 as against 95.4 mm; culmen from base 22.9 as against 22.1 mm; the tail of the female too damaged for meaningful comparison. The present specimens help to fill a great geographic gap in the range, as indicated by actual specimen records, in Hall and Moreau (1970:map 168).

*Phyllanthus atripennis bohndorffi* (Sharpe). — The Capuchin Babbler is a common bird in the forests of the Ouossi River area. Six adults, 3 of each sex were taken between 5 and 16 June (4 netted, 2 shot); all with small or only slightly enlarged gonads; weights males 80, 84, 90 g; females 86, 86 and 94 g respectively. These specimens are all typical *bohndorffi* and show no approach to *haynesi* of northern Cameroon although 1 male has two dark brown feathers among the gray ones on one side of the crown; they agree closely with a series from western Uganda. The Ouossi region adds an intermediate locality of record in the distribution shown for the species in Hall and Moreau (1970:map 175).

Subfamily Sylviinae

*Cisticola natalensis strangei* (Fraser). — Two males, testes slightly enlarged, were taken at the forest edge 15 and 20 June; weights 23 and 26 g.

*Camaropectera brevicaudata tincta* (Cassin). — Three males, all with large gonads, were netted in the forest undergrowth 4 to 12 June; weights 11, 12 and 12 g.

\**Camaropectera superciliaris flavigularis* Reichenow. — One male, testes large, was taken in dense growth at the forest edge 4 June; weight 10 g.

\**Camaropectera chloronota toroensis* (Jackson). — Three males, testes slightly or not enlarged, netted in forest undergrowth 1 and 2 June, weights 10.5, 11 and 12 g, constitute a very considerable northwestern extension of the

known range of the species. They agree well with west Ugandan examples and are, accordingly, placed with that race.

\**Macrosphenus flavicans hypochondriacus* (Reichenow). — One male with small testes, netted in forest undergrowth 10 June, weight 14 g, extends the previously known range of the race *hypochondriacus* northwestward about 200 miles.

*Hyliota flavigaster flavigaster* Swainson. — Two adults, one of each sex, male with enlarged testes, female with small ovary, were collected at the edge of the forest 12 and 13 June, foraging in the tree tops with a party of *Parus leucomelas*; weight male 13 g, female 12.5 g. Judging by the distribution shown in Hall and Moreau (1970:map 259) these specimens fill a considerable gap in the recorded range of the species.

*Hylia prasina prasina* (Cassin). — Apparently common in the Ouossi River area, 6 specimens, 3 of each sex, gonads varying from small to large, were netted in the forest undergrowth 1 to 10 June; weights males 14, 15, 15 g, females 12 g in each case.

#### Subfamily Muscicapinae

*Fraseria cinerascens cinerascens* Hartlaub. — This Flycatcher must be common in the Ouossi River forests, as 4 adults of each sex and 1 immature male were taken, chiefly in mist nets in the forest undergrowth, 31 May to 18 June; gonads small in most birds, large in 1 male taken 31 May; weights males 21.5 to 24.5 g (average 23), females 18 to 22 g (average 19.8).

*Myioparus plumbeus plumbeus* (Hartlaub). — A single male, testes not enlarged, one of a small flock seen at the edge of the forest, was collected 18 June. It is not fully adult, with a brownish wash on the breast and sides of the abdomen; weight 13 g. Hall and Moreau (1970:map 249) show no records for this Flycatcher from the southern part of the Central African Republic.

*Myioparus griseigularis griseigularis* (Jackson). — Three males, 2 with enlarged testes, 1 with small ones, 2 to 12 June; weights 14 g in each case; plumage somewhat abraded in all. These specimens agree closely with a series from western Uganda. The Ouossi River records add a locality in the middle of a considerable gap in the map in Hall and Moreau (1970:map 249).

\**Platysteira castanea castanea* (Fraser). — Two males and 1 female, all with enlarged gonads, were netted in dense forest undergrowth 4 and 9 June; weights males 13 and 14 g, female 16 g.

\**Trochocercus nigromitratus* (Reichenow). — One female, with ovary not enlarged, was taken in open undergrowth in riverine forest 6 June; weight 9 g. The distribution of this species in the Central African Republic must be limited to the forested areas of the south, along the border of the Republic of the Congo.

*Terpsiphone rufiventer ignea* (Reichenow). — Apparently common in the Ouossi River area, but previously reported only from the western part of the Central African Republic; 4 males, all with large testes, 2 females, with little or

no ovarian swelling, 7 to 18 June; weights males 14 to 15.5 g (average 14.9), females 15.5, 16 g. These specimens extend the known range of *ignea* northward a considerable distance, the previously reported limit being the Uelle River, Zaire. Like the Congo specimens of *ignea*, these birds have the rectrices brownish, only washed with rufous.

FAMILY PARIDAE

*Parus leucomelas guineensis* Shelley. — One male, testes not enlarged, was taken at the edge of the forest 8 June; weight 20 g; also seen 12 and 13 June.

FAMILY NECTARINIIDAE

*Anthreptes longuemarei haussarum* Neumann. — One male, 1 female, gonads not enlarged, were taken at the edge of the forest 7 and 13 June; weight male 14 g, female not recorded.

\**Anthreptes rectirostris tephrolaema* (Jardine and Fraser). — Five males, gonads varying from small to large, were taken in trees at the forest edge, 12 to 16 June; weights 10 g in 4 cases, 11 g in the other.

*Anthreptes collaris somereni* Chapin. — One male, testes enlarged, 3 females, ovaries small, were collected in fruiting trees at the forest edge 5 to 17 June; weight of male 10 g, females 8 g each.

\**Nectarinia seimundi traylori* Wolters. — One specimen, sex undetermined, was taken in a fruiting tree at the forest edge 15 June.

*Nectarinia olivacea cephalis* (Bates). — This Sunbird must be common in the Ouossi River area; 8 specimens, 3 males with large testes, 5 females with small to slightly enlarged ovaries, were taken in the riverine forest 31 May to 8 June; weights males 11, 11.5 and 12 g, females 9 g in 1, 10 g in the other 4 individuals.

\**Nectarinia cyanolaema octaviae* Amadon. — Two males with large testes were shot in fruiting trees at the forest edge 18 and 20 June; weights 15, 16 g.

*Nectarinia superba superba* (Shaw). — One male, testes large, was collected in tree tops at the forest edge 17 June; weight 17.5 g.

FAMILY EMBERIZIDAE

*Emberiza cabanisi cabanisi* (Reichenow). — One female, ovary not enlarged, was taken at the forest edge 31 May; weight 22 g.

FAMILY ESTRILDIDAE

*Parmoptila woodhousei woodhousei* Cassin. — One male, testes slightly enlarged, was netted in swampy undergrowth of the forest 10 June; weight 9.5 g, and extends the known range of this subspecies eastward about 500 miles along the northern limits of its range. In the Central African Republic it was

known earlier only from the extreme western area, bordering on Cameroon.

\**Nigrita bicolor brunnescens* Reichenow. — Two females, 1 with small and 1 with enlarged ovary, were taken near the forest edge 10 and 12 June; weights 13 and 15 g.

\**Nigrita canicapilla canicapilla* (Strickland). — Two females, 1 with enlarged, 1 with small ovary, were collected 15 and 19 June at the forest edge; weight 20 g each. The present birds are very slightly paler gray above than a series of *schistacea* from western Uganda, but the two races must meet not far to the east of the Ouossi River area. The birds had been eating small fruits, probably of the trees from which they were collected.

*Euschistospiza dybowskii* (Oustalet). — One female with small ovary, and 1 bird of undetermined sex (male by plumage), were collected in dense thicket at the forest edge 8 and 20 June; weight of male (?) 13 g, female 12 g; stomach contents grass seeds and insects. These specimens fill a considerable blank in the records shown by Hall and Moreau (1970:map 385).

\**Mandingoa nitidula schlegeli* (Sharpe). — One male, testes not enlarged, was netted in forest undergrowth 12 June; weight 11 g.

*Pyrenestes ostrinus ostrinus* (Vieillot). — The Black-billed Seed-cracker must be common in the Ouossi River area as 6 examples, all with small gonads, were taken in mist nets in the swampy forest undergrowth 2 to 19 June; weights males 21, 21.5, 22 g, females 21, 23, 23 g. Mackworth-Præd and Grant (1973:695-696) treat *ostrinus* and *rothschildi* as two sympatric species on the assumption that "it seems very doubtful that large-billed and small-billed birds would interbreed in any one locality . . ." On the other side of the argument, Chapin (1954:493) writes "that birds of differing sizes may mate with each other cannot be doubted" and gives specific instances. It may be that before man began to clear and otherwise intrude into previously uniformly forested areas there may have been separation of the two "species" but the fact that they do cross and that variants of all degrees of intermediate size occur together in many areas indicates that the birds do not "recognize" specific differences. And they are, biologically, the reliable judges. The present 6 birds show both *ostrinus* and *rothschildi* characters in bill size. A similar situation prevails in a long series of specimens from western Uganda.

\**Spermophaga ruficapilla ruficapilla* (Shelley). — The Red-headed Blue-bill must be very abundant in the Ouossi River area as 14 specimens, 8 males, all with small or only slightly enlarged testes, and 6 females, all with small ovaries, were taken, largely in mist nets, in the dense forest undergrowth 2 to 12 June; weights 22 to 27 g (average 24.3) in males, 24 to 28 g (average 24.8) in females. The present records extend the known range of the species over a hundred miles to the northwest.

#### FAMILY PLOCEIDAE

*Ploceus nigricollis nigricollis* (Vieillot). — One female, ovary slightly enlarged, was collected in a fruiting tree at the forest edge 18 June; weight 31 g.

*Ploceus cucullatus bohndorffi* Reichenow. — Two males, testes enlarged, were taken at the forest edge 8 and 12 June; weights 41, 47 g.

\**Malimbus nitens microrhynchus* Reichenow. — Two females, ovaries not or only slightly enlarged, were netted in riverine forest undergrowth 4 and 15 June; weights 30, 34 g. These birds are small, wings 80 and 82.5 mm, and agree with a series from western Uganda. They extend the known range of *microrhynchus* about 300 miles to the northwest.

*Malimbus malimbicus crassirostris* Hartert. — Three specimens, all in non-breeding state, were taken 8 to 19 June; weight male 36 g, females 31 and 33 g. These birds are close to *crassirostris* from western Uganda and fill a sizeable gap in the data recorded in Hall and Moreau (1970:map 348).

#### FAMILY DICRURIDAE

*Dicrurus ludwigii sharpei* Oustalet. — The Square-tailed Drongo must be fairly common in the Ouossi River forests, as 5 specimens were taken, 3 males with enlarged or slightly enlarged testes, 2 females with small ovaries, 3 to 11 June; weights males 31, 31, 32 g, females 26, 30 g.

\**Dicrurus atripennis* Swainson. — One female, ovary slightly enlarged, was netted in open forest undergrowth 14 June; weight 42 g; stomach contents mainly beetles.

#### ACKNOWLEDGMENTS

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FOLIICOLOUS ASCOMYCETES 1:  
THE CAPNODIACEOUS GENUS SCORIAS,  
REPRODUCTION

*By* DON R. REYNOLDS



NATURAL HISTORY MUSEUM OF LOS ANGELES COUNTY

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FOLIICOLOUS ASCOMYCETES 1:  
THE CAPNODIACEOUS GENUS SCORIAS  
REPRODUCTION<sup>1</sup>

By DON R. REYNOLDS<sup>2</sup>

ABSTRACT: *Scorias spongiosa* (Schw.) Fries development is analyzed by use of sequential collections from Georgia. The soma develops during the fall to winter season. The morphology of the anamorphic centrum remains unchanged as the soma matures. The teliomorphic centrum is dothideaceous; a sterile element in this centrum is interpreted as laterally positioned periphyses; the ascus is functionally bitunicate. A protocol to substantiate definite proof of reproductive state pleomorphism is discussed.

INTRODUCTION

*Scorias* Fries, a classic North American representative of sooty mold Ascomycete fungi, is known in the earliest American mycological literature. This capnodiaceous genus is based on an early known North American species, *S. spongiosa* (Schw.) Fries. This fungus occurs in a typical sooty mold plant-surface habitat in saprobic association with insect exudate. Although the distribution of the fungus is known to be along the U.S. east coast from northern Florida to Maine, *S. spongiosa* has received little attention since its initial impact on mycological literature of the 19th century.

The labyrinthic stroma formed by the dark mycelial growth, preceding pseudothecium formation, was first termed "sponge." Initially Schweinitz (1822) and later Fries (1829) in the type description of the genus, commented on the waxlike appearance of the mycelium and the change in the "sponge" matrix from brittle to soft upon absorption of moisture. The name *Scorias* was utilized by Fries to denote the stromatal resemblance to slag as the structure developed on leaves and branches of the American beech, *Fagus grandifolia* L. *S. spongiosa* was illustrated by Ellis and Everhart (1892) with a drawing showing ascocarps and pycnidia (as "spermogonia") originating from the same

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

CHRISTOPHER DAVIDSON  
M.L. FARR  
JAMES KIMBROUGH

<sup>2</sup>Senior Curator of Botany, Natural History Museum of Los Angeles County, 900 Exposition Boulevard, Los Angeles, California, 90007. USA

"fertile branch." They placed the monotypic genus in a taxon, the Perisporiaceae, defined with "ostiolum obscure or wanting . . . opening irregularly." Von Hoehnel (1910) described the hyphae as copious, partially slimy and fused together bundlelike. He characterized (1909) the pseudothecium centrum as cartilaginous-gelatinous due to the nature of the component sterile elements. Ascus dispersal was attributed to an apical swelling of the centrum. "Ein ausgesprochenes Ostiolum fehlt stets." Few other morphological insights can be gleaned from subsequent literature (i.e., Lloyd 1921; Batista & Ciferri 1963b).

This paper concerns the developmental morphology of *Scorias spongiosa*. A taxonomic monograph of the genus *Scorias* Fries is to appear later as an additional contribution from ongoing studies focusing on foliicolous fungi.

#### MATERIALS AND METHODS:

The sequential collections selected for detailed analysis represent periodic sampling from Athens, Georgia — i.e. LAM 200001 (25 X 1971), LAM 200004 (12 XI 1971), LAM 200006 (02 XII 1971), LAM 200007 (20 XII 1971). Collection LAM 200008 (21 I 1972) was utilized for illustration of mature material; information from collection LAM 200000 (18 VIII 1973) was incorporated for data on early development. Additional specimens examined from Georgia included LAM 200002 (02 II 1972), LAM 200004 (09 II 1972), LAM 200005 (20 II 1972), LAM 200009 (05 IV 1972), LAM 200010 (24 IV 1970), LAM 200011 (11 V 1972), LAM 200012 (11 V 1970) and LAM 200013 (10 V 1973). Other herbarium specimens examined included those from BPI (Brown VII 1932, Shear 4 X 1935, Shear 1 II 1903); CUP (Howard Cayuga Flora 48), FLAS (1862, 1863, 1864, 21183, 46426); ILL (Rogers 14-15 III 1958), Ellis, North American Flora (1363 a & b), Ravanel Fungi Americana (334 and 1877). Schweinitz collections from herbaria E, FH, K, PH and UPS were additional non-Georgian specimens examined.

Fresh material and 2% KOH revived dry material were cut on a Bailey freezing microtome and mounted in lactophenol or lactophenol-cotton blue; additional material was killed and fixed in FAA, paraffin embedded and the resulting sections stained with hematoxylin and methylene blue.

Camera lucida drawings were made by DRR; composite drawings from direct observation of sectioned material were done by F.E. Runyan.

### RESULTS

#### THALLUS DEVELOPMENT

The general appearance of early thallus formation was as cream to buff colored tufts of mycelium on twigs and on some leaves of the American beech (LAM 200000). The fungus soma developed in accumulations of the exudate of the wooly aphid insect, which utilizes *F. grandifolia* as a host plant. Limited mycelial growth was seen on the ground at time of collection. The nonpig-

mented hyphae exhibited two distinct zones in the wall. In cross section of older hyphae (Fig. 1A), the outermost zone was widest, measuring an average  $15\mu$ . The outer boundary of the inner-wall zone was sharply delineated and measured approximately  $1\mu$  in diameter. The cell lumen containing the protoplast averaged  $6\mu$  in diameter. Cells were generally rectangular; size was variable (Fig. 1B). The outer-wall zone was present in the apical cell of presumed actively growing hyphae (Fig. 1C) and became wider in diameter than the inner-wall zone in cells progressively subtending the apical cell. The wall formed a constriction at sites corresponding to the location of septa traversing the cell lumen. In median cell focus, a centrally located gap could be detected in the isodiametric septa.

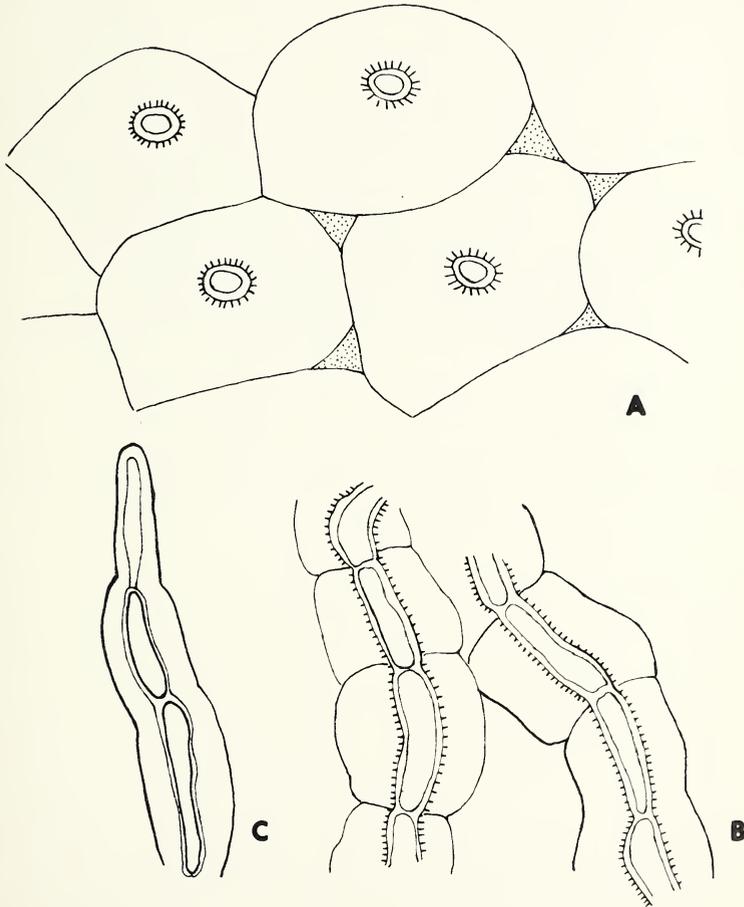


FIGURE 1. Hyphae. A. Cross section of hyphae, approx. 1300X; B. hyphae illustrating two wall zones, approx. 1000X; C. tip of young hypha, approx. 1000X.

Hyphal organization was effected largely by adherence of outer wall surfaces; reinforcement by cell fusions resulted in cytoplasmic continuity. Hyphae adhering together in small numbers for short distances, diverging individually or in small numbers and readhering with single or grouped hyphae, maintained a loose mycelial subiculum in localized areas on the supporting plant surface. The basic hyphal organization appeared as strands. Strand construction was similar throughout thallus development. The strand was usually rounded in a cross-section outline; the component hyphae were more or less parallel.

The somatic mycelium was well developed at a point in time represented by specimen LAM 200001. The hyphal wall construction was similar to that described in LAM 200000. The outer-wall zone measured 5-15 $\mu$  in diameter. An irregular verrucose deposition could be detected on hyphal surfaces in direct contact with other hyphal strands which were exposed to the atmosphere. The inner-wall zone measured approximately 1 $\mu$  in diameter. An interzonal area was identifiable which varied in width from almost nil to 1 $\mu$ ; it could be recognized by dark lines of varying length, oriented generally perpendicular to the axis of the hyphae, radiating from the outer surface of the inner-wall zone into the outer-wall zone. Pigmentation occurred first on exposed strand surfaces. The inner-wall zone of mature hyphal strands was initially achromatic and became darkened with a deposition of a pigment assumed to be melanin. The outer-wall zone was also initially achromatic and became darkened with a pigment similar to that of the inner zone, but of less intensity.

Mature stromata produced by the somatic mycelium of *S. spongiosa* had a definite internal structure (Figs. 2 & 3). Collection LAM 200013 is representative of mature stroma structure. It measured 11.6 cm in length and 5.5 cm at its highest point. Fig 2 is a diagrammatic representation of the stroma viewed lengthwise; Fig 3 represents a cross section at a level indicated by the arrow in Fig 2. The mycelial development radiated upward and outward from the supporting twig. The hyphae coalesced to form mycelial strands, which were

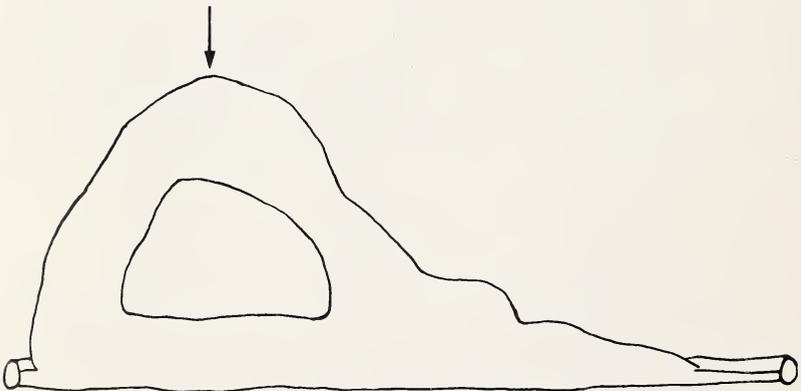


FIGURE 2. Diagrammatic representation of stroma lengthwise profile. Note enlargement of stroma in area represented by arrow in Figure 3.

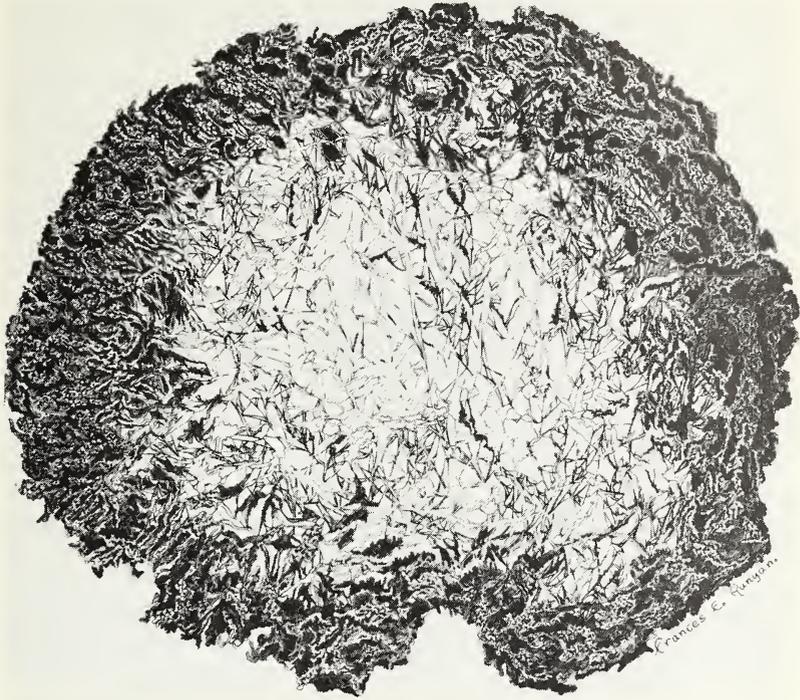


FIGURE 3. Cross-section view of mature stroma, approx. 3X. Supporting twig would be located at lower center portion.

largest in the lower center of the stroma. These central strands were formed in a lacunate region within the stroma which was also the highest portion (Arrow, Fig. 2; Fig. 3). Above the central labyrinth, the mycelial strands branched more frequently resulting in a compacted layer 1-2 cm deep, which formed the outermost region of the stroma. Reproductive structures ultimately developed on the exposed surface of the stroma. In the outermost compacted region of developing stroma, the hyphae comprising the outer layers of the component mycelial strands were fully pigmented; hyphal walls in the inner mycelial strand core were hyaline to yellowish. In mature stroma (Fig. 3) collected in late spring and bearing pseudothecia (LAM 200013), the strands in the outermost compacted portion were fully pigmented and most were surrounded by a nonpigmented layer representing the individual hyphae of new growth on the strand surface.

The dry stroma enlarged on contact with moisture. A rough estimation was made of structure modification upon wetting by calculating weight increase. Sections cut of collection LAM 200013 were weighed before and after wetting in a 10% formalin solution. An average 1.4% increase in weight was noted. Lack of appropriate material precluded confirmation of these data by use of additional stroma.

## CONIDIOGENY

A phialidic anamorphic centrum was present at the tips of the mycelial strands in collections LAM 200000 and LAM 200014 on the cream to buff-colored tufts of mycelium (Fig. 4). Within the hyaline strand apex, the conidiogenous system was initiated by profuse transverse cell division in the centrally positioned parallel hyphae.

The short cells of the centrally located dividing hyphal strands were distinct from larger elongate cells of the hyphae in the outermost strand layers. Additional hyaline cells were produced from these short cells, which in turn branched toward the strand center. Sympodial branching was initiated from a site immediately below the apical septum and generally opposite a conidiogenous site (Fig. 8B). Limited apical expansion resulted in a branched system of phialogenic hyphae of one to several cells in length. Phialospores were produced from usually only one place on the conidiogenous cell near the uppermost septum, less frequently in the middle of the cell, or at the hyphal tip (Fig. 8A-E). No observations were made on initial spore development from living material. The first conidium was apparently formed as a small tubular protrusion which was blown out from the conidiogenous cell (Fig. 8A). Successive spores were produced through a collarette (Fig. 8D, E).

A dark brown pigment appeared in the inner-wall zone of the short-celled hyphae from which the conidiogenous centers were initiated, as well as in cells of adjacent strand hyphae with longer cells. The outermost nonpigmented hyphae of the strand apex was separated from the enlarged conidiogenous centers from this time on. Lateral expansion of the anamorphic centrum coincided with proliferation of conidiogenous hyphae and production of conidia; the conidia became compacted in the middle of the conidiogenous center, creating a locule. A necklike extension was developed beyond the sporogenous area by a convergence and elongation of a layer of dark strand hyphae surrounding a central cylinder of nonbranching sterile hyaline phialogenic hyphae. The outer darkly pigmented hyphal layer eventually ceased to grow; the hyaline inner layer of hyphae extended beyond the outer layer, became reflexed, resulting in what Batista and Ciferri (1963a) referred to as a fimbriated ostiole. Conidia appeared to be initially forced through a space between the hyphae of the hyaline core, thus creating a channel to the end of the neckline extension. These and subsequent conidia were exuded in a slimelike matrix which collected as a droplet at the apex of the neck.

The phialidic anamorphic centrum was present on the surface of the well-developed stroma; it was well represented in October collections as well as in collections from later in the year. Initiation of these conidium forming areas is identical to that described from collections LAM 200000 (Fig. 5); the resulting conidia were identical. However, the phialidic anamorphic centrum was formed in short mycelial strands of darkly pigmented hyphae which radiated from the stroma surface. The length of the subtending strand varied. None of these pycnidium-like structures was seen in this later stage to have an apical continuation of the outer mycelial strand hyphae into a necklike extension.



FIGURE 4. Asexual fruit body with phialidic anamorphic centrum, approx. 300X.

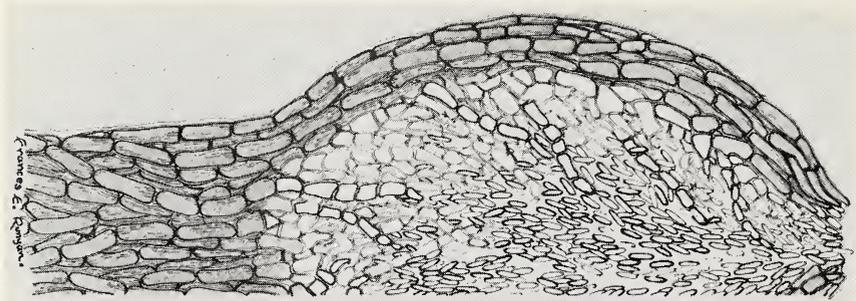


FIGURE 5. Asexual fruit body with phialidic anamorphic centrum, approx. 1000X.



FIGURE 6. Stroma surface detail illustrating ascocarps, approx. 30X.

#### ASCOGENY

Ascocarp formation was initiated by internal proliferation within a mycelial strand found on the stromatal surface (Fig. 6) and culminated in a prehyemial structure designated here the protopseudothecium. Eight or more individual hyphal strands from the surface network recoalesced in strand forma-

tion. Elongation of the strand appeared to be from the apical ends of the component hyphae. The mycelial strand organization was initially similar to that found in the central and compacted areas of the stroma, whereby parallel anastomosing hyphae formed into a rounded branch; the relative position of hyphae in the outer to central areas remained constant. All cells were found to be melanin-like pigmented. The onset of protopseudothecial differentiation was signaled by three areas of hyphal proliferation. A mycelial strand where a protopseudothecium was to be initiated was comprised of several hyphal zones; configuration patterns could be discerned in the outermost hyphal layers, in the middle hyphal layers and in the remaining innermost hyphae. The outermost layers did not depart from the basic parallel strand pattern (Fig. 7B). The hyphae in the middle layers began three-dimensional dichotomous and trichotomous branching. The cells were shorter but similar in cell shapes as compared to the outer most parallel hyphae (Fig. 7D). The hyphae in the innermost layers proliferated by formation of small isodiametric hyphae. These frequently branched, intermingled hyphae were generally oriented inwardly, perpendicular to the strand axis (Fig. 7E). All hyphae in the protopseudothecium had the basic 2-zone wall construction described earlier. Pigmentation developed in the outer layers containing the parallel, and the di- and trichotomously branched hyphae (Fig. 7B, C), but not in the isodiametric hyphae in the center of the protopseudothecial strand (Fig. 7D, E). Development of the outer layers of protopseudothecial strand kept pace with innermost core layer so that the pigment containing layers surrounded the inner core of hyaline isodiametric hyphae at all times. Proliferation of the latter and subsequent increase in width began in the lower portion of the protopseudothecium and became widest in the center of the ascocarp and terminated in an ostiole at the uppermost part.

Thus, the basic ascocarp subtended by a stalk (Fig. 7A) was formed before appearance of the ascogenous system. No further strand development appeared to occur after the inner core of hyaline hyphae was produced in the protopseudothecium. The portion of the protopseudothecial strand forming the ascocarp wall appeared plectenchyma-like in that the intertwined cells became affixed together, presumably by wall fusion. However, the centrally located nonpigmented hyphae retained their individual identity (Fig. 7E). In a longitudinal section of a protopseudothecium, the tissue might appear as pseudoparenchyma in both the wall and the central mycelial mass. This effect, as represented in the drawings such as those by Batista and Ciferri (1963b) for *S. spongiosa*, is due to the intermingled, highly-branched hyphae in the pigmented and nonpigmented layer in section showing the lumen of component cells from various angles separated by the wide walls.

The ascogenous system (Fig. 7F) appeared at the lower end of the pseudothecium. No ascogonium was detected; asci appeared to originate as croziers on proliferating ascogenous hyphae. Asci matured first in the center of the developing hymenium. The ascus wall was isodiametrically thickened only until the ascus mother cell elongated to full size. An ascus devoid of spores was cylindrical (Fig. 8F). The elongating ascus mother cells appeared to push up-

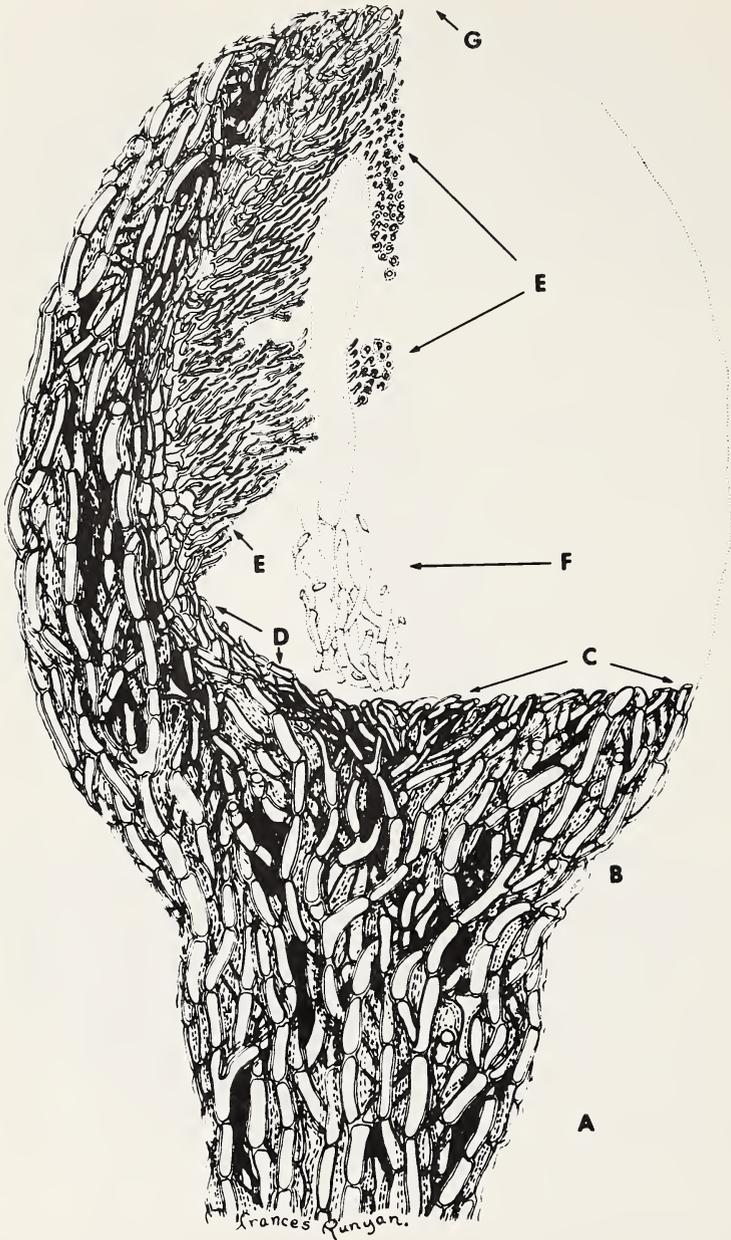


FIGURE 7. Ascocarp, approx. 1000X. A. mycelial strand subtending ascogenous center as stalk; B. base of ascocarp; C. dark tissue layer delimiting ascocarp; D. inner zone of hyaline hyphae; E. lateral periphyses lining locule; F. ascogenous hyphae bearing asci; G. ostiole.

ward among the nonpigmented hyphae occupying the center of the pseudothecium (Fig. 7). As the hymenium developed, the nonpigmented hyphae were displaced from the lower 75 percent of the original areas they occupied. The interface at the place of origin of nonpigmented hyphae with pigmented strand hyphae, effectively limited displacement. The resulting distortion created space within the pseudothecium (Fig. 7).

The shape of an ascus containing spores had been modified to obpyriform; the wall of such an ascus was thickened at the ascus apex with an evident *nasse apicale* (Reynolds 1971) and tapered in width toward the ascus base (Fig. 8G). Mature ascospores were hyaline and traversed by three septa. Discharged asci were found to have a discernible outer tunica surrounding a tubular inner tunica. Ascospores were frequently seen attached to the outer surfaces of ascocarps, some having germinated. No ascus was found to be discharged intact from the ascocarp as suggested by Ellis and Everhart (1892), although in some preparations, pressure applied to a coverslip would result in dislocation of individual asci and whole hymenia through the ostiole.

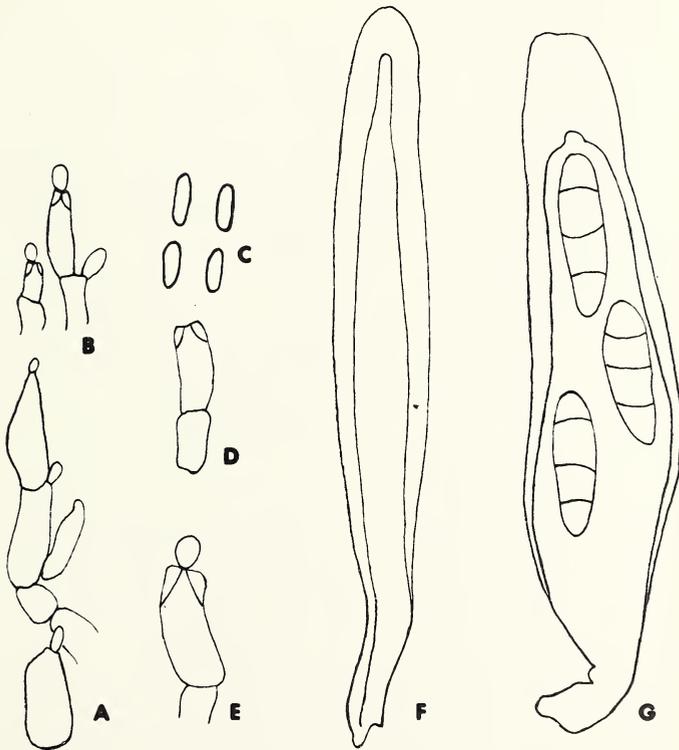


FIGURE 8. Phialides and asci, approx. 2000X. A, B. enterblastic monophialidic conidiophores bearing young conidia; D, E. phialides with collarettes; C. conidia; F. young ascus before ascosporeogenesis; G. mature spore-bearing ascus.

## DISCUSSION

The terms teliomorphosis and anamorphosis have been introduced (Hennebert and Weresub 1977) in relation to a restatement of the International Code of Botanical Nomenclature, Article 59, "Names of fungi with a pleomorphic life cycle and of fossils assigned to form genera." These terms refer to basic reproductive modes of the holomorphic fungus and were defined as follows: teliomorphosis — "characterizing form that is involved in producing meiotic diaspores — in Ascomycetes, an ascocarp or its equivalent producing asci and ascospores. . . ."; anamorphosis — "The imperfect state . . . the asexual mitotic diaspore expression of a fungus . . ."

The term anamorphic centrum is utilized here as a Deuteromycete application of the Luttrellian Ascomycete centrum concept; this and other related terms are defined as follows: teliomorphic centrum = centrum sensu Luttrell (1951); anamorphic centrum = the reproductive or conidiogenous system component of an asexual fruit body; phialidic anamorphic centrum = an anamorphic centrum where the conidium is enteroblastically produced via a phialide.

The conidiogenous system described here consists of enteroblastic, basically monophialidic, conidiophores resembling that of two epimycotic Coelomycete genera. The illustrations by Seeler (1943) of *Eleuthoromycella mycophyla* von Hoehnel and especially *Eleutheromyces subulatus* (Fr.) Fuckel indicate strikingly similar acropleurogenous branched conidiophores. Both species are described as having wall tissue which is pseudoparenchymatous (textura angularia) rather than of parallel, somewhat gelatinized hyphae (textura oblita), as found in *S. spongiosa*. The pigmentation of *E. subulatus* is a nectriaceous burnt sienna, and that of *E. mycophyla* is carbonaceous. The walls of *S. spongiosa* pycnidia range from hyaline to melinoid.

Only one anamorphosis is associated with the life history of *S. spongiosa*. The term anamorphic centrum has been used to emphasize a continuity in terms of the conidiogenous system and the conidia produced in association with the stroma in all stages of development. Morphological forms of the asexual fruit body found here can be assigned to various pycnidial genera. Following Batista and Ciferri (1963a), these would be *Leptoxyphium* (globose, sessile, with no neck), *Podoxyphium* (globose stalked, with no neck) and *Microxyphium* (cylindrical, with a neck). Hughes (1976) speculatively refers to similar morphological forms as *Polychaeton* and *Conidiocarpus* (and perhaps *Scolecoxyphium*). The position of the anamorphic centrum in the rapidly expanding and rounding mycelial strands (i.e., LAM 200000) would seemingly cause a cylindrical pycnidium-like structure. Continued growth of the surrounding hyphae would produce a "neck." This observation is made especially clear when conidiogenous systems are to be found centrally located in mycelial strands with the ostiole eliminated by the continued growth of the strand tip. The conidiogenous systems found in the more mature stroma develop at the ends of narrow hyphal strands. Unlike the pycnidia with a "neck," these strands extend from the surface of a stroma and terminate with the formation of the conidiogenous center.

Therefore, the generic concepts of these pycnidiate fungi as set forth in literature such as Batista and Ciferri (1963a) and Hughes (1976) are questionable; many of these appear to be based on growth cycle artifacts given undue taxonomic significance. Experimental data derived from pure culture work would go far in resolving the problem. Detailed observations on a chronologically obtained series of collections from a single natural locality, such as utilized in this study, may prove a valid alternative.

The teliomorphic type is modified dothideaceous. The ascus produced by *S. spongiosa* is functionally bitunicate; microscopic mounts reveal the nasse apicale apparatus proposed by Chadefaud and explained by Reynolds (1971). The sterile elements peripherally produced from the wall, which hang into the locule, are not pseudoparaphyses sensu Wehmeyer. Therefore, in agreement with von Arx and Müller (1975), the concept of these structures as pleosporaceous (Corlett 1973), is rejected. These structures originate as outgrowths from the pseudoparenchymatous peripheral layer of the ascocarp locule and the ostiole. The term for these structures in an ostiole is periphyses. Because they are produced to a lower level in the ascocarp but are not attached in the hymenium as are paraphyses and additionally are not involved in centrum formation as are pseudoparaphyses, they are regarded as laterally positioned periphyses or periphysoids (Barr 1976). Samuels (1973) discussed centripetal paraphyses and apical paraphyses as found in unitunicate species.

In *Scorias*, as in other Ascomycetes, taxon definition is typed with the teliomorphosis. No Ascomycete species is known to produce more than one teliomorphosis sexual state, but many are known which produce one or more anamorphoses from the same mycelium or thallus. My attempts to work with *Scorias spongiosa* in artificial culture failed to yield the desired reproductive states. Instead, a hopefully acceptable compromise has been utilized involving sequentially collected herbarium specimens, which is similar to that utilized by Luttrell and Muthappa (1974). Holomorphic data was derived from collections taken periodically from a particular locality over a time span during which the fungus developed in nature. Additional and supportive information was derived from usual herbarium specimens available on loan from the institutions previously mentioned. Consequently, the author is reasonably convinced, in absence of definite proof sustained by data from artificial culture methods, that the stroma development is accurately presented for a localized strain of *S. spongiosa*, and that the reproductive states are likely to be those actually produced by the species, rather than being associated with the stroma of *S. spongiosa* by virtue of habitat preference of sooty mold fungi with similar morphological features.

Imperative in profiling the capnodiaceous whole-organism is an absolute certainty that the alternate reproductive states are biologically associated. Müller (1971), in a review of perfect-imperfect connections in Ascomycetes, pointed out that use of pure culture techniques has allowed definite proof of connections between the teliomorphosis and any anamorphoses produced by one organism. Biological connection of alternate states are definitely proved in

artificial cultivation, where this method is possible, by use of spore-to-spore cultivation, or by germination of one spore form to give rise to a mycelium in culture which produces an alternate state. Definite proof of biological connection is lacking, and only suspected, where demonstration of a single hyphal strand organically connecting several alternate states is found in randomly obtained herbarium specimens.

My concept of sooty mold fungi is derived from several thousand collections I have made in all of the neotropical countries and in some areas of the paleotropics, on the examination of all herbarium specimens I can locate which have been cited in the literature, and from attempts at experimental culture work with field-derived isolates. Consequently, I strongly advocate cognizance of the specialized microenvironment into which sooty mold fungi have adapted when systematic judgments are formulated as well as in the perception of pleomorphic or alternate reproductive state relationships. Therefore, especially in capnodiaceous fungi, systematic relationships should be determined from data derived from artificial culture of the species as well as from specimens collected in nature. Analytical analysis of the holomorphic sooty mold species demands a nonintuitive laboratory protocol in order that realistic taxonomic innovation can be made.

The intuitive "analytical analysis" of the interpretation of the sooty mold fungi was summarized by Hughes (1976). This viewpoint is in direct contrast to the rendering of systematic judgment which incorporates experimental data derived from a protocol utilizing pure culture techniques such as that demonstrated by Simmons (1969), or a chronologically obtained series of specimens from a single natural collection locality such as that utilized by Luttrell and Muthappa (1974). Hughes advocated *prima facie* establishment of alternate reproductive state association in the sooty mold colony as may be found in randomly collected herbarium collections. The *a priori* taxonomy proposed by Hughes (1976) contains the highly interesting, but biased, insight of a Fungi Imperfecti specialist. However, his philosophical commentary was unfortunately expressed in nomenclatorial jargon and, lacking experimental data, falls short of proper systematic documentation.

The annual growth and reproduction cycle detected in the sooty mold fungus *S. spongiosa* is regarded as indicative of efficient utilization of available microenvironmental resources under the influence of overall seasonal changes. This species and others in the family Capnodiaceae von Hoehnel exhibit morphological and life-history features, which would give advantages in coping with the stressful plant surface-atmosphere environment in which they exist. Thus, concepts of thallus and fruit body development should be justifiably influenced by habitat-related data. The sooty mold colony produced in nature by the capnodiaceous fungi should basically be regarded as an environmentally influenced association of species (Reynolds 1975; Reynolds and Pohlad 1974). Any attempt at analytical analysis of the fungi in the plant surface microenvironment will have to be based on a convincing, nonintuitive demonstration of

biological relationships between teliomorpheses and anamorpheses of fungi which thrive in this habitat. Definite proof of these relationships is necessary because ultimately any patterns of reproductive state associations should be reflected in the taxonomy of these highly evolved Ascomycetes.

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OTOLITHS AND OTHER FISH REMAINS  
FROM THE CHUMASH MIDDEN AT RINCON POINT (SBa-1)  
SANTA BARBARA-VENTURA COUNTIES, CALIFORNIA

*By* RICHARD W. HUDDLESTON and LLOYD W. BARKER

NATURAL HISTORY MUSEUM OF LOS ANGELES COUNTY

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OTOLITHS AND OTHER FISH REMAINS  
FROM THE CHUMASH MIDDEN AT RINCON POINT (SBa-1),  
SANTA BARBARA-VENTURA COUNTIES, CALIFORNIA<sup>1</sup>

By RICHARD W. HUDDLESTON<sup>2</sup> and LLOYD W. BARKER<sup>3</sup>

ABSTRACT: Material from a Chumash village site yielded 45 species of fishes (29 kinds of bony fishes, and 16 kinds of sharks, skates and rays). The fish remains, ranging in size from less than 1 to 75 mm, consisted of otoliths, teeth, jaws (dentary, premaxillary and palatines), vertebrae, stings, dermal denticles, dorsal spines and scales. As indicated by the species recovered, the Chumash inhabitants fished from surface regions and surf zones to depths exceeding 60 feet, utilizing hook and line, gill nets, traps, beach seines, harpoons, spears and capture by hand. The most abundant identified remains were otoliths of *Genyonemus lineatus*, scales of *Sardinops caeruleus*, and dermal denticles of *Squatina californica*. None of the identified remains showed signs of having been altered or modified for use in ornamentation. Comparison of the fishing habits of the inhabitants of SBa-1 and Ven-3 in Ventura indicated a similar level of advancement, which was superior and more fishery-orientated than Ora-190 in Orange County and SLO-2 in San Luis Obispo County.

INTRODUCTION

Prior to the completion of this study Lloyd W. Barker lost his life acting as an observer for the California Department of Fish and Game aboard a commercial sealion capturing vessel, which capsized in the Santa Barbara channel. Because of his untimely death, any errors or omissions are the responsibility of RWH.

Fish and other faunal remains of midden sites usually have appeared in archaeological literature as simple lists of identifications without any interpretation or significance. In particular, remains of fishes have been neglected, often being identified only as "fish" or "shark". Otoliths (fish earstones) play an important role in the identification of fishes recovered from middens. The use of otoliths in archaeological work is not new, being employed first in the

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

JOHN E. FITCH

W.I. FOLLETT

ROBERT J. LAVENBERG

<sup>2</sup>Section of Vertebrate Paleontology, Natural History Museum of Los Angeles County, 900 Exposition Boulevard, Los Angeles, California 90007.

<sup>3</sup>Deceased.

latter part of the nineteenth century (Ihering 1891). It was not until 1969, however, that otoliths were used on a large scale (Fitch 1969a). Fitch noted approximately 19 species of fishes represented by otoliths from a midden in Ventura County.

All bony fishes (fishes other than sharks, skates, rays and chimaeroids) possess some type of discrete aragonitic concretion in the semicircular canals of the otic capsules, called otoliths. Although not well understood, the otolith aids in the hearing and balance of the fish. Since almost all species of fishes have distinctive otoliths, their specific identifications can be made with adequate comparative material.

Bony fishes possess three pairs of otoliths; the sagittae, lapilli and asterisci. Of these, the sagitta generally is the largest, most frequently encountered, and most relied upon for taxonomic interpretation. Many conclusions have been drawn regarding the Indians' fish-eating habits, based upon the quantity of fish vertebrae (unidentified as to species) present in a given sample from different levels of the midden. Fitch (1972) states that these conclusions are untrustworthy, and normally indicate only that fishes were present; they do not furnish an index of numerical abundance or importance.

A relationship exists between otolith lengths and fish lengths, and once this relationship has been defined for a given species, a reliable estimate of a fish size can be ascertained from a single midden otolith. Otoliths can be deposited in middens by predators through their digestive systems, by scavengers at the midden, or by the Indians. Otoliths that have passed through digestive systems indicate signs of erosion on all surfaces. Species that unlikely would be captured by the inhabitants for food because of their small size or living depth could be of predator origin in the midden, and this often can be determined by the degree of surface erosion. Caution must be used in interpreting these otoliths in relation to the food habits and fisheries of the Indians. Indians sometimes would consume whole small fishes (Follett 1967), which offers the possibility that some of the small eroded otoliths could reflect passage through human digestive systems. Whether these eroded otoliths have passed through a human or nonhuman digestive system often can be determined by examining the habits of the fish in question. For example, Fitch (1969a) noted a myctophid otolith (*Ceratoscopus townsendi*) from a Ventura midden. The depth at which this lantern fish lives (rarely coming within 600 feet of the surface) as well as its extremely small size (about three inches) was sufficient evidence to indicate that this fish had not been captured directly by the inhabitants nor passed through a human digestive system; rather, it was probably from the stomach of some predator.

#### METHODS AND MATERIALS

We recovered less than a hundred pounds of midden material from the site. Our methods of preparing and examining the field sample followed closely methods discussed by Fitch (1967, 1969a, 1972). The field sample was soaked

in a large tub of water, then passed through a ¼-inch mesh screen. The retained screenings were set aside to dry. Material not retained by the first screen was then passed through an 18-mesh screen. These screenings were dried in an oven at a temperature of 250-300°F. The material that was not retained by this second screen was passed through a 30-mesh screen. Due to the abundance of ash and charcoal in the midden "dirt" and its tendency to cling to all other materials, a secondary screening was necessary. The freshly dried screenings were soaked separately in a solution of one part liquid bleach and two parts water for several minutes, then rescreened. This made the screenings cleaner and reduced them in weight by ten percent. These procedures greatly enhanced our ability to recognize the fish remains and decreased the time required to examine the sample. The ¼-inch screenings were examined by eye for the larger fish remains, whereas the 18- and 30-mesh screenings were sorted a spoonful at a time under a binocular microscope.

### HISTORY AND PREVIOUS DIGGING

The Rincon site (SBa-1) became a historic point of contact with the landing of Juan Rodriquez Cabrillo in October 1542. The village, which was called Xucu by the Indians, was visited several times in succeeding centuries: Sebastian Vizcaino, 1602-1603(?); Gaspar de Portola, 1770; and Juan Bautista Anza, 1776. The Rincon area had been ravaged heavily prior to our study. A massive amount of material was removed by Stephen Bowers, an amateur archaeologist, in the early 1870's, but there are no reports on his findings, and the material subsequently has become lost (Rogers 1929). Leon De Cessac, a French archaeologist, probably worked at the site during the early 1870's but these reports remain unverified. Rincon was worked partly in the 1920's by archaeologists D.B. Rogers, the Catlin brothers and W.C. Toby and Jesse Wood. In 1930, Ronald Olson excavated three cemeteries (Olson 1930). Marshall McKusick surveyed the Rincon Point area in 1959 for the University of California at Los Angeles (UCLA) Archaeological Survey. W.H. Harrison and Patricia Lyon, then with the University of California, Santa Barbara, excavated several burials in 1959 and 1960. Patrick Finnerty, formerly of UCLA, excavated two areas in 1961 and 1964 (Finnerty 1961, 1964). Personnel representing the UCLA Archaeological Survey have done the remainder of the excavations: three test pits in April 1963 and extensive excavations in the summer of 1966. Unfortunately, the control column from the 1966 excavation was discarded without having been examined. John E. Fitch, California Department of Fish and Game, removed several hundred pounds of material during the 1966 UCLA excavations and reported three species of fishes: northern anchovy (*Engraulis mordax*), pacific sardine (*Sardinops caeruleus*), and Pacific hake (*Merluccius productus*). Six other species were found but not specifically identified (Fitch 1969b). Fitch gave us his material and we have incorporated it into this report. Most of the Rincon publications report on aspects other than faunal remains. Evans, Grossman and Toney (1968:36)

mention fish remains but state only that "The remains of fish, mainly vertebrae, were numerous and appear to represent shallow water species."

### SPECIES ACCOUNTS

It is difficult to present the species accounts in both an archaeological and an ichthyological approach. We have tried to simplify the matter by separating the elasmobranchs (Sharks, skates and rays) from the teleosts (bony fishes). In each of the two groups, taxa are arranged alphabetically by family, and within each family by genus and species. Common names are listed after each scientific name.

#### ELASMOBRANCHS

##### Alopiidae – Thresher sharks

*Alopias vulpinus* – Thresher shark. — Along the west coast of North America the thresher shark ranges from central Baja California north to the Strait of Juan de Fuca, but also is found in all warm seas. Threshers are known to attain a length of at least 5.5 m (18 feet, Joseph 1954). This shark lives near the surface, probably not descending to depths greater than 200 m; they rarely are found near shore. Indians probably utilized a harpoon in obtaining them. Thresher shark remains have been reported from a midden site in Alameda County (Follett 1975a).

Material: 1 jaw tooth; Fig. 1B.

##### Carcharhinidae – Requiem sharks

*Galeorhinus zyopterus* – Soupfin shark. — Soupfin sharks are large, attaining lengths to 2 m (6.5 feet, Miller and Lea 1972). They are found off Chile and Peru in the southern Hemisphere and from San Juanico Bay, Baja California, to northern British Columbia in the Northern Hemisphere. South of Point Conception this shark often inhabits waters several hundred feet deep (Fitch 1968).

Soupfin shark remains also have been recovered from Ventura (Fitch 1969a, 1975; Follett 1965) and Los Angeles counties (Follett 1963a; Frey 1974; Tartaglia 1976), and at Point St. George site (Gould 1966).

Material: 13 jaw teeth; Fig. 1I.

*Mustelus californicus* – Gray smoothhound. — Gray smoothhounds reach lengths of just over 1.5 m (5 feet, Fitch 1972), and range from Mazatlan, Mexico, to Cape Mendocino, California. They are common in shallow water off southern California where they could have been taken easily by gill nets, hook and line or beach seines, by the Indians.

Remains of gray smoothhounds have been reported from middens in Ventura (Fitch 1969a), Orange (Fitch 1975) and San Diego Counties (Follett 1976).

Material: 2 jaw teeth; Fig. 2A.

*Prionace glauca* – Blue shark. — The blue shark ranges throughout warm

seas. In the eastern Pacific, they are found from Chile to the Gulf of Alaska but are absent in the tropics. Individuals off California are usually shorter than 1.8 m (6 feet, Fitch 1972). The Indians probably used harpoon and hook and line to capture this species. Blue shark remains have been recovered also from middens in Los Angeles (Follett 1963b), San Luis Obispo (Fitch 1972), and Orange Counties (Fitch 1975).

Material: 1 jaw tooth. Fig. 1H.

*Triakis semifasciata* – Leopard shark. — The leopard shark has been taken from Mazatlan, Mexico, to Oregon and in the Gulf of California. They are common along beaches in bays and attain lengths of 2 m (6.5 feet, Miller and Lea 1972). The Indians could have captured this shark by harpoon, spear, hook and line, traps or beach seines.

Leopard shark remains have been recovered from archaeological sites in Ventura (Fitch 1969a; Follett 1933, 1965), Los Angeles (Follett 1963a, 1963b, 1969), Orange (Fitch 1967, 1975; Follett 1966), Marin, Monterey and San Luis Obispo (Follett 1964, 1974, 1972a; Fitch 1972), Alameda and Contra Costa Counties (Follett 1975a, 1975b), and also from Santa Catalina Island (Tartaglia 1976).

Material: 3 jaw teeth, Fig. 2D.

#### Dasyatidae – Stingrays

*Dasyatis dipterura* – Diamond stingray. — This large ray ranges from Paita, Peru, to Kyuquot, British Columbia. They are known to attain a weight of 25 kg. (113-½ pounds, Miller and Lea 1972). Diamond stingrays are found in shallow areas to depths of 18 m (55 feet, Miller and Lea 1972) preferring regions of sandy bottom, where they lie on the substrate and cover themselves with sand. The Indians could have captured this species with hook and line, spear or harpoon while fishing in shallow nearshore areas.

The diamond stingray has been reported from only one other midden (Fitch 1975).

Material: 4 jaw teeth. Fig. 2E.

#### Heterodontidae – Horn sharks

*Heterodontus francisci* – Horn shark. — This small nonaggressive shark is found in the Gulf of California and along the coasts of the Californias to Monterey Bay, reaching a length of just over one meter (3 feet 2-½ inches, John Fitch, personal communication). Horn sharks are most frequently found in shallow water in rocky bottom habitats, but they may descend to depths of 164 m (492 feet, Miller and Lea 1972). Fitch (1969a) suggests that horn sharks may have been captured by the Indians while free diving as well as with hook and line and possibly with traps.

Horn shark remains have been recovered from Indian middens in Orange and Ventura Counties (Fitch 1967, 1969a; Follett 1933).

Material: 4 jaw teeth, 1 dorsal spine. Fig. 2F,G,H.

## Hexanchidae – Cow sharks

*Notorynchus maculatus* – Sevengill shark. — Sevengill sharks range in the north Pacific from San Carlos Bay, Baja California, to northern British Columbia. The maximum known length is 2.6 m (8 feet-6 inches, Bohnam 1942). These sharks commonly are found in bays, but south of Point Conception they usually inhabit deeper waters of 200 m (600 feet, Fitch 1969a) or more. The Indians probably captured this species using hook and line in deep water.

Remains of sevengill sharks have been found in middens near Ventura (Fitch 1969a, 1975) and in Marin County (Follett 1968).

Material: 1 jaw tooth, Fig. 1E.

## Lamnidae – Mackerel sharks

*Carcharodon carcharias* – White shark. — The white shark has a worldwide distribution, and is found in the eastern Pacific from Chile to Alaska. There is an endemic population off California. They probably are not uncommon as reported in the literature (Bigelow and Schroeder 1948; Miller and Lea 1972). Whites are one of the largest sharks attaining lengths of at least 6.4 m (21 feet, Randall 1973). The Indians could have captured this shark by use of a harpoon.

White shark remains have been reported from sites in Ventura (Fitch 1975; Follett 1933, 1965) and Los Angeles Counties (Tartaglia 1976), and two sites in southern New England (Waters 1967).

Material: 3 jaw teeth, Fig. 1D.

*Isurus oxyrinchus* – Shortfin mako. — The shortfin mako reportedly attains a length of 3.9 m (13 feet, Miller and Lea 1972) and weight of 454 kg (1000 pounds, Miller and Lea 1972), but a specimen measuring 3.5 m (11 feet-5 inches, Huddleston unpublished data), harpooned off Anacapa Island in August and weighing 466 Kg (1030 pounds, Huddleston unpublished data), appears to be the largest eastern Pacific one (S.P. Applegate, personal communication). In the eastern Pacific the shortfin mako ranges from Chile to the Columbia River. The Indians probably caught this shark with harpoon.

Remains of shortfin makos have been recovered previously from midden sites in Ventura (Fitch 1969a, 1975; Follett 1933, 1965; Tartaglia 1976) and Los Angeles Counties (Follett 1963a, 1963b, 1969; Tartaglia 1976) and from Santa Catalina Island (Tartaglia 1976).

Material: 4 jaw teeth. Fig. 1A.

## Myliobatidae – Eagle rays

*Myliobatis californica* – Bat ray. — Bat rays range from the Gulf of California to Oregon. They have been known to attain a width of about 1.4 m (4 feet-9 inches, Miller and Lea 1972), and a weight of 95 kg (210 pounds, Miller and Lea 1972), but most individuals weigh less than 23 kg (50 pounds, Fitch 1969a). They have been found from the surface to depths of 45 m (150 feet,

Miller and Lea 1972). Bat rays commonly are found in bays and shallow water over sandy or muddy bottoms. Large individuals could have been captured by hook and line, and it is possible that the Indians utilized the caudal stings of these and other rays for harpoon points.

Bat ray remains have been recovered from several other middens in Ventura (Fitch 1969a, 1975; Follett 1933, 1965; Tartaglia 1976), Los Angeles (Follett 1963a, 1969; Frey 1974; Meighan 1959; Tartaglia 1976) Orange (Follett (1966), Marin (Follett 1968, 1974), Santa Barbara (Harrington 1928), San Luis Obispo Counties (Fitch 1972).

Material: 57 jaw teeth. Figs. 2J,K.

#### Rhinobatidae – Guitar fishes

*Rhinobatos productus* – Shovelnose guitarfish. — The shovelnose guitarfish is found from the Gulf of California to San Francisco Bay, but recent reports indicate that it ranges only as far north as Capitola. This cartilaginous fish has been reported to attain a length of about 1.5 m (61.5 inches, Miller and Lea 1972). They are found from the surface to depths of about 13.5 m (45 feet, Miller and Lea 1972), preferring sandy or muddy bottoms. Sometimes shovelnose guitarfish feed in such shallow water as to be nearly beached by the breaking surf. At such times they are taken easily by spear or hand. It is also possible that the Indians used hook and line.

Remains of the shovelnose guitarfish have been recovered from other midden sites in Ventura (Fitch 1969a; Follett 1933; Tartaglia 1976), Orange (Fitch 1967, 1975), and Los Angeles Counties (Follett 1963a, 1963b; Tartaglia 1976) and Santa Catalina Island (Tartaglia 1976).

Material: 1 jaw tooth. Fig. 2C.

#### Scyliorhinidae – Cat sharks

*Cephaloscyllium ventriosum* – Swell sharks. — Swell sharks are found from Chile to Monterey Bay, including Guadalupe Island and the Gulf of California. This shark is very abundant around islands south of Monterey Bay, but not those south of Magdalena Bay. Swell sharks prefer rocky kelp bed habitat from shallow water to depths of over 400 m (1380 feet, Miller and Lea 1972); they attain lengths of about one meter (3 feet, Miller and Lea 1972). When caught or threatened they have the ability to inflate their stomachs with air — a possible defensive mechanism. The Indians probably captured this shark using traps in shallow rocky areas, although some could have been taken by hook and line. Swell sharks are reported to be of very poor flavor and the Indians probably did not actively fish for them (S.P. Applegate, personal communication).

Swell shark remains also have been recovered from a midden in Ventura County (Fitch 1969a).

Material: 4 jaw teeth, Fig. 1F.

## Squalidae – Dogfish sharks

*Squalus acanthias* – Spiny dogfish. — The spiny dogfish has been found in the temperate and subarctic regions of both the Atlantic and Pacific Oceans. In the eastern Pacific, this shark has been found off Chile and from Sebastian Viscaïno Bay, Baja California, to Alaska. They reach lengths of 130 cm (4 feet 3 inches, Bonham, Sanford, Clegg and Bucher 1949), and occasionally travel in schools in those waters above 390 m (1200 feet, Miller and Lea 1972). Off California they usually are found in depths between 33 and 66 m (100-250 feet, Fitch 1969a). The Indians could have utilized hook and line as well as gill nets to capture this species.

Spiny dogfish remains have been recovered also from Indian middens in Ventura and San Luis Obispo (Fitch 1969a, 1972), and Los Angeles Counties (Tartaglia 1976). This species has also been noted from midden sites in British Columbia, Canada (Niblack 1890; Stewart ms).

Material: 25 jaw teeth. Fig. 1G.

## Squatinae – Angel sharks

*Squatina californica* – Pacific angel shark. — The Pacific angel shark is found off Chile and from the Gulf of California to southeastern Alaska, but is not common north of Point Conception and has not been reported from Canada (Hart 1973). This shark has been known to reach a length of 1.8 m (5 feet, Miller and Lea 1972) and a weight of 27 kg (60 pounds, Miller and Lea 1972). Pacific angel sharks prefer shallow water, dwelling on the bottom in sandy or muddy areas. They have been observed from depths between about 3 to 45 m (8 to 150 feet, Fitch 1969a), but prefer a depth of about 20 m. Although the Indians could have used a beach seine to capture this species they probably captured them on hook and line or by harpoon.

Remains of the Pacific angel shark have been recovered from middens in Los Angeles (Follett 1963a, 1963b, 1969; Frey 1974; Tartaglia 1976), Ventura (Fitch 1969a, 1975; Follett 1965; Tartaglia 1976), Orange (Fitch 1967), and San Luis Obispo Counties (Fitch 1969a).

Material: 9 jaw teeth, 365 dermal denticles. Fig. 1C.

## Unidentified elasmobranch remains

Three fragments of caudal stings were recovered from SBA-1. Unfortunately caudal stings generally are not useful for making specific identifications because of their similarity. Two fragments of large caudal stings were recovered from the road level sample near the area where most of the *Myliobatis californica* teeth were recovered (Fig. 2I, one only). However, they were not associated with this material and it is possible that they belong to *Dasyatis dipterura*, which has a similar type of caudal sting. The third smallest fragment was found in one of the hill samples and although it could have been from a small *Myliobatis californica* it possibly was from *Urolophus halleri*, the round

stingray. Both species are extremely abundant off southern California in shallow sandy regions, but because of its small size and fragmented nature the sting cannot reliably be assigned to either ray.

Material: 3 caudal stings. Fig. 2I.

#### TELEOSTS

##### Atherinidae – Silversides

*Atherinops affinis* – Topsmelt. — Topsmelt range from Santa Maria Bay, Baja California, to Vancouver Island, British Columbia, and attain a length to 365 mm (Schultz 1933). Topsmelt inhabit bays and kelp beds living at or near the surface. They possess small mouths and thus would have been difficult to take by hook and line. The Indians probably used beach seines to obtain this species.

Fitch (1969a, 1972) reported otoliths *A. affinis* from sites in Ventura and San Luis Obispo Counties.

Material: 7 otoliths. Fig. 3A.

*Atherinopsis californiensis* – Jacksmelt. — Jacksmelt are known from Santa Maria Bay, Baja California, to Yaquina Bay, Oregon. Although reported to reach a length of 22 inches, the largest measured individual was 448 mm (17½ inches, Miller and Lea 1972). Jacksmelt are common along coasts, bays and kelp beds. Beach seines probably were used to obtain this species.

An otolith of *A. californiensis* has been reported from a midden near Ventura (Fitch 1969a); it also has been reported from Marin (Follett 1974), San Diego (Follett 1976) and Alameda Counties (Follett 1975a).

Material: 3 otoliths. Not figured.

##### Batrachoididae – Toadfishes

*Porichthys notatus* – Plainfin midshipman. — Plainfin midshipmen have been found in the Gulf of California and range from Gorda Bank, Baja California, to Sitka, Alaska. They are found near the surface and to depths of about 330 m (1000 feet, Miller and Lea 1972). South of Point Conception they usually are confined to deeper waters (Hubbs and Schultz 1939). However, during “nesting” season it is possible to capture juveniles as well as adults from under rocks by hand in the intertidal. Plainfin midshipmen spend daylight hours burrowed in the bottom sediments, emerging at night to seek food. The single otolith recovered from SBa-1 was that of a juvenile and showed signs of digestive wear; it probably was from the stomach of a predator captured by the Indians.

Remains of *P. notatus* have been reported from middens in Ventura (Fitch 1969a), San Luis Obispo (Fitch 1972), Los Angeles (Fitch 1975) and Alameda Counties (Follett 1975a).

Material: 1 otolith. Fig. 3C.

## Bothidae – Lefteyed flounders

*Paralichthys californicus* – California halibut. — California halibut are found from Magdalena Bay, Baja California, to Quillayute River, British Columbia, and an isolated population occurs in the Gulf of California. They have been known to reach a length of 1.8 m (5 feet, Fitch 1969a), and a weight of 33 kg (72 pounds, Fitch 1969a). They are uncommon north of Morro Bay. California halibut usually are found in shallow water at depths of less than 36 m preferring sandy habitat. During the spawning season (from February through July) they frequent shallower water where they could have been captured easily by hook and line and beach seines.

Remains of California halibut have been reported from middens in Los Angeles (Follett 1963b, 1969; Tartaglia 1976), Orange (Follett 1966), and Ventura Counties (Fitch 1969a, 1975; Follett 1933; Tartaglia 1976), and from midden sites along the coast of British Columbia (Boas 1895, 1916; Niblack 1890; Leechman 1973; Ducker 1955, 1965; Sapir 1915; Garfield 1939, 1966; Stewart ms).

Material: 1 Premaxillary. Fig. 6F.

## Carangidae – Jacks and pompanos

*Seriola dorsalis* – Yellowtail. — The schooling yellowtail range from Chile to southern Washington and also are found in the Gulf of California. They attain a length of 1.8 m (5 feet, Miller and Lea 1972) and a weight of 36 kg (80 pounds, Miller and Lea 1972). Generally they live near the surface but may descend to 24 m. The Indians probably captured this species by hook and line in offshore areas.

Yellowtail remains have been reported from middens in Los Angeles (Follett 1963a, 1963b, 1969; Tartaglia 1976) and Ventura Counties (Tartaglia 1976).

Material: 1 vertebra. Not figured.

*Trachurus symmetricus* – Jack mackerel. — Jack mackerel, a schooling species, are known from Magdalena Bay, Baja California, to southeastern Alaska, and from offshore to several hundred kilometers. They sometimes are found inshore around rocky headlands. Fitch (1972) reported that a 5.25 pound (2.4 kg) jack mackerel measured 28.5 inches (724 mm) in total length and possessed otoliths 11.4 mm in length. *Trachurus symmetricus* is reported to reach a length of just under one meter (32 inches, Miller and Lea 1972). They live in the upper 45 m. The Indians probably captured this species with hook and line or gill nets.

Jack mackerel remains also have been reported in midden sites in Ventura (Fitch 1969a), San Diego (Fitch 1969b), San Luis Obispo (Fitch 1972) and Los Angeles Counties (Tartaglia 1976).

Material: 1 otolith. Not figured.

## Clinidae – Kelpfishes

*Neoclinus uninotatus* – Onespots fringehead. — Onespots fringeheads are known only from Ensenada, Baja California, to Bodega Bay, a restricted geo-

graphic distribution. They are a nearshore species occurring in waters 3 to 27 m (10-90 feet, Miller and Lea 1972) deep, and reach lengths to 247 mm (9 inches, Miller and Lea 1972). The eroded condition of the otolith recovered from SBA-1 indicated that it probably had passed through the digestive system of a predator captured by the Indians. The otolith is from a specimen too small to have been captured by the gill nets used for white croakers, although many are taken by hook and line.

*N. uninotatus* remains have not been reported from any other midden. Material: 1 otolith. Fig. 3B.

#### Clupeidae – Herrings

*Sardinops caeruleus* – Pacific sardine. — Pacific sardines are schooling fish with a broad distribution in the eastern Pacific from Guaymas, Mexico, to Kamchatka. They have been known to reach lengths of about 39.4 cm (approximately 16 inches, Miller and Lea 1972). Scales of *S. caeruleus* are distinctive among the clupeids. The transverse slits and perforations in the scale are distinctive for identification. Scales of *S. caeruleus* were exceedingly abundant throughout the samples examined with the exception of those from the slope of Rincon Hill. This species was probably captured by beach seines or gill nets. Follett (1965, 1968, 1969, 1972a, 1976) reported remains of *S. caeruleus* (as *S. sagax*) from the Conejo Rock Shelter, Tomales Bay site, Century Ranch site, Mission La Soledad cemetery and a site at Rancho Carrillo, Ventura, Marin, Los Angeles, Monterey, and San Diego Counties; Fitch (1972, 1975) noted their remains at sites in San Luis Obispo and Ventura Counties.

Material: 3 otoliths. Fig. 3D.

#### Embiotocidae – Surfperches

*Amphistichus argenteus* – Barred surfperch. — Barred surfperch range from Playa Maria Bay, Baja California, to Bodega Bay, attaining lengths to 43 cm (17 inches, Fitch 1969a) and a weight of two kg (4.5 pounds, Fitch 1969a). This species is most abundant in breaking surf and other shallow waters, particularly sandy bottom areas; they rarely are captured in rocky areas. Barred surfperch have been captured at the surface to depths of 73 m (240 feet, Miller and Lea 1972). This species probably was captured by beach seines, although large individuals could have been taken by hook and line.

Barred surfperch remains also have been recovered from midden sites in Orange (Fitch 1967), Ventura (Fitch 1969a, 1975; Tartaglia 1976; Follett 1933) and Los Angeles Counties (Tartaglia 1976).

Material: 1 jaw tooth. Fig. 5A.

*Cymatogaster aggregata* – Shiner surfperch. — The shiner surfperch is a small fish; most individuals are shorter than 177 mm. They range from San Quintin Bay, Baja California, to Port Wrangell, Alaska, and have been taken from the surface to depths of about 136 m (480 feet, Miller and Lea 1972). Shiner surfperch usually prefer water shallower than 18 m. This species, which

does not exceed 100 g (¼ pounds, Fitch 1972) in weight, probably was captured by the Indians using beach seines.

Fitch (1972), reported shiner surfperch otoliths from a midden site at Diablo Cove, San Luis Obispo County.

Material: 2 otoliths. Fig. 3G.

*Damalichthys vacca* – Pile perch. — The pile perch has been taken from Guadalupe Island to Port Wrangell, Alaska. They are recorded from surface waters to depths of 45 m (140 feet, Miller and Lea 1972). A record-sized specimen measured 44.2 cm (17.4 inches, Fitch 1969a) and weighed slightly less than 1.8 kg (4 pounds, Fitch 1969a). The pile perch is found over sandy and rocky bottom habitat as well as around kelp beds. The Indians probably captured pile perch using hook and line and possibly gill nets and beach seines.

Follett (1964) found pile perch remains from the Drakes Bay site and Fitch (1969a, 1972) reported their remains from Ventura and San Luis Obispo Counties. They also have been reported from midden sites in Marin (Follett 1967), Monterey (Follett 1973), Ventura and Los Angeles Counties (Tartaglia 1976).

Material: 2 pharyngeal bones, 58 pharyngeal teeth. Fig. 5B,E.

*Hyperprosopon argenteum* – Walleye surfperch. — This surfperch ranges from Point Rosarito, Baja California, to Vancouver Island, British Columbia, including Guadalupe Island. They have a recorded size to 30.5 cm (12 inches, Miller and Lea 1972). A 27.3 cm (10-¾ inch, Fitch 1969a) fish weighed just over 397 g (14 ounces, Fitch 1969a). The walleye surfperch has been known from surface waters to a depth of 18 m (60 feet, Miller and Lea 1972). They prefer sandy bottom or flat rocky habitat. This species probably was captured by the Indians using beach seines.

Walleye surfperch remains have been recovered from middens in Ventura and San Luis Obispo Counties and Drakes Bay (Fitch 1969a, 1972; Follett 1964).

Material: 2 otoliths. Fig. 3I.

*Phanerodon furcatus* – White seaperch. — White seaperch have been captured from Point Cabras, Baja California, to Vancouver Island, British Columbia. They have been known from the surface to depths of 42.4 meters (140 feet, Miller and Lea 1972). This species travels in loose schools over sandy bottoms. A record-sized specimen weighed about 369 grams (13 ounces, Fitch 1969a). The Indians probably captured this species using beach seines near shore and gill nets in deeper waters.

Previously white seaperch have been recovered from a midden in Ventura County (Fitch 1969a).

Material: 5 otoliths. Fig. 3H.

Embriotocids — (genus and species undetermined). — Of the 19 species of surfperches that are found in marine waters off California, 17 occur off southern California. Of these, one is found only around islands, thus there are 16 possible marine species that could have been captured by the inhabitants of SBA-1. It is possible that some of the 227 unidentified pharyngeal teeth be-

longed to some of the other species not listed above or from freshwater sources.

Material: 227 pharyngeal teeth. Not figured.

#### Engraulidae – Anchovies

*Engraulis mordax* – Northern anchovy. — The northern anchovy is one of the most abundant fishes off our coast. This schooling fish has been found from Cape San Lucas, Baja California, to Queen Charlotte Island, British Columbia. They are known to attain a length of 229 mm (9 inches, Miller and Lea 1972) but specimens over 177 mm are rare. During fall and winter, northern anchovies apparently move offshore and return inshore during spring (Baxter 1966). During the day, anchovies remain well below the surface, rising to the surface at night. They are consumed by nearly all predatory fishes off California as well as by birds and marine mammals. The Indians could have caught *E. mordax* by beach seine, although some of the otoliths show signs of digestive wear and were probably from stomachs of predators captured by the Indians.

Northern anchovy remains have been reported from midden sites in Orange (Fitch 1967), Ventura (Fitch 1969a, 1975) and Los Angeles Counties (Fitch 1975; Tartaglia 1976). Fitch (1969b) previously reported otoliths of *E. mordax* from SBa-1.

Material: 148 otoliths. Fig. 3E.

#### Labridae – Wrasses

*Oxjulis californica* – Senorita. — This small wrasse has been taken from Cedros Island, Baja California, to Sausalito, California. Ranging from surface waters to depths of 54.5 m (180 feet, Miller and Lea 1972), seniorita prefer shallow water rocky habitat with kelp vegetation. A 229 mm (9-inch, Fitch 1968) individual weighed 113 g (4 ounces, Fitch 1968). The Indians probably caught this species with gill nets.

*O. californica* remains have been reported from midden sites in San Luis Obispo (Fitch 1972), Ventura and Los Angeles Counties (Tartaglia 1976).

Material: 2 otoliths, 7 premaxillary bones, 26 pharyngeal bones. Figs. 3F; 5A; 6C.

*Pimelometopon pulchrum* – California sheephead. — California sheephead range from Cape San Lucas, Baja California, to Monterey, with an isolated population in the northern Gulf of California. Although abundant in southern California waters, it is not common north of Point Conception. This fish is abundant in thick kelp beds and slightly rocky habitat. They are known to reach a length just under one meter (3 feet, Miller and Lea 1972) and a weight of 16.5 kg (36.25 pounds, Fitch 1968). The Indians could have captured California sheephead by hook and line, in traps, or by free diving, especially on offshore islands.

California sheephead remains also have been recovered from many other midden sites: Arroyo Grande, Point Mugu, Arroyo Sequit, Century Ranch, La

Jolla, Santa Catalina Island and San Pedro (Wallace 1962; Follett 1933; Mitchell 1959; Follett 1963a, 1963b; Shumway, Hubbs and Moriarty 1961; Meighan and Eberhart 1953; Meighan 1959; Frey 1974), and from Orange (Fitch 1967), Ventura (Fitch 1969a; Tartaglia 1976) and Los Angeles Counties (Tartaglia 1976).

Material: 1 jaw tooth. Fig. 5C.

#### Merlucciidae – Hakes

*Merluccius productus* – Pacific hake. — The Pacific hake ranges from Magdalena Bay, Baja California, to Alaska and along the Asiatic coast; there is an isolated population in the Gulf of California. They have been known to reach a length of nearly one meter (3 feet, Fitch 1972) and a weight of 3.6 to 4.5 kg (8 to 10 pounds, Fitch 1972). Although found from the surface to depths of 1000 m (3000 feet, Miller and Lea 1972), most individuals off California inhabit waters shallower than 270 m (750 feet, Fitch 1972). The Pacific hake is a schooling fish that moves inshore and offshore much the same as the northern anchovy, and is preyed upon heavily by marine mammals. No Pacific hake remains were recovered from the samples examined by us, but Fitch (1969b) reported jaw fragments and vertebrae of Pacific hake from a sample (general sample) he examined from the slope region of Rincon Hill.

Pacific hake remains have been recovered from Indian midden sites in Ventura and San Luis Obispo Counties and at Tomales Bay and Point St. George (Fitch 1969a, 1969b, 1972; Follett 1968; and Gould 1966).

Material: Jaws, vertebrae. Not figured.

#### Sciaenidae – Croakers

*Cynoscion nobilis* – White seabass. — White seabass are found from Magdalena Bay, Baja California, to Juneau, Alaska, with an isolated population in the northern Gulf of California. Although reported to grow as large as 41 kg (90 pounds, Miller and Lea 1972), a 38 kg (83.75 pound, Fitch and Lavenberg 1971) individual is recognized as the world record. The white seabass prefers depths of 21 to 45 m (75 to 150 feet, Fitch and Lavenberg 1971) but has been taken from surface waters to depths of 121 m (400 feet, Miller and Lea 1972). Although large adults have few natural enemies, the largest of the two sagittae that we recovered at SBA-1 was eroded, indicative of digestive wear possibly due to consumption by a large predator. Otoliths of *C. nobilis* have been used by California's Indians for necklace ornaments (Fig. 7). The Chumash probably caught white seabass on hook and line while fishing just offshore.

*C. nobilis* remains have been found at Malaga Cove and Santa Catalina Island (Walker 1951; Meighan 1959), Arroyo Sequit and Century Ranch sites (Follett 1963a, 1963b; Mitchell 1959), Ventura (Fitch 1969a, 1975; Tartaglia 1976), San Nicolas Island (Charles Rozaire, Natural History Museum of Los Angeles County, personal communication), Marin (Follett 1974), Contra Costa (Follett 1975b) and Los Angeles Counties (Tartaglia 1976), and a midden

site at Punta Pequena, San Juanico Bay, Baja California (Huddleston, unpublished data).

Material: 2 otoliths. Figs. 4A, B.

*Genyonemus lineatus* – White croaker. — White croakers attain lengths to 412 mm (15.4 inches, Miller and Lea 1972). They have been found from Magdalena Bay, Baja California, to Vancouver Island, British Columbia, but are not common north of San Francisco Bay. White croakers prefer sandy or muddy bottom habitat and frequently are taken in shallow waters, although they have been known from depths of 188 m (330 feet, Miller and Lea 1972). A random sample of 100 *G. lineatus* otoliths from SBA-1 ranged in size from 7.0 to 12.5 mm representing fish from 152 to 266 mm in length. This narrow size range indicates a selective method of fishing, probably the use of gill nets.

Remains of *G. lineatus* were reported previously from SBA-1 and near Ventura (Fitch 1969b, 1969a, 1975), Conejo Rock shelter and a site near La Jolla (Follett 1965; Shumway et al. 1961), San Diego County (Follett 1976) and from a site in San Pedro (Frey 1974).

Material: 932 otoliths. Fig. 4C.

*Seriphus politus* – Queenfish. — This fish is found from west of Uncle Sam Bank, Baja California, to Yaquina Bay Oregon, but is rare north of Monterey. Queenfish attain lengths of 305 mm (12 inches Fitch 1972) and a weight just over 284 g (10 ounces, Fitch 1972). They prefer much the same habitat as the white croaker, and most of the individuals probably were captured in gill nets along with the white croakers. Queenfish are not taken as easily by hook and line as white croakers, but it is possible that some were captured that way.

Fitch (1969a, 1972, 1975) reported *S. politus* otoliths from sites in Ventura and San Luis Obispo Counties.

Material: 42 otoliths. Fig. 4D.

#### Scombridae – Mackerels and Tunas

*Pneumatophorus japonicus* – Pacific mackerel. — This transpacific species is found in the eastern Pacific from Chile to the Gulf of Alaska. Attaining a length of 635 mm (25 inches, Miller and Lea 1972) and a weight of 2.9 kg (6-½ pounds, Miller and Lea 1972), this schooling species is found from the surface to depths of 45.5 m (150 feet, Miller and Lea 1972). The Pacific mackerel, like the bonito, will take nearly any bait, and the Indians probably captured them by the use of hook and line.

Follett (1963a, 1963b, 1965) reported Pacific mackerel remains from two sites in Los Angeles County and from the Conejo Rock Shelter in Ventura County. Fitch (1969a, 1975) reported their remains from midden sites near Ventura, and Follett (1976) reported their occurrence from a site in San Diego County. They have also been reported from a midden site at Cape Brinera (Sidimi) USSR (Besednov 1973).

Material: 4 otoliths. Figs. 4E.; 6A.

*Sarda chiliensis* – Pacific bonito. — The schooling Pacific bonito ranges

from Chile to the Gulf of Alaska but is absent in tropical waters and uncommon north of Point Conception. They have been reported to attain a length of just over one meter (40 inches, Miller and Lea 1972). A 686-mm (27 inches, Fitch 1969a) specimen weighed 4.8 kg (10-½ pounds, Fitch 1969a). This fish usually travels at or near the surface and will take nearly any bait. The Indians probably captured Pacific bonito with hook and line. Follett (1933, 1963a, 1963b) reported Pacific bonito remains from two middens in Los Angeles County and from one in Ventura County. Fitch (1969a) noted their remains from a Ventura County midden and Tartaglia (1976) noted them from sites in Ventura and Los Angeles Counties.

Material: 33 dentaries. Fig. 6B.

#### Scorpaenidae – Rockfishes

*Sebastes atrovirens* – Kelp rockfish. — The kelp rockfish ranges from Pt. San Pablo, Baja California, to Timber Cove, Sonoma County. They have been known to attain a length of 425 mm (16-¾ inches, Fitch 1969a) and a weight of just over 1.4 kg (3 pounds, Fitch 1969a). Kelp rockfish inhabit depths from subtidal to 45.5 m (25 fathoms, Phillips 1957) but are most abundant at about 10 m or less. The inhabitants of SBA-1 probably caught kelp rockfish by hook and line in shallow water just offshore or in traps.

Remains of *S. atrovirens* also have been reported from a midden in San Luis Obispo County (Fitch 1972).

Material: 1 otolith. Fig. 4F.

*Sebastes diploproa* – Splitnose rockfish. — This deep-living rockfish ranges from north of San Martin Island, Baja California, to Prince William Sound, Alaska. They are known to reach a length of 457 mm (18 inches, Miller and Lea 1972) and a depth of 473 m (250 fathoms, Phillips 1957). The single broken otolith recovered from SBA-1 showed little digestive wear. Because this species has not been known to come nearer the surface than 212 m (700 feet, Miller and Lea 1972) it may not have been captured directly by the Indians. We suspect that it was derived from the digestive system of a deep-feeding predator such as a marine mammal, which was captured by the Indians.

Remains of *S. diploproa* have not been reported from any other midden.

Material: 1 otolith. Fig. 4H.

*Sebastes goodei* – Chilipepper. — *S. goodei* have been captured from Magdalena Bay, Baja California, to near Cape Scott on the northwest coast of Vancouver Island, British Columbia. They range from the surface to great depths. The deepest recorded specimen was taken at 327 m (1080 feet, Miller and Lea 1972); the largest specimen captured measured 559 mm (22 inches, Phillips 1957). Chilipeppers frequently are captured by sport fishermen, but only from skiffs or boats anchored or drifting over deep rocky habitat. Although young individuals usually remain in shallow water, all of the otoliths we recovered at SBA-1 were from adult fish. The Indians probably captured this fish by hook and line while fishing in deep water.

Follett (1963a) reported *S. goodei* from a midden in Los Angeles County. Material: 9 otoliths. Fig. 4G.

*Sebastes miniatus* – Vermilion rockfish. — Ranging from San Bonito Island, Baja California, to Vancouver Island, British Columbia, this rockfish has been captured at a depth of 200 m (110 fathoms, Phillips 1957); juveniles prefer shallow water. Vermilion rockfish attain lengths of 762 mm (30 inches, Phillips 1957). The Indians probably caught this species while fishing with hook and line in intermediate depths. Remains of vermilion rockfish have been recovered from Indian middens at Pt. St. George and Scripps Estate (Gould 1966; Shumway et al. 1961).

Material: 2 otoliths. Fig. 4I.

*Sebastes* spp. – (Species undetermined). — At least 58 species of rockfishes (genus *Sebastes*) inhabit waters off California. Some of the fragmented *Sebastes* otoliths we recovered from SBa-1 probably belonged to one or more of these species.

#### Serranidae – Sea basses

*Stereolepis gigas* – Giant sea bass. — Sometimes placed in the family Percichthyidae (temperate basses), the giant sea bass has been taken from the Gulf of California to Humbolt Bay, but is not abundant north of the Channel Islands off southern California. A record specimen weighing 252 kg (557 pounds, Fitch and Lavenberg 1971) was caught in 1962. An individual weighing 197 kg (435 pounds, Fitch and Lavenberg 1971) was found to be 72 to 75 years old (Fitch and Lavenberg 1971). Large individuals prefer rocky bottom habitat and depths of 35 to 46 m, just outside kelp beds. During the spawning period, which is from June to September, large individuals are relatively abundant in shallow waters where they can be taken easily with hook and line.

Fitch (1969a) reported branchiostegal rays of *S. gigas* from a midden near Ventura.

Material: 1 vertebra. Fig. 5I.

#### Sphyraenidae – Barracudas

*Sphyraena argentea* – Pacific barracuda. — Ranging from Cape San Lucas, Baja California, to Kodiak Island, Alaska, the Pacific barracuda reaches a length of 1.2 m (46-½ inches, Fitch and Lavenberg 1971) and a weight of 7.7 kg (18 pounds 3 ounces, Fitch and Lavenberg 1971). There is an unverified record of 1.5 m. Most common south of Morro Bay, this schooling species remains near shore in depths from the surface to 18.8 m (60 feet, Miller and Lea 1972). Schools of juveniles will sometimes wander into shallow bays. Although today barracudas often are captured by gill nets, the inhabitants of SBa-1 probably took barracudas by hook and line.

Remains of Pacific barracuda have been recovered from midden sites in Ventura (Fitch 1969a, 1975; Follett 1933, 1965; Tartaglia 1976), Los Angeles

(Follett 1963b, 1969; Tartaglia 1976) and San Diego Counties (Follett 1976). Material: 6 otoliths. Figs. 5D, 6C, D, E.

#### Xiphiidae – Swordfish

*Xiphias gladius* – Swordfish. — This species is found worldwide in warm and temperate seas, but in the eastern Pacific it is found from Chile to Oregon. The swordfish occurs off our coast only during a few summer months each year. They frequently rest at the surface but have been seen at depths greater than 666 m (2000 feet, Fitch and Lavenberg 1971). The largest recorded specimen measured 4.5 m (14 feet 11- $\frac{1}{4}$  inches, Fitch and Lavenberg 1971) and weighed 535 kg (1182 pounds, Fitch and Lavenberg 1971). This specimen was captured off the coast of Chile in 1953. The Indians probably obtained swordfish with harpoons during summer months.

Swordfish remains have been reported from midden sites in Ventura County (Fitch 1969a; Follett 1933) and from the Burton Mound Site (Harrington 1928).

Material: 7 vertebrae. Figs. 5F, G.

#### ELEMENTS OF IDENTIFICATION

Otoliths were by far the most important element in identifying teleosts from SBA-1. Twenty of the 29 species (representing 69 percent) were identified from otoliths; the next most useful elements were premaxillaries, pharyngeal bones, dentaries and vertebrae. Four species were identifiable by each of these elements, representing only 14 percent of the teleost species. For identifying elasmobranchs, which do not possess otoliths, teeth were the most important element. All 16 of the sharks were identifiable on the basis of teeth alone. One species also was identified from dermal denticles and another by a dorsal fin spine, each representing less than 6.5 percent of the elasmobranch species. Small mesh screens are not only necessary for retaining small otoliths, but are important in the collecting of elasmobranch remains. From the  $\frac{1}{4}$ -inch screenings a total of four species could be identified; from the 18-mesh, eight species; and from the 30-mesh, 11 species. Six species of four families were retained only by the 30-mesh screen. Utilizing screens smaller than 30- or 32-mesh is not practical. There are otoliths which will pass through such screens, but they represent fishes that would not likely have been utilized as food by the Indians who inhabited these sites. It would be desirable to examine a large midden sample with 30-mesh screens, but if a shortage of time makes this impossible at least a 6 $\times$ 6-inch control column should be given this fine screening examination.

#### OTOLITHS IN ORNAMENTATION

A necklace in the Natural History Museum of Los Angeles County (LACM) no. A. 5600/99 from a San Nicolas Island site, mentioned by Fitch



TABLE 1 (Continued)

Scientific name	otolith	pre-max.	pharyngeal bone	vertebrae	dentary	jaw teeth	pharyngeal teeth	scales	palatines	dorsal spines	caudal stings
Teleosts (continued)											
<i>Seriola dorsalis</i>				1							
<i>Seriphus politus</i>	42										
<i>Sphyaena argentea</i>	6	X		X	X					X	
<i>Trachurus symmetricus</i>	1										
<i>Xiphias gladius</i>				7							
(*) Wing spines.											
(**) Dermal denticles.											

(1969a), is constructed of white seabass otoliths and *Olivella* shells (Fig. 7). The 30 otoliths (14 right sagittae + 16 left sagittae) have been drilled through the thick knob-like protrusion on the outer face. The otoliths apparently were drilled part way through on one side and then turned over and completed from the other side. The hardness of otoliths as well as their vulnerability to fracture when drilling pressure is applied indicates that great patience was required to complete this necklace. None of the otoliths from SBa-1 showed any signs of such drilling or unnatural modification.

Also in the LACM collection is an artifact (no. L.2100. A. 902.70-1) from another midden in Los Angeles County (LAN-174) in which white croaker otoliths were used in a decoration (Fig. 8) believed to be a portion of a water jug (C. Rozaire, personal communication). Small pebbles and shell fragments are embedded randomly in the asphalt; these are probably a natural encasement. A faint fabric-like pattern is detectable on part of the asphalt surface. Sixteen white croaker sagittae (22 present in an earlier photograph) also are embedded in the asphalt in an "L"-shaped pattern. All of the otoliths are embedded with the outer face showing and nearly all with the end pointing inward. There is no apparent pattern in the placement of right and left sagittae. Three white croaker sagittae were loose in the bottom of the tray and several "empty" otolith impressions can be seen in the "L"-shaped pattern in the asphalt. It is assumed that the otoliths are merely a form of decoration; no other explanation is suggested at present. None of the otoliths recovered from SBa-1 shows any asphalt or tar residues to suggest their possible use as ornaments, trinkets or fetishes.

#### COMPARISON BETWEEN THE FISH REMAINS AND FISHING TECHNIQUES OF SBa-1 AND OTHER SITES

The oceanic environment adjacent to SBa-1 and Ven-3 in Ventura County is nearly identical, both sites possessing offshore kelp beds, sandy regions and

nearby rocky habitat; and similar species of fishes inhabit their coastal regions. The similarity of the fishing cultures of these two villages is reflected in the fish remains (Table 2). Thirty-one (72 percent) of the 41 species from SBA-1 (which likely were captured by the inhabitants as food items) also were recovered from the Ven-3 midden. Of the species thought to have been captured directly by the inhabitants, 48 percent from SBA-1 probably were captured by hook and line compared to 52 percent from Ven-3. Twenty-eight percent of the species of SBA-1 probably were captured by gill nets compared to 33 percent from Ven-3. Probable beach seine captures accounted for 40 percent of the species from SBA-1 and 44 percent of the species from Ven-3. Eight percent of the species of SBA-1 were captured by other methods compared with 11 percent of the species of Ven-3. These figures are only approximate since in several cases some of the species probably were captured by more than one method. Unfortunately, there are no age-data correlations between our samples from SBA-1 and those from the Ven-3 site reported by Fitch (1969a). It is apparent that these two villages were utilizing similar fishing techniques and were oriented strongly towards a marine fishery. This is in contrast with the inhabitants of Ora-190 in Orange County, who apparently utilized only hook and line and traps in taking fish (Fitch 1967). The inhabitants of SLO-2, San Luis Obispo County, also were apparently not fishery oriented, although they occupied the same site for several thousand years: "There is no evidence that they progressed beyond a hook and line fishery . . ." (Fitch 1972).

### ELASMOBRANCH REMAINS

The relative scarcity of shark teeth in the SBA-1 midden when compared to the total number of vertebrae recovered is perhaps the result of one or two factors. First, sharks could have been decapitated at or near their point of capture or at a "cleaning station", reducing the total weight to be carried and the chance of being "bitten". Second, the teeth could have been utilized in some form of ornamentation or other artifact usage, but there is no indication of this.

### ANALYSIS OF FISH REMAINS

In attempting to analyze the fishery habits of the inhabitants of SBA-1 we selected only the bony fishes for which an approximate minimum number of individual (MNI) fish could be determined. Further, we utilized only those species that were presumed to be food sources. We omitted the anchovies because it was not possible to determine how many of the otoliths were from stomachs of predators captured by the Indians. The number of otoliths for each species was divided by two (since each fish has two sagittae), a practice which assumes that both right and left sagittae were recovered, but if not true, establishes a minimum number. For other elements (identifications based solely on vertebrae, etc.) only a MNI of one was interpreted, although in the case of the

TABLE 2

Scientific name	Occurrence in Ven-3	Probable method of capture			
		Hook and line	Beach seine	Gill net	Other
Elasmobranchs					
<i>Alopias vulpinus</i>					X
<i>Carcharodon carcharias</i>					X
<i>Cephaloscyllium ventriosum</i>	X				X
<i>Dasyatis dipterura</i>		X			X
<i>Galeorhinus zyopterus</i>	X	X			
<i>Heterodontus francisci</i>	X	X			
<i>Isurus oxyrinchus</i>	X	X			X
<i>Mustelus californicus</i>	X	X	X		
<i>Myliobatis californica</i>	X	X	X		
<i>Notorynchus maculatus</i>	X	X			
<i>Prionace glauca</i>		X			
<i>Raja</i> spp.	X	X			
<i>Rhinobatos productus</i>	X		X		
<i>Squalus acanthias</i>	X	X			
<i>Squatina californica</i>	X	X			
<i>Triakis semifasciata</i>	X	X	X	X	
Teleosts					
<i>Amphistichus argenteus</i>	X		X		
<i>Atherinopos affinis</i>	X		X		
<i>Atherinopsis californiensis</i>	X		X	X	
<i>Cymatogaster aggregata</i>			X		
<i>Cynoscion nobilis</i>	X	X			
<i>Damalichthys vacca</i>	X		X		
<i>Engraulis mordax</i>	X		X		
<i>Genyonemus lineatus</i>	X			X	
<i>Hyperprosopon argenteum</i>	X		X		
<i>Merluccius productus</i>	X	X			
<i>Oxyjulis californica</i>				X	
<i>Paralichthys californicus</i>	X	X	X		
<i>Phanerodon furcatus</i>	X		X	X	
<i>Pimelometopon pulchrum</i>	X	X			X
<i>Pneumatophorus japonicus</i>	X	X			
<i>Sarda chiliensis</i>	X	X			
<i>Sardinops caeruleus</i>			X	X	
<i>Sebastes atrovirens</i>		X			
<i>Sebastes goodei</i>		X			
<i>Sebastes miniatus</i>		X			
<i>Seriphus politus</i>	X			X	
<i>Sphyræna argentea</i>	X	X			
<i>Stereolepis gigas</i>	X	X			
<i>Trachurus symmetricus</i>	X	X		X	
<i>Xiphias gladius</i>	X				X

swordfish the seven vertebrae could have come from seven different individuals.

Since it was not possible to determine the MNI for the elasmobranchs because of the abundance of teeth in a single jaw, no attempt was made to indicate preference or selective fishing for this group. According to present-day taste standards the thresher shark is considered choice, followed closely by the white shark and the shortfin mako, but all of these are fast-swimming forms and not easily taken (S.P. Applegate, personal communication).

A minimum of 538 bony fishes was represented by the teleost remains. Although we considered 23 species to be potential food fishes, 19 of these constituted only 6.4 percent MNI; whereas white croaker constituted 86.6 percent MNI. Single representatives of such large fishes as the giant sea bass and swordfish would yield large poundage of food, but the relative scarcity of their remains in SBa-1 tends to indicate only limited or occasional usage and we do not believe that they were relied upon heavily for food. The large percentage of white croaker suggests strongly that the Indians either preferred this species or else it was easy to catch and not undesirable.

Although a hook and line fishery would account for the greatest diversity of teleostean species when compared with other fishing methods used by the Indians, it could not have accounted for more than 6.6 percent of the MNI. Beach seining probably took the second greatest number of species, but only 2.76 percent MNI. Fewer species were taken by gill netting but this method apparently accounted for nearly 92 percent MNI. All other methods yielded only a fraction of one percent MNI. Gill netting is indicated as the primary method of fish gathering.

## DISCUSSION

Fish remains were very scarce in all samples obtained from the slope of Rincon Hill. The slope area is believed to be an older region of occupation, estimated to be 2000 to 1000 B.C. (Evans et al. 1968). Three radiocarbon dates obtained from samples collected by Lyon and Harrison in 1959-60, were 1320 B.C.  $\pm$  250 years, 1470 B.C.  $\pm$  130 years and 1580 B.C.  $\pm$  60 years (Radiocarbon 1963:290). Sufficient fish remains were recovered from Rincon Hill to indicate that fish were utilized in the Indians' diet. The lack of variety, the absence of open ocean or deep dwelling species, and the overall sparseness of the fish remains indicate a minimal usage of fish as a food source. This probably reflects inadequate technical skills or inefficient fishing methods at that stage of cultural development.

This is in contrast with the lower and more recently occupied region of the SBa-1 complex. Based on the fish material we recovered the occupants of the lower area displayed highly advanced fishing techniques and depended upon the sea as a primary source of food. The occupation of this lower region persisted into historic times.

Among the samples from the lower region were remains of many pelagic or open ocean fishes, species which could not have been captured from shore.

Based on the life habits of the fishes (presumably these habits have not changed in the last several thousand years), the inhabitants of this lower region were utilizing crafts to carry them well beyond the surf zone and kelp beds where they harpooned swordfish, white sharks, thresher sharks, blue sharks and shortfin makos. With deep hook and line fishing they were able to take skates, spiny dogfish and rockfish; closer to shore, hook and line methods were practical in kelp bed areas to obtain California sheephead. In shallow waters and surf zones beach seines would explain the presence of smaller-mouthed fishes such as topsmelt, jacksmelt, and some of the small surfperches as well as bat rays and sting rays. Use of gill nets was demonstrated by the abundance of white croaker otoliths of nearly identical sizes. Fishes that inhabit shallow water and are approached easily, such as the shovelnose guitarfish and the horn shark, could have been taken by hand or spear.

A variety of fishing gear has been reported for the Chumash: plank canoes, harpoons, fish spears, harpoon arrows, shellfish hooks, bone fish hooks, traps and nets (Hoover 1973; Richie and Hager 1973). Concerning the SBA-1 sites only shell fish hooks have been reported (Evans *et al.* 1968). Evans *et al.* (1968:24-25) described a "donut-shaped stone" as follows: "One artifact . . . is a round cobble which has had a cylindrical hole (which) contains a large amount of asphaltum." This stone was nine centimeters in diameter, 6.8 cm thick and had a bore diameter of 3 cm. It is obvious from this description that they were dealing with a stone fishing weight (sinker) probably similar to those illustrated by Hoover (1973, plate 4, fig. B and C). Vague descriptions of "pointed bone artifacts" and "hammered stones" by Evans *et al.* (1968) render it impossible to determine if some of these materials were remnants or represented bone fish hooks, bone gorges, or fishing weights. Such artifacts should have been present at the site.

Olson (1971) noted that "ear bones" could at times be of value in age determination but failed to mention their significance in establishing specific identifications. Further, he suggests that the lack of fish remains in some sites could be due to the possible cartilaginous skeletal elements such as found in *Salmo*; this theory overlooks the fact that *Salmo* otoliths, as with most otoliths, are aragonitic in composition. Even fishes which possess poorly ossified skeletal structures, if present in the midden, would leave behind their otoliths.

In his discussion on shark remains, Olsen (1971:2-6) states, "A number of cartilaginous fish are poisonous when eaten by man, and it is not known whether the recovered shark and ray elements are the residue of meals or represent some other use by man." S.P. Applegate (personal communication) states that none of the sharks or rays occurring in waters off North America is poisonous when eaten by man. Therefore, there is no reason to assume that the shark and rays recognized in a midden site do not constitute food items.

Unfortunately the randomness of our samples and the disrupted state of the Rincon site (SBA-1) prevented a study of an interesting transgression of the SBA-1 inhabitants from a terrestrial hunting to a marine-oriented people.

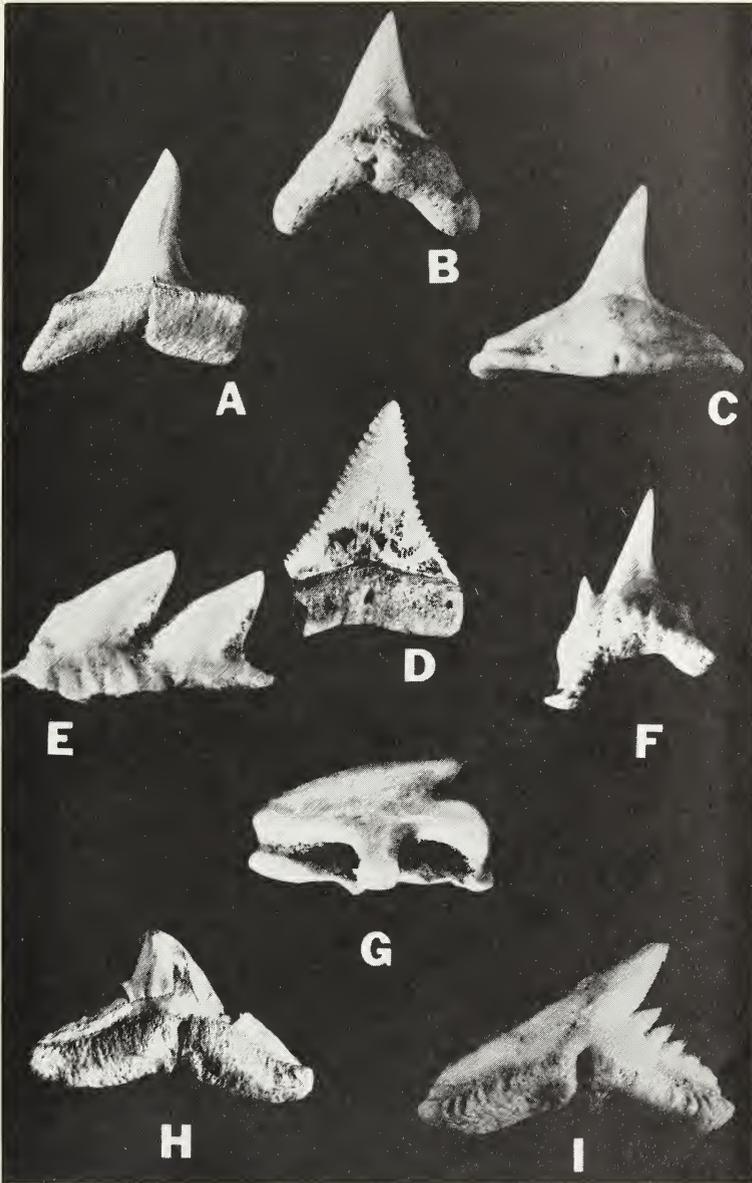


FIGURE 1. A *Isurus oxyrinchus* tooth, 18.9 mm high; B. *Alopias vulpinus* tooth, 6.0 mm high; C. *Squatina californica* tooth, 3.8 mm high; D. *Carcharodon carcharias* tooth, 22.5 mm high; E. *Notorynchus maculatus* incomplete tooth, 9.0 mm length of base; F. *Cephaloscyllium ventriosum* tooth, 2.7 mm high; G. *Squalus acanthias* tooth, 3.7 mm length of base; H. *Prionace glauca* worn tooth, 8.5 mm high; I. *Galeorhinus zyopterus* tooth, 4.1 mm high.

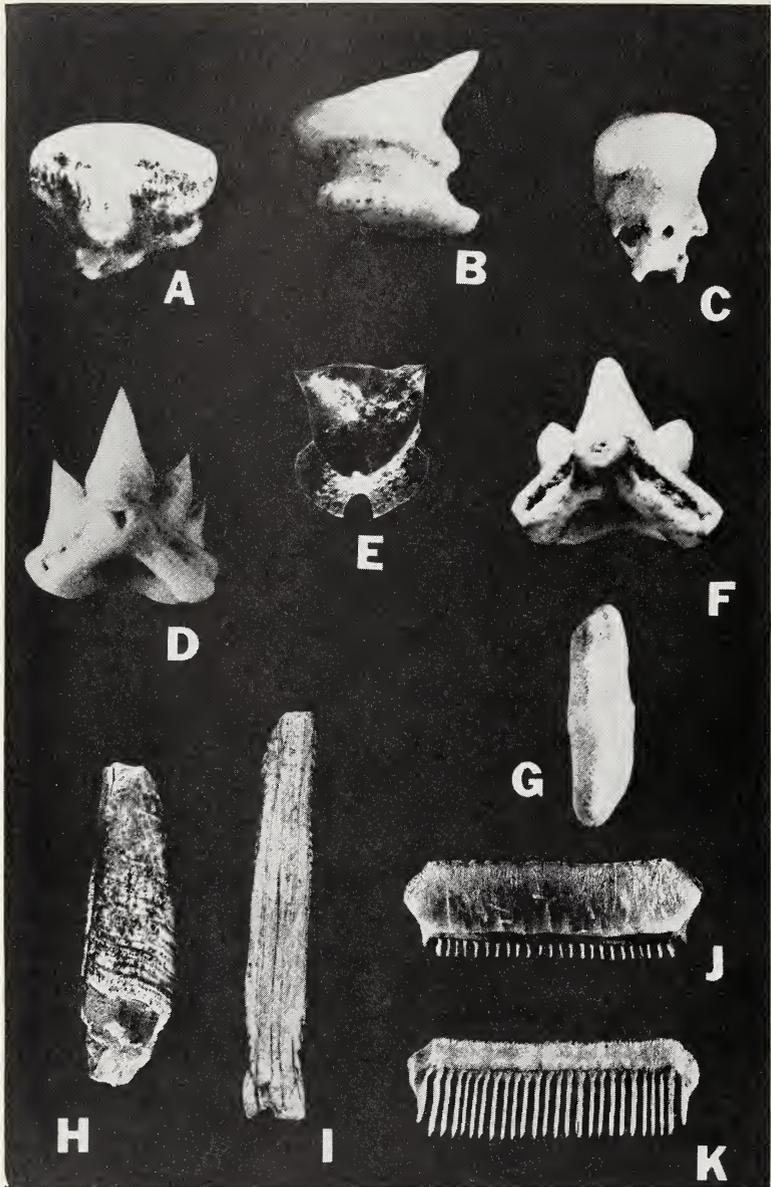


FIGURE 2. A. *Mustelus californicus* tooth, 1.1 mm high; B. *Raja* sp. tooth, 2.1 mm high; C. *Rhinobatos productus* tooth, 1.4 mm high; D. *Triakis semifasciata* tooth, 3.2 mm high; E. *Dasyatis dipterura* tooth, 1.7 mm high; F. *Heterodontus francisci* anterior tooth, 2.9 mm high; G. *Heterodontus francisci* posterior tooth, 7.6 mm high; H. *Heterodontus francisci* incomplete dorsal spine, 31.4 mm; I. Myliobatoidei incomplete caudal sting, 49.0 mm; J. *Myliobatis californica* dorsal view median tooth, 26.3 mm length of base; K. *Myliobatis californica* ventral view median tooth.

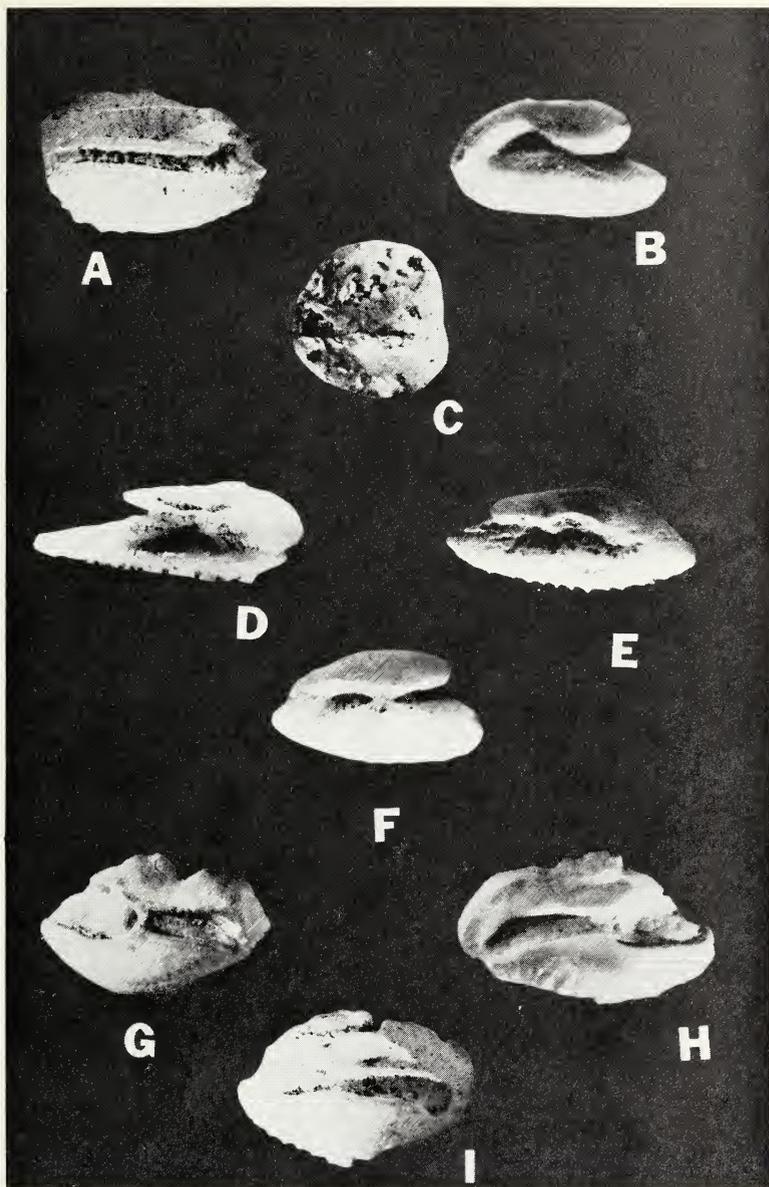


FIGURE 3. A. *Atherinops affinis* left sagitta, 5.1 mm; B. *Neoclinus uninotatus* left sagitta, 1.9 mm; C. *Porichthys notatus* eroded right sagitta, 1.3 mm; D. *Sardinops caeruleus* right sagitta, 3.5 mm; E. *Engraulis mordax* right sagitta, 4.0 mm; F. *Oxyjulis californica* left sagitta, 1.9 mm; G. *Cymatogaster aggregata* right sagitta, 6.7 mm; H. *Phanerodon furcatus* right sagitta, 8.4 mm; I. *Hyperprosopon argenteum* right sagitta, 6.7 mm.

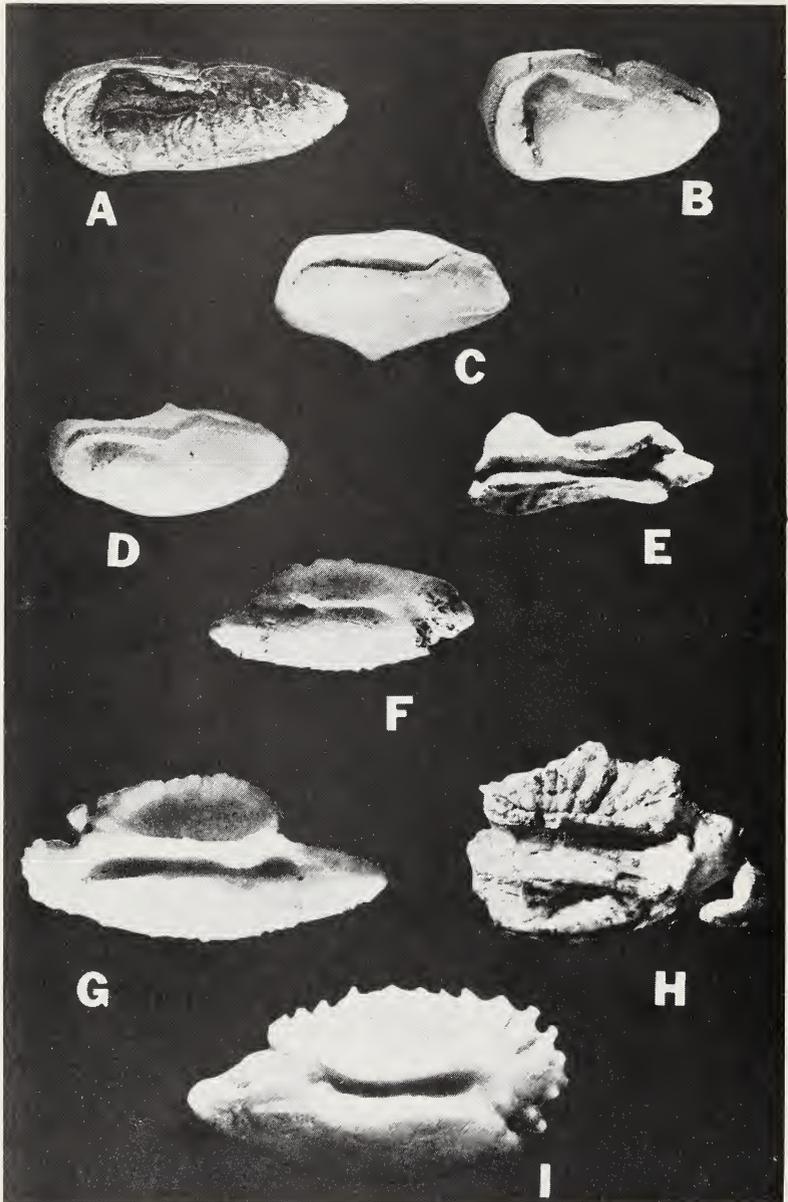


FIGURE 4. A. *Cynoscion nobilis* eroded left sagitta, 25.7 mm; B. *Cynoscion nobilis* left sagitta, 21.1 mm; C. *Seriphus politus* left sagitta, 9.3 mm; D. *Genyonemus lineatus* left sagitta, 18.0 mm; E. *Pneumatophorus japonicus* left sagitta, 5.3 mm; F. *Sebastes atrovirens* right sagitta, 10.1 mm; G. *Sebastes goodei* left sagitta, 19.8 mm; H. *Sebastes diploproa* eroded right sagitta rostrum missing, 10.2 mm; I. *Sebastes miniatus* right sagitta, 18.7 mm.

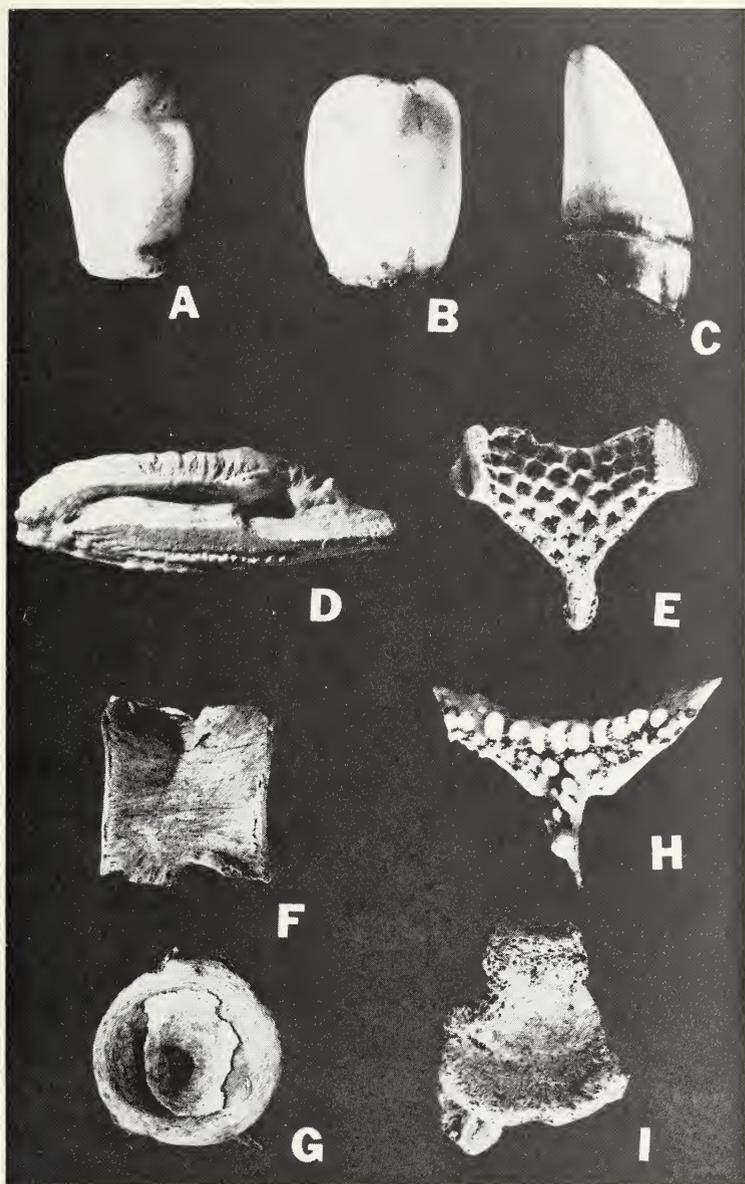


FIGURE 5. A. *Amphistichus argenteus* pharyngeal tooth, 4.8 mm; B. *Damalichthys vacca* pharyngeal tooth, 6.0 mm high; C. *Piomelometopon pulchrum* tooth, 7.3 mm high; D. *Sphyræna argentea* left sagitta, 15.2 mm; E. *Damalichthys vacca* lower pharyngeal bone, 26.2 mm wide; F. *Xiphias gladius* vertebra, 46.9 mm length; G. *Xiphias gladius* end view of vertebra, 47.6 mm diameter; H. *Oxyjulis californica* lower pharyngeal bone, 5.2 mm wide; I. *Stereolepis gigas* vertebra, 60.0 mm high.

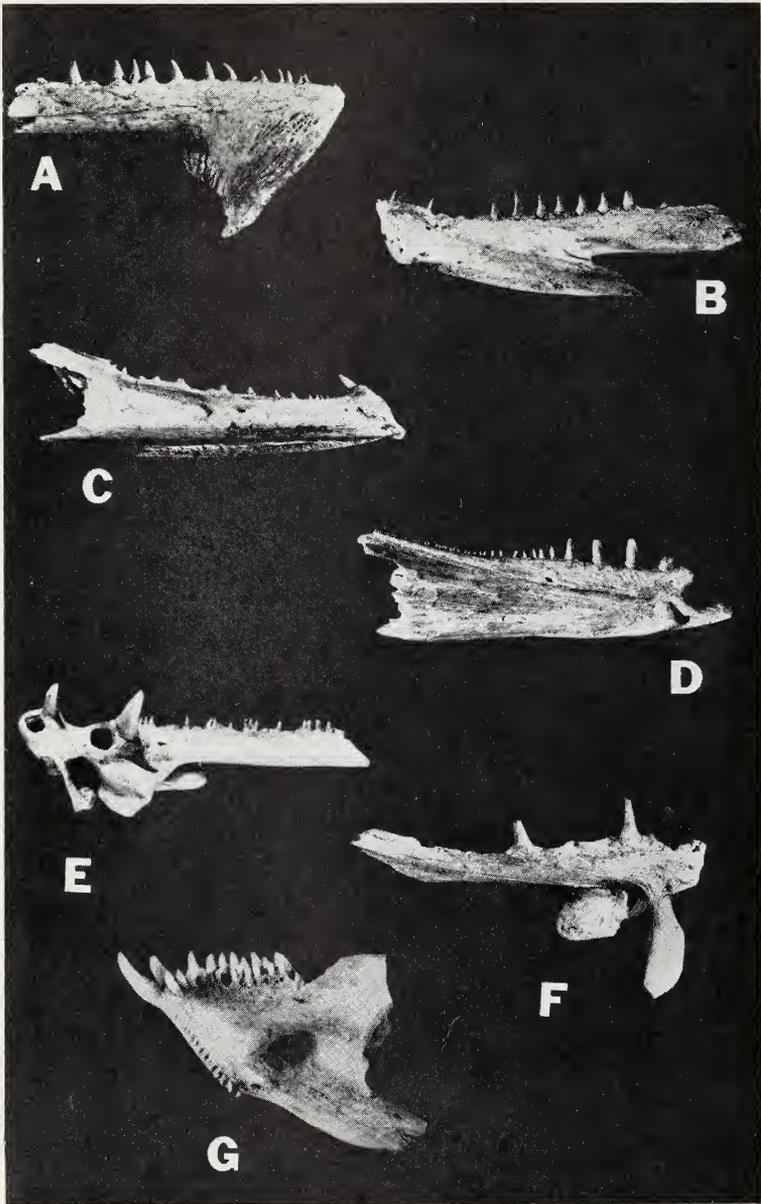


FIGURE 6. A. *Pneumatophorus japonicus* incomplete right dentary, 42.9 mm B. *Sarda chiliensis* left dentary, 56.3 mm; C. *Sphyraena argentea* right dentary, 64.4 mm; D. *Sphyraena argentea* right palatine, 51.8 mm; E. *Sphyraena argentea* incomplete right pre-maxillary, 30.3 mm; F. *Paralichthys californicus* incomplete left pre-maxillary, 45.1 mm; G. *Oxyjulis californica* right dentary, 10.9 mm.

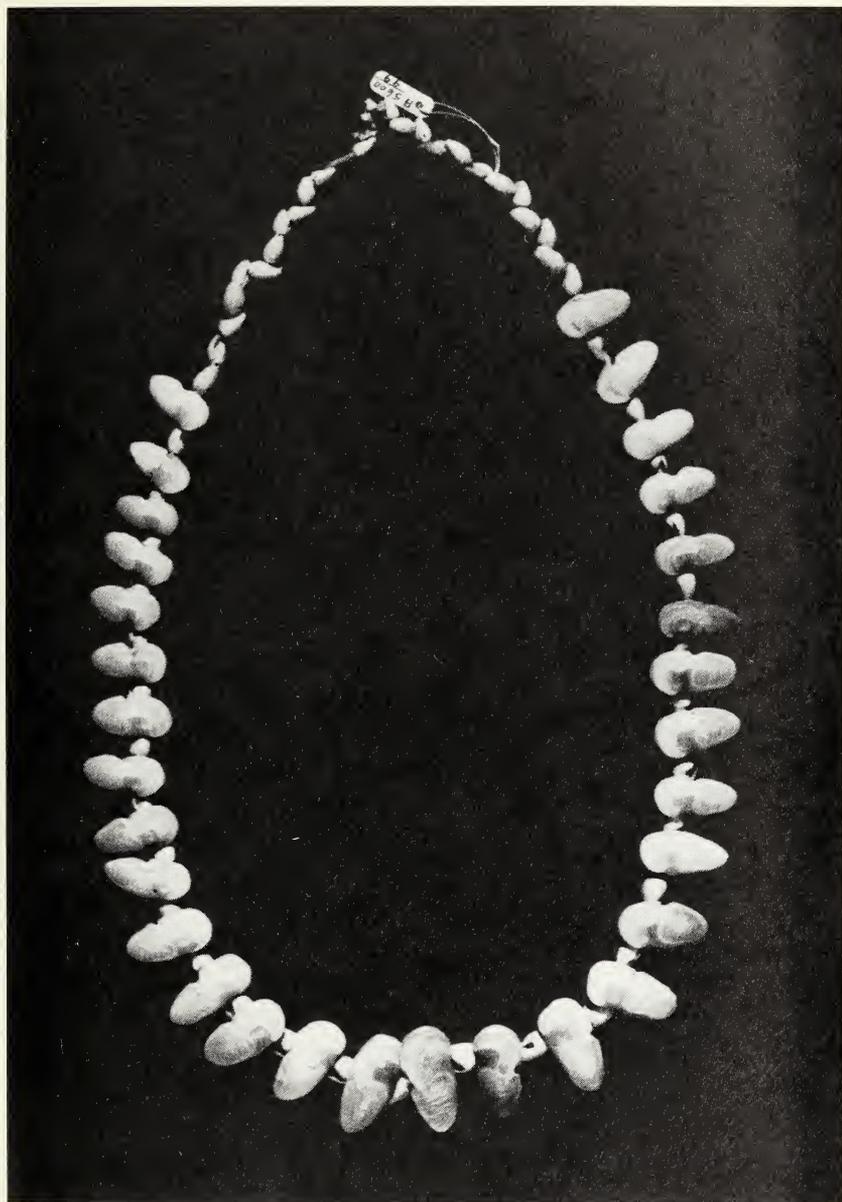


FIGURE 7. Necklace, LACM no. 5600/99, constructed with *Cynoscion nobilis* otoliths and *Olivella* shells.



FIGURE 8. Fragment of "water jug" LACM no.L.2100.A.902.70-1 containing otoliths of *Genyonemus lineatus*.

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LATE MIOCENE MARINE BIRDS  
FROM ORANGE COUNTY, CALIFORNIA

*By* HILDEGARDE HOWARD

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CONTRIBUTIONS IN SCIENCE

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# LATE MIOCENE MARINE BIRDS FROM ORANGE COUNTY, CALIFORNIA<sup>1</sup>

By HILDEGARDE HOWARD<sup>2</sup>

ABSTRACT: Bone fragments from five sites in the Late Miocene Monterey Formation at Laguna Niguel, Orange County, California, represent at least 14 species of marine birds, *Gavia brodkorbi* n. sp., *Diomedea* ?*californica*, *Diomedea* sp., *Puffinus barnesi* n. sp., *Oceanodroma* sp., *Osteodontornis orri* Howard, *Morus lompocanus* (Miller), *Morus magnus* n. sp., ?*Miosula media* Miller, ?*Uria* sp., ?*Cephus* sp., ?*Aethia* sp., *Fraterculini* gen. and sp. indet., and *Praemancalla wetmorei* Howard. The avifauna suggests a slightly younger phase of the Late Miocene than another avifauna previously reported from the Monterey Formation in Laguna Hills, three miles northward.

## INTRODUCTION

In 1969, during the excavation for the North American Rockwell Building (now United States General Services Administration Building) on El Lazo Road in Laguna Niguel, Orange County, California, fossiliferous sands and siltstones of the Late Miocene Monterey Formation (Clarendonian correlative) were exposed. Marine mammals and birds were collected in the actual building excavation and, from 1969 to 1976, in adjacent hillsides within a half-mile radius of the El Lazo site.

The localities, all of which bear Natural History Museum of Los Angeles County (LACM) locality numbers, are listed below (numbers in parentheses indicate the number of avian bones found). Detailed locality descriptions with reference to the San Juan Capistrano Quadrangle, U.S.G.S. 7.5 minute, 1948 edition, are on file in the Section of Vertebrate Paleontology, LACM.

LACM Loc. 3185 — Aliso Creek. From coarse yellow sand. (3)

LACM Loc. 6901 — El Lazo Road. In laminated gray to white siltstone. (1)

LACM Loc. 6902 — El Lazo Road. From coarse yellow sands overlying siltstones described in LACM 6901. (21)

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

LAWRENCE G. BARNES

STORRS L. OLSON

STUART WARTER

<sup>2</sup>Chief Curator Emeritus, Natural History Museum of Los Angeles County, 900 Exposition Boulevard, Los Angeles, California 90007.

- LACM Loc. 6906 — Site of excavation for North American Rockwell Building on El Lazo Road. In yellow sands and laminated gray siltstone. (21)
- LACM Loc. 7136 — Moulton Parkway. In phosphatic pebble bed, in a gray siltstone. (5)

### MATERIAL

Fifty-one avian bone fragments were recovered from the Laguna Niguel localities. These are in the collections of the Natural History Museum of Los Angeles County (LACM). Thirty-nine are identified and assigned to seven families.

Comparative fossil material used in connection with this study is largely in the LACM collections and includes, in addition to LACM types and referred specimens, casts of types of *Gavia concinna* Wetmore 1940; *Diomedea californica* Miller 1962; *Puffinus conradi* Marsh 1870; *P. diatomicus* Miller 1925; *P. inceptor* Wetmore 1930; *P. mitchelli* Miller 1961; *P. priscus* Miller 1961; *Osteodontornis orri* Howard 1957; *Sula willetti* Miller 1925; *Morus lompocanus* (Miller 1925); *Miosula media* Miller 1925; *Palaeosula stocktoni* (Miller 1935); and *Uria antiqua* (Marsh 1870).

In addition, the following material was made available on loan: from the Museum of Comparative Zoology, Harvard University (MCZ), referred tibiotarsus (Wetmore 1943) of *Diomedea anglica* Lydekker 1891; from the Museum of Paleontology, University of California, Berkeley (UCMP), type and reverse of type of *Miosula media* Miller 1925, and figured specimens of *Morus lompocanus* (Miller 1925:pls. 7 and 9); from the United States National Museum of Natural History (USNM), previously unreported referred humerus and ulna of *Miocepphus mcclungi* Wetmore 1940, identified by Storrs Olson.

Recent skeletal material used for comparison is largely from the LACM collections, but also includes skeletons of Alcidae obtained on loan from the Museum of Vertebrate Zoology, University of California, Berkeley (MVZ) and California State University, Long Beach (CSLB), and a skull of *Morus bassanus* lent by Pierce Brodtkorb, University of Florida, Gainesville (PB).

### HISTORICAL REVIEW

Miller (1925) was the first to document Miocene birds from marine deposits in California, naming three species of sulids, a shearwater, a godwit and an auklet from the Late Miocene diatomaceous shales of the Sisquoc Formation near Lompoc, Santa Barbara County. Within the next ten years three sites in Los Angeles County yielded Late Miocene avian fossils: the Modelo Formation at Calabasas (Miller 1929), and the Monterey Formation at Lomita and San Pedro (Miller 1935). Also, in the same decade (1925-1935), the first avian bones from the Middle Miocene (Round Mountain Silt) Sharktooth Hill

Bonebed were recorded (Wetmore 1930). By the end of 1935, 11 species had been described.

No further marine birds from the California Miocene were added until the 1950's when a flagstone quarry in the Monterey Formation in Tepusquet Canyon, Santa Barbara County, yielded two avian skeletons. Both were described under extinct families (Howard 1957a and 1957b). Later excavations in the San Fernando Valley and at El Sereno, Los Angeles County, yielded additional records of some of the previously described species and added a new sulid (Howard 1958, and Howard and White 1962). Miller (1951) described a storm petrel during this decade, from the Capistrano Formation near San Juan Capistrano, Orange County. The age of the deposit was given as Middle Miocene, but is now considered to be either Late Miocene or Early Pliocene (Fife 1974:19).

The 1960's added two Miocene bird localities in California: the Jewett Sand at Pyramid Hill, Kern County (Early Miocene) yielded a single bone described in a new family related to the cormorants (Howard 1969), and a large collection from the Monterey Formation at Leisure World, Laguna Hills, Orange County added five new species (Howard 1966a and 1968). Also, within the last 16 years, five additional species have been described from the Sharktooth Hill Bonebed (Miller 1961 and 1962; Howard 1966b; Warter 1976).

In seven of the 11 areas in California from which Miocene marine birds have been previously obtained, the specimens occur as partial skeletons or skeletal impressions on slabs of shale. Such specimens include the types of 12 of the 26 recorded species. While these specimens provide information on the proportions of the birds involved, the finer details of structure are usually not clearly preserved. Consequently it becomes difficult to compare these specimens with the isolated, mineralized bone fragments obtained from localities such as Sharktooth Hill, Pyramid Hill, Laguna Hills Leisure World, or the area discussed herein.

In the following list of species from previously recorded marine Miocene sites in California, those based on partial skeletons in shale slabs are marked with an asterisk.

#### Procellariiformes

Diomedidae: *Diomedea californica* Miller 1962; *D. milleri* Howard 1966.

Procellariidae: \**Puffinus diatomicus* Miller 1925; *P. inceptor* Wetmore 1930; *P. mitchelli* Miller 1961; *P. priscus* Miller 1961; *P. calhouni* Howard 1968; *Fulmarus hammeri* Howard 1968.

Hydrobatidae: \**Oceanodroma hubbsi* Miller 1951.

#### Pelecaniformes

Pseudodontornithidae: \**Osteodontornis orri* Howard 1957.

Sulidae: \**Sula willetti* Miller 1925; \**Sula pohli* Howard 1958; \**Morus lompocanus* (Miller 1925); *M. vagabundus* Wetmore 1930; \**Palaeosula stocktoni* (Miller 1935); \**Miosula media* Miller 1925.

Phalacrocoracidae: \**Phalacrocorax femoralis* Miller 1929.

Plotopteridae: *Plotopterus joaquinensis* Howard 1969.

Anseriformes

Anatidae: *Presbychen abavus* Wetmore 1930.

Falconiformes

Pandionidae: *Pandion homalopteron* Warter 1976.

Charadriiformes

Scolopacidae: \**Limosa vanrossemi* Miller 1925.

Alcidae: *Aethia rossmoori* Howard 1968; \**Cerorhinca dubia* Miller 1925;  
*Alcodes ulnulus* Howard 1968; *Praemancalla lagunensis* Howard  
1966.

Passeriformes

Palaeoscinidae: \**Palaeoscinis turdirostris* Howard 1957.

The species represented at Laguna Niguel bring the total for the Alcidae to five identified species, and the totals for the Procellariidae and the Sulidae to seven species each. The Order Gaviiformes (Gaviidae, 1 species) is added to the California Miocene list.

SYSTEMATICS  
ORDER GAVIIFORMES

FAMILY GAVIIDAE — LOONS  
GENUS *Gavia* FORSTER 1788  
*Gavia brodkorbi* NEW SPECIES

FIGURE 1 A, B

*Holotype*. — Complete left ulna, LACM 31173, collected by Marion J. Bohrer, 1969, from locality LACM 6906.

*Diagnosis*. — Ulna relatively short and stout; proximally, attachment for anterior articular ligament short and broad (roughly triangular), and prominently set off from shaft, with brachial impression deeply rimming its palmar edge; distal tip of external cotyla bent toward shaft, with short scar running mediad directly beneath, confining small radial impression; distally, large carpal tuberosity jutting abruptly from shaft.

*Measurements*. — Greatest length 81.0 mm, breadth across proximal cotylae 9.4 mm, breadth of shaft at middle 4.9 mm, greatest breadth of distal and (through carpal tuberosity) 11.3 mm, depth of distal end through external crest of trochlea 7.5 mm, length of attachment for anterior articular ligament 4.4 mm, breadth of same 4.0 mm.

*Etymology.* — The species is named in honor of Pierce Brodkorb in recognition of his many contributions to Paleornithology, including a review of fossil loons.

*Discussion.* — The fossil ulna is 25 mm (23.6%) shorter than the minimum for this element in four LACM specimens of the Red-throated Loon, *Gavia stellata* (Pontoppidan 1763), but is relatively stouter. The proximal radial impression is more confined than in *G. stellata*, *G. pacifica* (Lawrence 1848), or *G. immer* (Brunnich 1764). Distally, the carpal tuberosity is more square in outline than in these Recent loons. The short, broad attachment of the anterior articular ligament, also, is distinct (the attachment is longer and more oval in the Recent species).

A photograph of an ulna of *Colymboides minutus* Milne-Edwards 1867 from the Early Miocene of France, illustrated by Storer (1956, Fig. 1, g) shows the attachment of the anterior articular ligament to be broad and short. Storer, however, notes that, unlike the ulna of all Recent loons, this element of *Colymboides* lacks the groove bordering the attachment posteriorly. This groove is present in *G. brodkorbi*. Furthermore, the carpal tuberosity in *Colymboides* is less abruptly projected than in *G. brodkorbi* or in any of the Recent loons.

The only previous Miocene record of the genus *Gavia* was based on a poorly preserved tibiotarsus from the Calvert Formation, Maryland, cited by Wetmore (1941) as *Gavia* sp. Four species have been described from the Pliocene: *Gavia portisi* (Regalia 1902), Middle Pliocene of Italy; *Gavia concinna* Wetmore 1940, Early Pliocene of Florida and Middle and Later Pliocene of California; *Gavia palaeodytes* Wetmore 1943, Early Pliocene of Florida; *Gavia howardae* Brodkorb 1953, Late Pliocene of California.

According to Brodkorb (1953), who reviewed these species, *Gavia portisi* is known only from a cervical vertebra that is nearly as large as that of *G. immer*. The type of *G. concinna* is an ulna much larger than that of *G. brodkorbi* (breadth across proximal cotylae 11.6 mm), and is further distinguished by a longer attachment for the anterior articular ligament. *G. palaeodytes* is known from coracoid, humerus and femur, all equal to, or slightly larger than comparable specimens of *G. stellata*, hence larger than would be expected for *G. brodkorbi*.

*Gavia howardae* was described from an incomplete humerus with two additional humeral specimens referred (all LACM). The smallest referred humerus provides a measurement of length (from distal end to distal tip of deltoid crest) of 91.5 mm, which is 14% less than the minimum for this same measurement in *G. stellata* (106.5 mm). The type of *G. howardae* is incomplete, but appears to have been longer than the referred specimen (possibly within 7 mm of the minimum for *G. stellata*). Relative breadth is difficult to determine in these incomplete specimens. They appear, however, to be of less stocky proportions than the ulna of *G. brodkorbi*. Qualitatively there is little on which to base comparison of the humerus of *G. howardae* with the ulna of *G. brodkorbi*. However, the long, narrow attachment for the anterior articular

ligament on the humerus of *G. howardae* closely resembles the condition found in *G. stellata* and is unlikely to correspond with the unusually short, broad attachment for this ligament on the ulna of *G. brodkorbi*.

ORDER PROCELLARIIFORMES  
FAMILY DIOMEDEIDAE — ALBATROSSES  
GENUS *Diomedea* LINNAEUS 1758  
*Diomedea* ?*californica* MILLER 1962

FIGURE 2 C

*Referred material.* — Distal end of tibiotarsus, LACM 37629, from locality LACM 6906.

*Discussion.* — Four species of fossil albatrosses have been previously named: *D. californica* Miller 1962 and *D. milleri* Howard 1966b, from the Middle Miocene of Sharktooth Hill, California; *D. thyridata* Wilkinson 1969, from the Late Miocene of Australia; and *D. anglica* Lydekker 1891, from the Pliocene of England (type) and Florida (specimen referred by Wetmore 1943).

*D. milleri* was described from an ulna with referred tarsometatarsus, both of which are smaller than comparable elements of *D. nigripes* Audubon 1839. *D. thyridata*, described from a rostrum, is likened in characters and size (Wilkinson 1969) to *D. melanophris* Temminck 1828. It would appear, therefore, that both *D. milleri* and *D. thyridata* were species whose size range was below that possible for the species represented by the tibiotarsus in the present collection.

*D. californica* and *D. anglica*, both described from the tarsometatarsus, were larger species than either *D. milleri* or *D. thyridata*. The referred specimen of *D. anglica* is a distal end of tibiotarsus. This specimen (MCZ 2328) was made available for the present study (Fig. 2, B). In distal breadth LACM 37629 from Laguna Niguel is only slightly larger than MCZ 2328. It differs from the latter, however, in less depression of the supratendinal bridge, and in having a well-developed, papilla-like internal ligamental attachment. In both of these characters LACM 37629 resembles *D. exulans* Linnaeus 1758, whereas MCZ 2328 more closely resembles *D. albatrus* Pallas 1769, in which the bridge is more depressed and the ligamental attachment is only a scar. Both fossil specimens differ from *D. exulans* in more horizontal position of the lower opening of the tendinal canal, but in MCZ 2328 the opening is more restricted in lateral extent than in LACM 37629.

Comparison of the Laguna Niguel specimen with *D. californica* rests entirely on size, as no tibiotarsus assignable to this species has yet been forthcoming from the Sharktooth Hill Bonebed. A second tarsometatarsus (LACM 18203) from that locality is, however, now at hand. This is slightly larger, but otherwise similar to the holotype. The distal breadths in the two tarsometatarsi of *D. californica* are 92.3% (holotype) and 96.4% (LACM 18203, referred) of

this dimension in a tarsometatarsus (LACM Bi230) of *D. exulans*. Compared with the tibiotarsus of the same specimen of *D. exulans*, the distal breadth of tibiotarsus LACM 37629 from Laguna Niguel is 96.7% (Table I). It appears reasonable, therefore, to assign this specimen to *D. californica*. However, being unable to compare it with a tibiotarsus from the type locality of *D. californica*, the assignment is tentative.

*Diomedea* SP. INDETERMINATE

FIGURE 2 A, D

*Referred material.* — Proximal section of humerus, LACM 58544, from locality LACM 6902, and distal end of radius, LACM 31172, from locality LACM 6906.

*Discussion.* — These poorly preserved wing bones are notably smaller relative to those of *D. exulans* than is the case with the tarsometatarsi of *D. californica* or tibiotarsus LACM 37629. They are somewhat smaller, also, than a distal end of humerus from the Sharktooth Hill Bonebed previously referred to *D. californica* (Howard 1966b) (see Table I).

The incomplete humerus lacks the tip of the internal tuberosity, the bicipital crest and a large portion of the deltoid crest. It resembles the humerus of *D. exulans* in the broad curvature of the anconal face of the shaft, but the area immediately below the head is less depressed. On the palmar surface, the enlarged distal tip of the deltoid crest resembles the condition in *D. exulans*, but the crest is much shorter in the fossil. The radius is too poorly preserved for analysis, but provides a measurement of distal breadth (Table I).

FAMILY PROCELLARIIDAE — SHEARWATERS  
GENUS *Puffinus* BRISSON 1790

Four wing bones are referable to the genus *Puffinus*. Thirteen species of middle to late Tertiary shearwaters of this genus have been described from Europe and North America, eight of which are from the west coast (see Brodkorb 1963b, and Howard 1968 and 1971).

After consideration of these species, and careful comparison with specimens of all those from California, I find it necessary to add still another species, which I refer to the subgenus *Puffinus*.

*Puffinus barnesi* NEW SPECIES

FIGURE 1 E, F

*Holotype.* — Left humerus lacking proximal end, LACM 42652, collected by W. Earl Calhoun, July 1969, from locality LACM 6906.

*Diagnosis.* — Humerus with shaft laterally compressed above distal end,

TABLE 1

Comparison of Fossil and Recent Specimens of *Diomedea*

	Measurements in Millimeters				Ratio Fossils to Recent (In Per Cent)		
	<i>D. calif- ornica</i> *	<i>D. sp.**</i>	<i>D. ang- lica***</i>	<i>D. exu- lans****</i>	<i>D. calif- ornica</i> *	<i>D. sp.**</i>	<i>D. ang- lica***</i>
Tarsometatarsus							
Distal breadth	20.6-21.5	....	19.3	22.3	92.4- 96.4	....	86.5
Breadth shaft	9.0-10.0	....	....	9.1	96.8-109.0	....	....
Proximal breadth	....	....	20.7	23.2	....	....	89.1
Tibiotarsus							
Distal breadth	....	20.6	20.2	21.3	....	96.7	94.8
Breadth shaft	....	10.0	9.5	10.0	....	100.0	95.0
Humerus							
Proximal breadth	....	39.2	....	48.5	....	80.8	....
Distance head to end deltoid crest	....	64.5	....	83.7	....	77.0	....
Distal breadth	27.5	....	....	31.6	87.0	....	....
Radius							
Distal breadth	....	11.7	....	14.6	....	80.0	....

\*Type and referred specimens from Sharktooth Hill

\*\*Specimens from Laguna Niguel (tibiotarsus referred *D. ?californica*)

\*\*\*Type tarsometatarsus, referred tibiotarsus

\*\*\*\*LACM no. Bi230

but slightly rounded in contour; internal side of distal end relatively short in anconopalmar dimension, and anconal tip swollen laterally; impression of brachialis anticus small, and short in proximo-distal dimension; ectepicondylar process situated relatively near to distal end; attachment of anterior articular ligament turned slightly laterally rather than facing directly palmar.

*Measurements.* — Length from distal end to distal tip of deltoid crest 67.0 mm (estimated total length 80 mm), breadth of distal condyles 7.7 mm, depth of internal side of distal end 8.4 mm, distance from distal surface of condyle to proximal edge of ectepicondylar process 9.5 mm, shaft dimensions near distal end 3.5 mm in breadth, 5.7 mm in depth, shaft dimensions (middle) 3.9 mm in breadth, 5.9 mm in depth.

*Etymology.* — The species is named for Lawrence G. Barnes in recognition of his paleontological studies of the marine vertebrates of the west coast.

*Discussion.* — The holotype of *P. barnesi* is comparable in general size to the humerus of *Puffinus opisthomelas* Coues 1864. Although the shaft is compressed laterally as in that Recent species, it is slightly more rounded and less bladelike in the fossil.

With the exception of *Puffinus tedfordi* Howard 1971, from the Almejas

Formation of Cedros Island, Baja California, Mexico, and *P. arvernensis* Milne-Edwards 1871, from the Early Miocene of France, all previously described Tertiary representatives of this genus are known from the humerus. Shufeldt (1896) referred a humerus to *P. arvernensis*, but according to Storrs Olson (personal communication), who has examined the specimen, it comes from a Pleistocene locality and should be assigned to the Recent species *Puffinus puffinus* (Brunnich 1764). The holotypes of both *P. tedfordi* and *P. arvernensis* are tarsometatarsi. In both species, this element suggests a stouter bird than is represented by the wing of *P. barnesi*.

Judging from the descriptions given by Milne-Edwards (1874), the type humeri of his species *Puffinus aquitanicus* and *P. antiquus*, from the Middle Miocene of France, both exceed *P. barnesi* in size. Also, as indicated by a cast of the type of *P. conradi* Marsh 1870 (LACM C688), that species was markedly larger than *P. barnesi*. At the opposite extreme, Brodkorb's (1963a:161) measurements of the type humerus of his species *P. micraulax*, from the Hawthorne Formation, Early Miocene of Florida, show that species to be notably smaller than *P. barnesi*.

Original material or casts of all the California species of Tertiary *Puffinus* have been examined, including toponotypical specimens of humeri referable to *P. mitchelli* Miller 1961 (LACM 17500) and *P. priscus* Miller 1961 (LACM 17502 and LACM 18140) recovered since the last report on the avifauna of the Middle Miocene of Sharktooth Hill (Howard 1966b).

Of the California species, the humeri of *P. felthami* Howard 1949 (Middle Pliocene of Orange County) and *P. mitchelli* are larger than *P. barnesi*. *P. inceptor* Wetmore 1930 (Middle Miocene, Sharktooth Hill) agrees in some dimensions, but the marked medial thrust of the internal condyle and the greater anconopalmar dimension of the internal side of the distal end are distinctive characters of *P. inceptor*. Also, the brachial impression in that species is more distally developed. In *P. calhouni* Howard 1968 (Late Miocene, Orange County) and *P. priscus* the shaft is more compressed and bladelike than in *P. barnesi*. The ratio of breadth to depth of shaft near the distal end in *P. barnesi* is 61%, in *P. calhouni* 50%, and in *P. priscus* 48-53%.

An excellent relief cast (LACM C692) from the holotype skeletal impression of *P. diatomicus* Miller 1925 (Late Miocene, Lompoc) clearly reveals characters of the palmar aspect of the distal end of the humerus. The impression of the brachialis anticus is more distally extended than in *P. barnesi* and the ectepicondylar process is placed higher above the distal end (11.6 mm from distal surface of condyle to proximal tip of process).

Most closely approaching *P. barnesi* in general size are the paratype and referred humeri of *P. kanakoffi* Howard 1949 (LACM specimens), from the San Diego Formation. This Pliocene species is distinguished, however, by a longer brachial impression, less rounded shaft (though less compressed than in *P. priscus*), less inflated anconal tip of the internal condyle, and more palmar-facing attachment for the anterior articular ligament.

*Referred material.* — A left ulna, lacking the olecranon (LACM 42654)

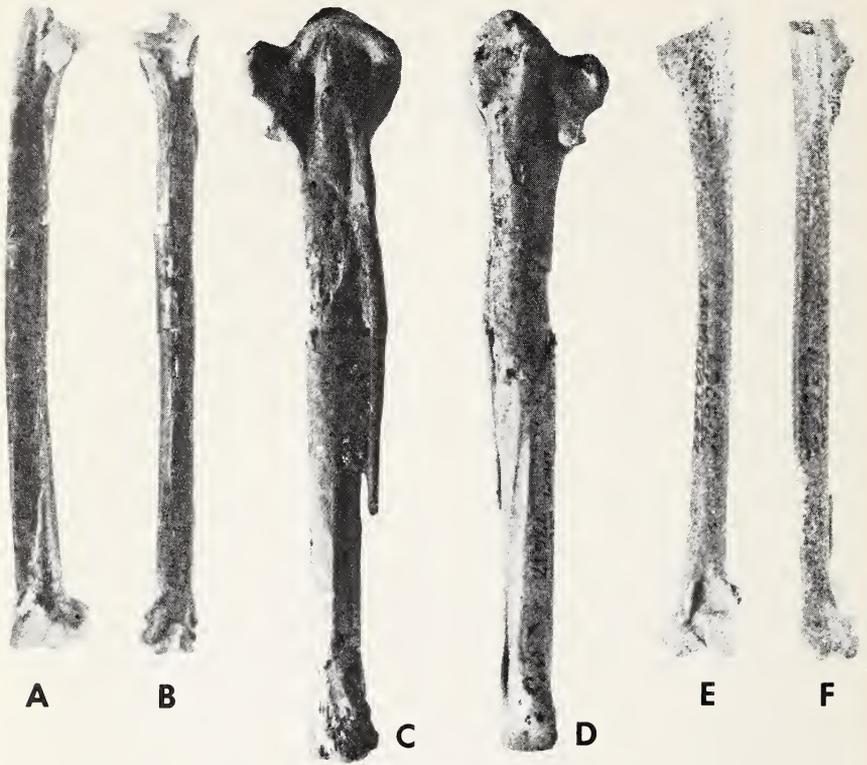


FIGURE 1. A, B, *Gavia brodkorbi* n. sp. holotype ulna, LACM 31173, internal and palmar views. C, D, *Morus lompocanus* Miller referred carpometacarpus, LACM 77697, internal and external views. E, F, *Puffinus barnesi* n. sp. holotype humerus, LACM 42652, palmar and internal views. X 1

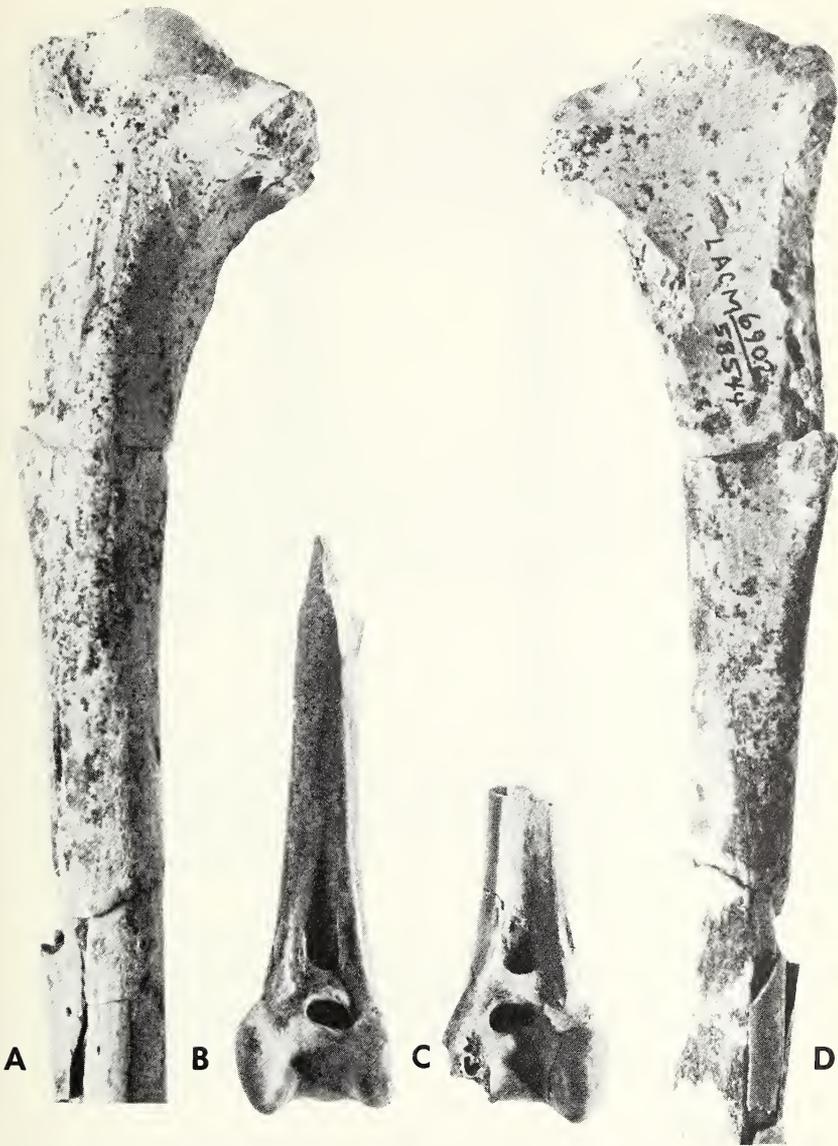


FIGURE 2. A and D, *Diomedea* sp. indet., proximal portion of humerus, LACM 58544, anconal and palmar views. B, *Diomedea anglica* Lydekker, referred distal end of tibiotarsus from Pierce, Florida, MCZ 2328, anterior view. C, *Diomedea ?californica* Miller, referred distal end of tibiotarsus, LACM 37629, anterior view. X 1



FIGURE 3. A and D, *Osteodontornis orri* Howard, referred proximal half of left carpometacarpus, LACM 53906, posterior and internal views. B, C, *Morus magnus* n. sp. holotype carpometacarpus, LACM 37632, internal and external views. X 1

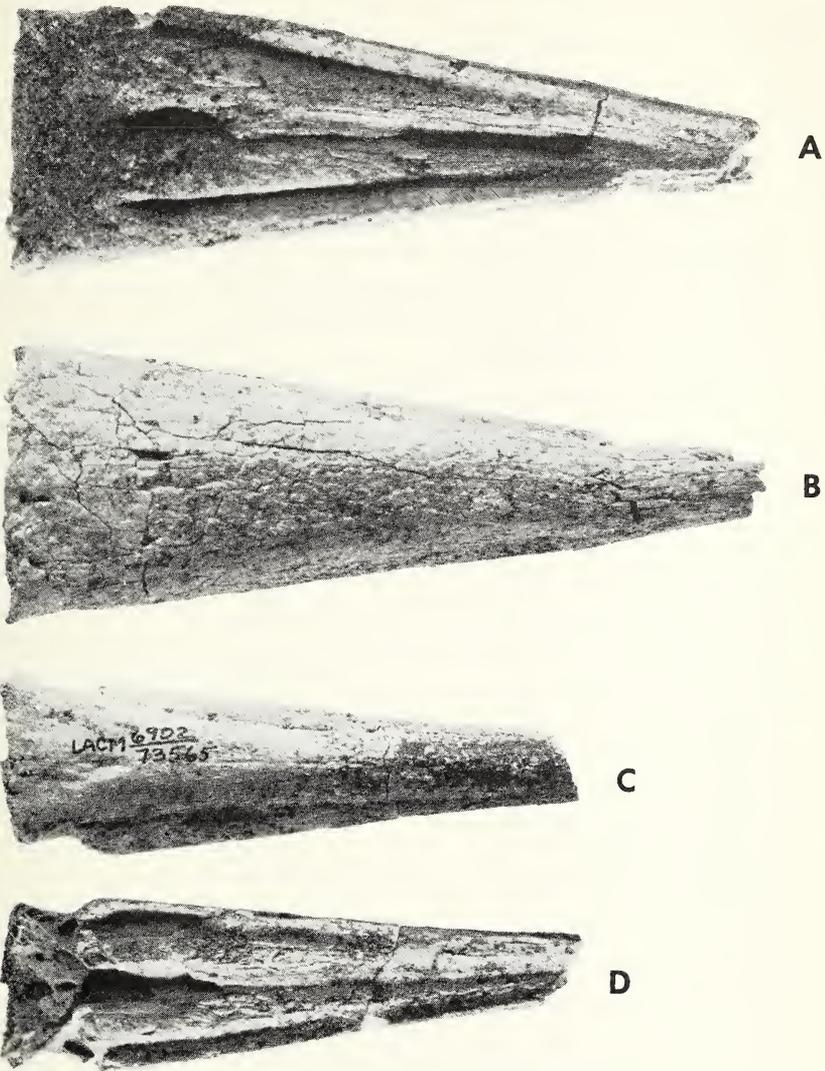


FIGURE 4. A, B, *Morus magnus* n. sp., referred rostrum, LACM 77696, ventral and dorsal views. C, D, *Sulidae* sp. indet., rostrum, LACM 73565, dorsal and ventral views. X 1

from the type locality, LACM 6906. Although smaller than would be expected for the wing of the same individual as the holotype, this specimen (like the humerus) falls within the size range of *P. opisthomelas*. (ulnar length, 68.3-76.3 mm), though near the minimum; the holotype humerus is near the maximum size of *P. opisthomelas*. The few characters discernible in the poorly preserved ulna are: carpal process as in *P. opisthomelas*, shorter than in a topotype ulna of *P. kanakoffi* (LACM 2821, previously unreported), and more abruptly projected; external cotyla not prominently projected palmar; ridge present from external cotyla to shaft; attachment for anterior articular ligament seemingly more protruding than in *P. opisthomelas*; but the area is broken.

Measurements of ulna: length to intercotylar ridge 70.8 mm, breadth of proximal end 6.5 mm, greatest breadth of distal end 6.4 mm, depth through external crest of trochlea 5.3 mm, shaft dimensions (middle) 3.5 mm × 5.3 mm.

Another poorly preserved fragment of a distal end of an ulna (LACM 52748) from locality LACM 7136, has a distal breadth of approximately 6.3 mm. A wing phalanx (digit 2, phalanx 1), LACM 53925 from locality LACM 3185, measures 20.4 mm in length, which is within the size range of this element of *P. opisthomelas*. These two specimens are tentatively assigned to *P. barnesi*.

FAMILY HYDROBATIDAE — STORM PETRELS  
GENUS *Oceanodroma* REINCHENBACH 1852  
*Oceanodroma* SP. INDETERMINATE

*Referred material.* — A single incomplete right tarsometatarsus, LACM 42659, from locality LACM 6902, represents this family and genus.

*Discussion.* — The specimen resembles this element in *O. melania* (Bonaparte 1854), but is slightly longer. The length from distal end to proximal tip of hypotarsus is 31.5 mm. The distal end appears to be narrower than in *O. melania*, but the preservation is such that accurate measurement is impossible.

The only previously recorded Tertiary storm petrel is *O. hubbsi* Miller 1951, from the Capistrano Formation (Late Miocene-Early Pliocene), Orange County, a few miles south of the Laguna Niguel localities. The tarsometatarsus is represented in the type, partial skeleton, of this species preserved in shale. Miller (1951) gives the length of this element as 22.4 mm, markedly less than even the incomplete measurement possible on the specimen now at hand.

ORDER PELECANIFORMES  
FAMILY PSEUDODONTORNITHIDAE — BONY-TOOTHED BIRDS  
GENUS *Osteodontornis* HOWARD 1957  
*Osteodontornis orri* HOWARD 1957

FIGURE 3 A, D

*Referred material.* — Lower jaw fragment, LACM 22444, and carpometacarpus, LACM 53906, with portion of proximal end and shaft, both

from locality LACM 6902; portion of lower jaw, LACM 42656, with a single "tooth," from locality LACM 7136.

*Discussion.* — The jaw fragments resemble previously recorded specimens of *Osteodontornis* (Howard 1957a, and Howard and White 1962), although they seem somewhat smaller than the type of *O. orri*.

The fragment of carpometacarpus, however, conforms in size to the left carpometacarpus on the type skeleton, a cast of which is at hand. In fact, the specimen from locality 6902 fits exactly into the impression of the left carpometacarpus on type Slab No. 1 (LACM C703, Block No. 1), in which the large pisiform process has left a deep depression. The present specimen not only clarifies that this depression, was, indeed, made by the pisiform process, but also reveals other characters only suggested in the type, namely, the length of the process of metacarpal 1 and the great compression of metacarpal 3(M3) to metacarpal 2(M2). The very thin M3 is pressed against M2 even distal to the proximal metacarpal symphysis, and the symphysis itself extends almost to the level of the distal tip of the process of M1.

Metacarpal 1 is broken in both the type and LACM 53906, but the area of its attachment to the element as a whole is indicated in the type and clarified in the broken edges of the process on the carpometacarpus from Laguna Niguel. The length of M1 measured on LACM 53906, is 62.2 mm, approximately one-fourth the total length of the carpometacarpus as seen in the type (252 mm). Enough of the proximal end of LACM 53906 is preserved to obtain an approximate breadth of the proximal trochlea (15.2 mm). The antero-posterior dimension of the trochlea cannot be measured, but it is obvious that the posterior portion is short in distal extent. Shaft breadths of M2 and M3 are 11.0 mm and 4.0 mm respectively. The depth through the compressed M2 and M3 is 16.4 mm. The incomplete specimen measures 126.4 mm from trochlea to broken end of M2.

Except for a prominent pneumatic foramen above the pisiform process, which occurs in most sulids, there is nothing about this highly compressed carpometacarpus to relate it to the Pelecaniformes. I have previously contended (Howard 1957a) that the bony-toothed birds represent a distinct order, Odontopterigiformes.

#### FAMILY SULIDAE — BOOBIES AND GANNETS

The family Sulidae is the best represented family in the Laguna Niguel collection and the one which has presented the greatest difficulty in identification. Fifteen middle and late Tertiary sulids have been previously described from North America and Europe (see Brodkorb 1963b:257-261), eight of which are from California (six Miocene, two Pliocene). Five of the species are based on partial skeletons in shale slabs, the others on individual bones involving four different incomplete skeletal elements. A complete review of the known fossils of this family is greatly to be desired. This is a task that some energetic young paleontologist may profitably undertake.

Sixteen bones in the present collection are assignable to at least three species. In spite of the difficulty experienced in correlating the previously described species, I feel justified in describing one new species and in assigning several specimens to one previously described.

GENUS *Morus* VIELLOT 1816  
*Morus lompocanus* (Miller 1925)

FIGURE 1 C, D

*Referred material.* — Carpometacarpus, LACM 37634; distal end of ulna, LACM 37636; and distal end of femur, LACM 37633; all from locality LACM 6902; carpometacarpus, LACM 77697, from locality 6901; proximal end of tarsometatarsus, LACM 32428 from locality LACM 6906; proximal end of tarsometatarsus, LACM 42657, from locality LACM 7136; distal end of tibiotarsus, LACM 52217, from locality LACM 3185.

*Discussion.* — *Morus lompocanus* was described (Miller 1925) from the impression of a partial skeleton in a slab of diatomaceous shale from Lompoc, California. Although the holotype (UCMP 26544) was the only specimen described in the text, two other partial skeletons from the same site were so named and illustrated (op. cit.:pl. 7B and pl. 9). These referred specimens (UCMP 117309 and UCMP 115855), both bearing Miller's identification, as well as a cast (in relief) of the holotype (LACM C697) are at hand. On the basis of comparison of size with these specimens, the fossils from Laguna Niguel are referred to *M. lompocanus*.

The two carpometacarpi measure 94.7 mm (LACM 37634) and 95.7 mm (LACM 77697) in length. By comparison, a carpometacarpus (LACM Bi 1764) of a female *M. bassanus* (Linnaeus 1758) is 90.0 mm, and Miller (1935:78) records another of this Recent species at 94 mm. The referred carpometacarpus of *M. lompocanus* (UCMP 115855) is 96.6 mm. Other fossil sulids in which this dimension is known are: *Palaeosula stocktoni* (Miller 1935), 102 mm; *Miosula media* Miller 1925, 81 mm; *Sula willetti* Miller 1925, 70 mm; *S. pohli* Howard 1958, 69 mm; *Microsula avita* (Wetmore 1938), 75 mm.

Carpometacarpus LACM 77697, the better preserved of the two Laguna Niguel carpometacarpi (Fig. 1 C, D), is similar in the shape of the process of M1 to *Morus bassanus*. But where the small foramina occur in the modern species, there is a deep, slit-like foramen — one anterior to the pisiform process, and one in a similar position at the base of M1 on the external side of the proximal end. The fossil also resembles *Morus* in the absence of pneumatic foramina at the posterior edge of the trochlea. Details of qualitative characters are not discernible on the Lompoc specimens.

Ulna LACM 37636 resemble *Morus* rather than *Sula* in the pneumaticity of the palmar face of the carpal process, and the size of the process. It is of the same distal breadth (10.5 mm) as the ulna of *M. bassanus* LACM Bi 1764. Measurements of ulnar breadth cannot be made on *M. lompocanus*, but the Laguna Niguel specimen corresponds favorably with the impression of the element on Lompoc specimen UCMP 115855.

Femur LACM 37633 conforms in proportions to a raised mold of the element made from the type impression of *M. lompocanus*. Similar dimensions measured on the two specimens are identical: breadth across anterior face of distal end 13.9 mm, breadth of shaft 7.0 mm. *M. bassanus* LACM Bi 1764 is larger in these dimensions (14.2 mm and 7.5 mm, respectively).

Tibiotarsus LACM 52217 conforms in size with *M. lompocanus* specimen UCMP 115855 from Lompoc. The bridge is less vertical in position than in *M. bassanus*, the upper edge being tipped posteriorly. This is true, as well, of the type tibiotarsus of *Miosula recentior* Howard 1949 (LACM 2117) from the Pliocene of San Diego, California. But the latter is distinguished from the specimen now at hand by less vertically oriented condyles. Measurements of LACM 52217 are: breadth of distal end 13.7 mm, depth of distal end 12.4 mm, ratio of depth to breadth 90.5%. The same dimensions in *M. bassanus* LACM Bi 1764 are, breadth 13.0 mm, depth 12.0 mm, ratio depth to breadth 92%.

The two proximal ends of tarsometatarsi (LACM 32428 and LACM 42657) measure 12.8 mm and 12.9 mm in proximal breadth, respectively. A mold of the posterior surface of this element on the type specimen of *M. lompocanus* measures 12.8 mm proximally. The impression visible on Lompoc specimen UCMP 115855 measures 13.5 mm. *M. bassanus* and a mold of the tarsometatarsus in the type of *Miosula media* Miller 1925 are broader (14.5 mm and 14.1 mm, respectively).

#### *Morus magnus* NEW SPECIES

FIGURE 3 B, C; 4 A, B

*Holotype*. — Nearly complete left carpometacarpus, LACM 37632, collected by Marion J. Bohrer, 1969, from LACM locality 6906.

*Diagnosis*. — More than 20% longer than female specimens of this element of *Morus bassanus*. Area above pisiform process depressed, with small pneumatic orifice. Externally, a deep, slit-like depression at base of process of metacarpal 1.

*Measurements*. — Greatest length 116.1 mm, breadth proximal trochlea 11 mm (approximately), breadth of shaft 9.6 mm.

*Etymology*. — The species name *magnus* (Latin, great) refers to the large size of the skeletal elements described.

*Discussion*. — Owing to the poor preservation of the holotype carpometacarpus, size is the outstanding distinguishing character. Of previously described sulids, *Palaeosula stocktoni* most nearly approaches *M. magnus* in length of this element (102 mm), but is still 13% shorter. Characters of the carpometacarpus other than length are not clearly discernible on the type slab of *P. stocktoni* (cast, LACM C743). It has been shown, however (Howard 1958), that at least the humerus of *Palaeosula* is markedly distinct qualitatively from either *Morus* or *Sula*. *M. magnus*, on the other hand, resembles the living sulids.

From the elements known, none of the other middle to late Tertiary fossil sulids gives evidence of approaching *M. magnus* in size.

*Referred material.* — Distal end of humerus, LACM 32430, and shaft of femur, LACM 37628, both from the type locality, LACM 6906, collected by Bohrer in 1969; and rostrum, LACM 77696, from locality LACM 6902, collected by Jennifer Whistler, June, 1975.

The humerus resembles *Morus* in contrast to *Sula* in the absence of the deep pneumatic foramen undercutting the external side of the olecranal fossa. The flat surface of the attachment for the anterior articular ligament, and its length relative to the distal breadth of the element is also similar to *Morus*. The attachment, however, projects slightly more palmar at its proximal end than in *M. bassanus*, and, in this respect, resembles *Sula*. In breadth the element is 22% greater than in *M. bassanus*.

The fragmentary femur is 18% broader than in *M. bassanus* in least breadth of shaft, and appears to expand to even greater relative breadth farther distad. It is difficult to be certain of accurately reproducing the same measurement in the two specimens as the distal condyles are lacking in the fossil.

The rostrum resembles *Sula* in the broad arch of the nasals, but bears resemblance to *Morus* in the depression of the dorsal contour anterior to the hinge. This depressed area, however, is shorter than in *M. bassanus*. In greatest breadth, it exceeds the rostrum of *M. bassanus* by 31% (see Table 2).

#### ?*Miosula media* MILLER 1925

*Referred material.* — Tarsometatarsus lacking the proximal end, LACM 32431, from locality LACM 6906.

*Discussion.* — This specimen is heavier of shaft than the two proximal fragments of tarsometatarsus referred to *Morus lompocanus*. In breadth of distal end (17.6 mm) it is slightly larger than an incomplete mold of the tarsometatarsus made from the type skeletal impression of *Miosula media* (17.3 mm, approx.). Although neither the mold nor LACM 32431 is complete, both suggest a tarsometatarsus that is straighter of shaft than in *Morus*, but having the slightly raised internal trochlea characteristic of that genus as distinguished from *Sula*.

#### SULIDAE, spp. INDETERMINATE

*Referred material.* — A rostrum, LACM 73565, a proximal end of radius, LACM 58551, and a distal end of tibiotarsus, LACM 57834, all from locality LACM 6902; and a rostrum, LACM 37614, from locality LACM 6906.

*Discussion.* — Rostrum LACM 73565 (Fig. 4 C, D) bears strong resemblance to the cormorants in dorsal aspect, having deep lateral grooves setting off a narrow nasal process. There are, however, no dorsal foramina such as occur in *Phalacrocorax*. In palatal view, the resemblance is closer to the sulids. The palatines in the maxillo-palatine area are swollen, not flat, and are bordered laterally with wide, deep grooves. Posteriorly the maxillo-palatine area slants smoothly upward and bears very little perforation. In the slope of the area the specimen resembles *Morus*, in perforation it resembles

TABLE 2

Measurements (in millimeters) of *Morus magnus* and *M. bassanus*

	<i>M. magnus</i>	<i>M. bassanus</i> (LACM Bi 1764)
<i>Carpometacarpus</i>		
Greatest length	116.1	90.0
Breadth proximal trochlea	11.0 approx.	9.9
Breadth middle of shaft	9.6	7.4
Height process M1	16.0	12.0
<i>Humerus</i>		
Greatest breadth distal end	29.2	24.1
Depth distal end (externally)	17.0	14.4
Breadth of shaft immediately proximal to attachment for anterior articular ligament	22.8	17.0
<i>Femur</i>		
Least breadth shaft	8.9	7.1
Depth of shaft	9.6	7.5
<i>Rostrum</i>		
Breadth of frontonasal hinge	34.8	25.4-26.5*
Greatest depth	25.3	15.4-16.7*
Breadth nasal process	31.4	18.3-19.5*
Length	138.0 (estimate)	101.7-106.5*

\*Maximum measurements from rostrum PB 16291, minimum from LACM Bi 1765.

both *Phalacrocorax* and *Morus*, but not *Sula*. This area in *Sula* rises more abruptly and is well perforated. The lateral pneumatic openings are much reduced in comparison to those found in the cormorants, and compare more favorably with those of *Morus*. Measurements of LACM 73565: greatest breadth 22.2 mm (approximately), greatest depth, 15:1 mm, breadth nasal process 5.2 mm.

In view of the fact that Miller (1925) noted certain characteristics of *Miosula media* that are cormorant-like, it is possible that this rostrum may represent that species.

The second rostrum (LACM 37614) is typically sulid in all aspects. It is more massive than LACM 73565, but smaller than LACM 77696 referred to *Morus magnus*. Measurements: greatest breadth 24.0 mm, greatest depth 19.2 mm, breadth nasal process 21.8 mm.

The radius resembles *Morus bassanus* in general conformation and size, but is poorly preserved. The tibiotarsus is similar in characters of the distal end to LACM 52217 from Laguna Niguel, assigned to *Morus lompocanus*. The specimen is eroded so that measurements cannot be made precisely. It appears, however, to be narrower but relatively deeper than in LACM 52217, breadth of distal end 12.0 mm (approx.), depth of distal end 11.5 mm (approx.); ratio of depth to breadth 96%.

ORDER CHARADRIIFORMES  
FAMILY ALCIDAE — AUKLIKE BIRDS

*Discussion.* — In addition to the six bones of *Praemancalla wetmorei* (subfamily Mancallinae) described earlier (Howard 1976) from localities LACM 6902, 6906 and 3185, the alcids from Laguna Niguel are represented by five fragments assignable to the Alcinae. In view of the fact that comprehensive studies of Tertiary alcids are under way by Storrs Olson at the United States National Museum of Natural History (Atlantic avifauna) and G. Victor Morejohn at California State University, San Jose (Pacific avifauna), I have refrained from attempting to name these poorly preserved specimens.

Five middle to late Tertiary alcines have been previously described from the west coast: *Aethia rossmoori* Howard 1968, and *Cerorhinca dubia* Miller 1925, from the Late Miocene; *Brachyramphus pliocenens* Howard 1949, *Ptychoramphus tenuis* Miller and Bowman 1958, and *Cerorhinca minor* Howard 1971, from the Middle to Late Pliocene. East coast species are *Uria antiqua* (Marsh 1870), and *Miocepphus mcclungi* Wetmore 1940, from the Middle Miocene; and *Australca grandis* Brodkorb 1955, from the Middle Pliocene. A single species, *Uria ausonia* Portis 1887, is recorded from the Middle Pliocene of Italy (see Brodkorb 1967; and Howard 1968 and 1971). There is no indication that any of these species is represented by the material from the Laguna Niguel sites.

GENUS *Uria* BRISSON 1760  
? *Uria* sp.

*Referred material.* — An incomplete proximal end of humerus, LACM 52018, from locality LACM 6902.

*Discussion.* — This poorly preserved specimen resembles the humerus in the murrelets in the long, oval pectoral scar, and prominent head widening towards the internal side and overhanging a broadly depressed tricipital area between the pectoral scar and the internal tuberosity. Both the deltoid and the bicipital crests are incomplete. That which remains of the bicipital surface is prominently raised proximally and bordered medially below by a deep groove; the bicipital furrow is a deep notch. These characters are most closely matched by humeri of Recent *U. lomvia* (Linnaeus 1758).

Comparisons were made with a cast of the type of *Uria antiqua*, provided through the courtesy of Storrs Olson, United States National Museum of

Natural History. Olson (personal correspondence) now refers this species to the genus *Australca* Brodkorb 1965. The cast is not only larger, but is much flatter in the bicipital area than in the Laguna Niguel specimen.

GENUS *Cepphus* PALLAS 1769

?*Cepphus* sp.

*Referred material.* — A proximal end of ulna with incomplete olecranon, LACM 47045, from locality LACM 6906.

*Discussion.* — This specimen resembles the ulna of the Pigeon Guillemot, *Cepphus columba* Pallas 1811, in the rounded shaft lacking a distinct keel anconally, and in having the brachial impression bordering the attachment for the anterior articular ligament and extending farther proximally than in most other genera of alcines. However, the brachial impression is broader in the fossil, and more deeply undercuts the attachment for the anterior articular ligament than in the Recent species. Also the attachment for the ligament is more prominent and more square in outline.

The possibility that this specimen might represent the genus *Miocepphus* prompted me to contact Storrs Olson. He reports (personal correspondence) that "*Miocepphus mcclungi* is one of the commoner birds in the Calvert Formation of Maryland and Virginia and I have many specimens that have not been reported on in the literature." He provided me with the loan of a complete ulna and humerus which he said "certainly pertain to this species." In the ulna (USNM 237219) the attachment for the anterior articular ligament is less prominent and more elongated than in LACM 47045, the brachial impression is narrower, and the shaft more compressed. LACM 47045 is not related to *Miocepphus*, which accords with Olson's observation that "*Miocepphus* is not related to *Cepphus*" but to the "*Alca-Uria* group of Atlantic alcids."

GENUS *Aethia* MERREM 1788

?*Aethia* sp.

*Referred material.* — Incomplete humerus, LACM 37686, from locality LACM 6906.

*Discussion.* — LACM 37686 is the smallest of the alcine bones from Laguna Niguel. It is possibly related to the Auklet, *Aethia rossmoori* Howard 1968, described from an ulna (LACM 18948) with referred distal end of humerus (LACM 18949), collected in the Monterey Formation at Leisure World in nearby Laguna Hills (locality LACM 1945). LACM 37686 resembles the humerus of *A. rossmoori* in the rounded shaft, position of the brachial impression with slight rise bordering it externally, and attachment of the anterior articular ligament facing more palmar than laterally. It is, however, 15% larger than the specimen of *A. rossmoori*. Also, although the area of the tricipital grooves is abraded, the grooves appear to be less deeply incised than in modern species of *Aethia*, or *A. rossmoori*.

TRIBE FRATERCULINI  
GENUS AND SPECIES INDETERMINATE

*Referred material.* — Proximal end of humerus, LACM 42658, from locality LACM 7136, and distal end of humerus, LACM 37638, from locality LACM 6902.

*Discussion.* — Both humeral fragments resemble this element in the puffins (following Storer 1960:698, in segregating *Cerorhinca* in a tribe along with *Fratercula* and *Lunda*). The proximal portion (LACM 42658) resembles the type humerus of *Cerorhinca minor* Howard 1971 (LACM 15408), from the Pliocene of Baja California, Mexico, in the presence of a ridge from the head to the median crest, forming an internal border to the tricipital depression on the anconal surface below the head, and in the extension of the median crest to the border of the bicipital crest. In proximal breadth the Laguna Niguel specimen is 12.0 mm, which is markedly larger than this dimension in *C. minor* (10.5 mm). It is, in fact, closer in size to a humerus (LACM Bi 696) of *Lunda cirrhata* (Pallas 1769) which measures 12.2 mm in proximal breadth. Similarity to *Lunda* is seen in the extension of the pectoral attachment to the deepest part of the head, and, on the palmar side, the slight inset of the bicipital surface border from that of the bicipital crest. Similarity to *Fratercula corniculata* (Naumann 1821) is noted in the length of the bicipital surface, which becomes slightly pointed at its distal extreme. The tricipital depression below the head is shallower than in any of the specimens of Recent puffins at hand.

The distal portion of humerus (LACM 36738) also resembles this element in the Fraterculini. Its size suggests that it may belong to the same species as the proximal end discussed above.

The possibility that these two bones might be assignable to *Cerorhinca dubia*, described from the Late Miocene of Lompoc, was considered. However, their size seems to preclude this possibility. Miller (1925:116) gave the measurements of length for the type leg bones of *C. dubia* as 60 mm (tibiotarsus) and 29 mm (tarsometatarsus). These measurements in a series of ten specimens of *C. monocerata* (Pallas 1811) are 59.2 mm-60.0 mm, mean 62.9 mm (tibiotarsus), and 27.7 mm-30.6 mm, mean 29.1 mm (tarsometatarsus). The humeri from Laguna Niguel are relatively larger in comparison with the same series of skeletons of *C. monocerata*: proximal breadth (LACM 42658) 12.0 mm (*C. monocerata* 6.9 mm-11.3 mm, mean 10.6 mm); distal breadth (LACM 36738) 8.0 mm (*C. monocerata* 6.9 mm-7.8 mm, mean 7.2 mm).

GENUS *Praemancalla* HOWARD 1976  
*Praemancalla wetmorei* HOWARD 1976

No further material referable to this species has been found at Laguna Niguel since the type description, which included: holotype humerus, LACM 42653, paratype ulna, LACM 32429, and referred proximal end of humerus, LACM 32432, all from locality LACM 6906; complete radius, LACM 53907,

and scapular end of coracoid, LACM 37637, both from locality LACM 6902; and proximal section of carpometacarpus, LACM 52216, from locality LACM 3185.

### CONCLUSIONS

Seven families of marine birds are represented by the 39 identifiable avian bones from the Late Miocene deposits in Laguna Niguel. In the following list the numbers in parentheses indicate the number of specimens assigned to each species.

Gaviidae — Loons

*Gavia brodkorbi* new sp. (1)

Diomedeidae — Albatrosses

*Diomedea ?californica* (1)

*Diomedea* sp. indet. (2)

Procellariidae — Shearwaters

*Puffinus barnesi* new sp. (4)

Hydrobatidae — Storm Petrels

*Oceanodroma* sp. indet. (1)

Pseudodontornithidae — Extinct Bony-toothed Birds

*Osteodontornis orri* (3)

Sulidae — Boobies and Gannets

*Morus lompocanus* (7)

*Morus magnus* new sp. (4)

?*Miosula media* (1)

Sulidae, spp. indet. (4)

Alcidae — Auklike Birds

?*Uria* sp. (1)

?*Cepphus* sp. (1)

?*Aethia* sp. (1)

Fraterculini, gen. and sp. indet. (2)

*Praemancalla wetmorei* (6)

Five of the above families (Diomedeidae, Procellariidae, Pseudodontornithidae, Sulidae and Alcidae) are also represented in the larger collection of Late Miocene birds recovered earlier from locality LACM 1945 in Leisure World, Laguna Hills, about three miles north of Laguna Niguel (Howard 1968). However, few of the same species are listed from the two sites and none of those described as new from locality LACM 1945 is found in the Laguna Niguel area. From locality LACM 1945, 50% of the 120 bones identified are of the Procellariidae (4 species), with Sulidae (3 species) and Alcidae (5 species) constituting approximately 22% each. The remaining 6% include the Anatidae (2 species), Diomedeidae (2 species) and ?*Osteodontornis orri*.

At Laguna Niguel only 10% of the 39 identified bones are procellariid (1

species). The Sulidae are most abundant, making up 41%, followed by the Alcidae 28%. *Diomedea* and *Osteodontornis* constituting 7½% each, are relatively better represented than at locality LACM 1945. A loon (Gaviidae) and a storm petrel (Hydrobatidae), not present at LACM 1945, complete the avifauna. The Anatidae are not represented.

Although the deposits at both of these sites are in the Monterey Formation of Late Miocene (Clarendonian correlative) age, comparison of the two avifaunas strengthens the belief suggested by a comparison of the mancolline auks (Howard 1976) that the fauna from Laguna Niguel represents a slightly later time than that from locality LACM 1945. Not only is the mancolline auk, *Praemancalla wetmorei*, from Laguna Niguel further specialized for wing-propelled diving than is *P. lagunensis* from locality LACM 1945, but in the Laguna Niguel sites there is less indication of persistence of Middle Miocene species and a more definite representation of typical Late Miocene species. At locality LACM 1945, *Presbychen abavus* Wetmore 1930 and *Puffinus priscus*, both described from the Middle Miocene Sharktooth Hill Bonebed, are listed. Neither has been found at Laguna Niguel, although another species, *Diomedea californica*, described from the same locality, is tentatively identified. On the other hand the typically Late Miocene *Morus lompocanus*, which is only tentatively identified at locality LACM 1945, is the most abundant species at Laguna Niguel. *Osteodontornis orri*, tentatively listed from LACM 1945, on the basis of a single fragment, is definitely present at Laguna Niguel.

Some significance also may be attached to the occurrence of *Gavia* and *Oceanodroma* at Laguna Niguel. This is the first Miocene west coast occurrence of the loons (Gaviidae). The only previous record for *Oceanodroma* is *O. hubbsi* Miller in the Capistrano Formation, which is now considered to be of latest Miocene to early Pliocene (Hemphillian correlative) age (Fife 1974:19) rather than Middle Miocene as interpreted by Miller (1951).

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THE NET-WINGED MIDGES OF EASTERN NORTH AMERICA,  
WITH NOTES ON NEW TAXONOMIC CHARACTERS  
IN THE FAMILY BLEPHARICERIDAE (DIPTERA)

By CHARLES L. HOGUE

NATURAL HISTORY MUSEUM OF LOS ANGELES COUNTY  
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THE NET-WINGED MIDGES OF EASTERN NORTH AMERICA,  
WITH NOTES ON NEW TAXONOMIC CHARACTERS  
IN THE FAMILY BLEPHARICERIDAE (DIPTERA)<sup>1</sup>

By CHARLES L. HOGUE<sup>2</sup>

ABSTRACT: The single genus *Blepharicera* Macquart of the family Blephariceridae occurs in eastern North America, probably arriving historically via a continental connection with western Europe, and is now distributed through Appalachia, New England, the northern Great Lakes Region and southeastern Canada. Six species are recognized, discussed and figured: *B. capitata* (Loew), *cherokea* new species, *diminutiva* new species, *similans* (Johannsen), *tenuipes* (Walker), and *williamsae* (Alexander). Six larval types also are known but none definitely can be associated with adults (although three are provisionally identified). Pupal anatomy, with one exception, is homogeneous, defying species characterization.

The usefulness of taxonomic characters in the group is discussed including application of several new terms.

INTRODUCTION

The family Blephariceridae is represented in eastern North America by the single genus *Blepharicera*, in which six species are recognized presently. These species, here designated as the "Tenuipes Group," are extremely similar in all stages and undoubtedly arose from a single ancestral form. *Blepharicera* is now known to occur only in the northern hemisphere, ranging more or less continuously and narrowly across Asia through northern Spain, the Alps and Balkans, Caucasus, Himalayas, to Japan and North Korea. Species also are found disjunctly in northern Borneo, Thailand, Taiwan and neighboring China. This is a so-called "Tethyan distribution" and suggests, within the tenets of plate tectonics, that the genus originated in Laurasia and expanded to the south only as far as the northern margin of the Tethyan Sea.

Introduction to North America could have occurred via Europe-Newfoundland or Bering connections. I favor the former route for the Tenuipes Group because of the total lack of close relatives in western North America. (*B. ostensackeni* may form an exception but it is not clearly a member of this group.)

The western species of *Blepharicera* could have evolved secondarily from a western extension of this stock, but they are an assemblage of distinct species quite unlike the eastern species and I think it much more likely that they arrived independently from

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<sup>1</sup>REVIEW COMMITTEE FOR THIS CONTRIBUTION  
C. P. ALEXANDER  
DOUGLAS CRAIG  
JULIAN P. DONAHUE

<sup>2</sup>Senior Curator of Entomology, Natural History Museum of Los Angeles County, 900 Exposition Boulevard, Los Angeles, California, 90007.

one or more introductions over a Bering connection from eastern Asia. This thesis is supported further by the parallel occurrence in western North America of the genera *Bibliocephala* and *Philorus*, both of which have very close relatives in Japan and other parts of Asia. Unfortunately, there is no information on the occurrence of the genus in Alaska and northern and central Canada which could establish continuity between the eastern and western forms.

The eastern *Blepharicera* are now known from as far west as eastern Minnesota through southern Ontario and all the southeastern Canadian provinces, through New England and down the Appalachian cordillera to its southern extreme in Georgia. Included in this distribution are the Canadian provinces of Quebec, Ontario, Newfoundland, New Brunswick and Nova Scotia, and the American states of Maine, Vermont, New Hampshire, Minnesota, New York, Massachusetts, Connecticut, Pennsylvania, New Jersey, Maryland, Virginia, West Virginia, North Carolina, South Carolina, Tennessee and Georgia. I predict that they may eventually be discovered in extreme northeastern Alabama, eastern Kentucky and possibly Michigan and Manitoba.

This largely congruent distribution and the extreme morphological similarity of all the species has made it impossible, without rearings, to firmly establish associations of the immature with the adult stages. As many as three species can occur at the same locality, so that stages associated in single collections do not necessarily belong to the same species. A further barrier to relating the larvae to the adults is the total homogeneity of pupal morphology. Whereas identifiable pharate adults may be related to pupae by dissection, there is no way to transcend the gap between larva and pupa. The one exception to this is the distinctive form "F" with conspicuous median dorsal convexities on the abdomen of larva and pupa. Unfortunately, the one mature form "F" pupa available did not yield an identifiable female.

These difficulties have prevented me from definitely establishing stage associations in any species, and all identifications of immatures cited are provisional. Associations can be accomplished with certainty if specimens are individually reared, but this requires special care, time, and equipment. Very probable associations can be established if collecting is extensive and carefully done so that groups of larvae of all instars present, and pupae in close proximity (on the same boulder or area of a large rock face) and in the process of transformation, are preserved apart from other groups. Unfortunately, the material available for this study was totally inadequate for this application. In the taxonomic treatment below, I have relegated larvae to each of the species very tentatively and state my reason, albeit tenuous, for each association. I urge students of stream biology in the East to vigorously and carefully collect this genus so that these vagaries can be removed.

## TAXONOMIC CHARACTERS

### LARVAL CHAETOTAXY AND CUTICULAR SCLEROTIZATIONS

In my first attempts to separate the very similar larvae of the various species in this complex, I became aware immediately of the need to utilize new characters. Previously, the chaetotaxy has been almost totally ignored in taxonomic studies of larval

Blephariceridae, and no foundation existed upon which to assess possible useful character states. From the practical standpoint of need for a consistent terminology and to reveal some points for species discrimination, I undertook a preliminary study of the homologies (both serial and comparative between several genera) of the trunk setae; study of the head setae has been deferred.

After examining the first instar larvae of *Agathon comstocki* (Kellogg) (Fig. 1-western North America) and *Neocurupira chiltoni* (Campbell) (Fig. 2 - New Zealand) and later instars of numerous genera, it became apparent that, like those of most nematocerous families, blepharicerid larvae possess so-called primary sensilla which make up the complete complement of the first instar larva and a much larger number of secondary sensilla added in subsequent instars. The latter appear in addition to the primary sensilla after the first molt and continue to proliferate until maturity when the larva may be covered with a dense vestiture. In these later stages this homogeneity and density obscures the recognition of the primary sensilla, but these often retain some distinctive characteristic, such as larger alveolus, occurrence in pairs, darker pigmentation, larger size, association with a tubercle or plate, or unique shape.

These patterns are very constant and follow a basic plan described as follows for all except segments VIII - IX (refer to figures 1 - 2 and 30 for further explanation):

**tergal sensilla** (t)—most mesal series on the dorsum on all segments. Usually obliterated in later instars by proliferation.

**subtergal** (st)—next laterad to the tergal sensilla, on all segments. Always distinguishable in later instars by position, setiform shape and large alveolus.

**tergopleural** (tp)—two sensilla situated far laterad on all segments. Associated with the dorsolateral tubercle or plate in those forms with these structures. A close-set pair of long, setiform sensilla on the meso- and metathorax (although paired, not serially homologous with abdominal "geminate setae").

**pre-dorsopseudopodal** (pdpod)—in the first instar a single sensillum on the extreme base of the pseudopod on the abdominal segments; an isolated seta on the thorax. In later instars a group of setae on the anterobasal angle of the dorsal pseudopod when this organ is present.

**dorso-pseudopodal** ("geminate setae") (dpod)—a pair of conspicuous, always large, setiform sensilla on the anterolateral angle of the trunk segments and lateral margin of the cephalic division in instars II-IV; on the dorsal surface of the base of the pseudopod in the first instar. These sensilla are located at the apices of the dorsal pseudopods when this organ occurs and at the apex of the posterolateral lobe of the anal division (which is a dorsal pseudopod anatomically).

**pleural** (p)—a single seta, variously positioned on the lateral margin. Usually completely obscured by the secondary setae in later instars.

**sternopleural** (sp)—on the thorax of *Neocurupira chiltoni* a single, heavy seta between the conspicuous ventral substernal and lateral pleural hairs.

**substernal** (ss)—a large conspicuous seta on the venter of the thoracic segments, laterad of the sucker and minute **sternal** (s) setae.

**pedichetal** (pd)—This group is contained within the ventral sucker and consists of three minute setae. As shown by Craig (1967: fig. 13 and p. 202) the anteriormost sucker belongs to abdominal segment I, the posteriormost to abdominal segment VI.

Pedichetal sensilla, therefore, appear to be wanting from the venters of the thorax and anal division.

In addition to the relatively large setate sensilla, there are various minute sense organs (**intertergal-it**, **intersternal-is**, **intercalary-ic**), some appearing as minuscule hairlike processes, other as hairless rings (sensilla campaniforme). Their positions are very constant in all instars and species, so they offer little more taxonomically than reference points.

Segments VIII and IX of the anal division are recognizable dorsally by lines of sensilla and sclerites. The complements of both, however, are reduced and the nomenclature just given does not apply strictly. On segment VIII a tergal sensillum remains distinct but the others are grouped into a single pleural group. On segment IX, the terminal segment, only a pair of pleurals are apparent besides the conspicuous **terminal setae**.

Both primary and secondary sensilla may take a variety of shapes, often characteristic of genera and species. On the abdomen of the first instar of the two forms which I have studied, all the primary sensilla are setiform except the tergal (t) and the more lateral of the tergopleurals, both of which are lanceolate or coniform. This is also true of the thorax except for the tergals and intertergals which are coniform and the pleurals which are claviform.

This pattern persists in later larval instars of *Blepharicera*, except that the majority of the dorsal secondary sensilla assume varied coniform, claviform or capitate shapes and arrangements which confer to them diagnostic value.

The function of these organs is unknown. I doubt their sensory importance because of their density. Their dorsal position and the frequent occurrence of specimens with heavy growths of diatoms and algae and even mineral precipitates entangled and attached to them, suggests a function similar to that of the "tectorial" setae and spines of psychodid larvae (Vaillant 1959:41), be it to help anchor or hide the animal. The roughened surface produced may also act physically to reduce resistance with the water, like sclerotized projections which could have the same function as suggested by Hora 1930:255. The condition would appear to be specialized and apomorphic since few hairs is the rule in nematoceros and mecopterous larvae.

My study of chaetotaxy remains incomplete, requiring much material now unavailable of first instar larvae of many genera. I am continuing to work on an analysis of the homologies of the sensilla and hope eventually to propose a system of nomenclature useful to morphologists and taxonomists. For the present, I present detailed illustrations of the patterns of sensilla in these few species with only general topographic names for taxonomic reference.

Probably associated with these sensillar modifications is the tendency of many larvae (although not *Blepharicera*) to form dorsal sclerotizations since the positions of the latter generally coincide with the locations of the primary setae. The dorsal pseudopod (as in *Agathon* and *Philorus*) for example, always bears the large paired dorso-pseudopodal (dpod) setae at its apex. The blepharicerid taxonomist is advised, however, to homologize such plates, tubercles and other sclerotized processes with great caution because these structures take similar forms in unrelated species and genera.

## PUPAL STRUCTURES

With the exception of Species F, I have been unable to discover characters on the pupa which permit species discrimination. Part of the problem is the lack of complete material of all species. This most conservative of life stages shows no divergence of structure, even in detail, among these very closely related Eastern species. Size varies continuously from the smallest, *diminutiva*, to the largest, *williamsae*, so cannot be used as a discrete objective character.

## ADULT STRUCTURES

Aside from the number of bristles on the parietal sclerite of the head, which varies from none in most males to up to 50 in females of *williamsae*, there is little in the general anatomy of either sex to reliably distinguish the species.

It should be emphasized that the latter statement is also largely true of size and external body coloration, although these characters formed the basis of Alexander's key (1963:52-53). After trying to reconcile the several hundred adults used in the present study with this key, I have come to the conclusion that coloration in this species group is a character of very limited use because, (1) it varies continuously from species to species (smaller species tending to be paler than larger) and (2) its interpretation is too easily confused by the condition and age of the specimen when killed, presence of grease, and the angle of lighting and viewing. Regarding this last point, I should explain that the integument induces interference phenomena in light rays reflected from it and it displays spectral colors when viewed from oblique angles. Thus, the pigmentary colors are obscured and distorted by other than perpendicular viewing and the thorax seems to change in color from gray to brown as the specimen is rotated under the stereoscopic microscope.

The most useful species characters in this group, as with most nematoceros Dip-tera, are to be found in the genitalia. In the male the following three character complexes are those applied mainly: (1) shape of the apex and shaft of the parameres; (2) shape of the apices of the penis filaments; and (3) shape of the IXth tergite lobes. All tend to be simpler in the smaller species, a fact which throws some light on the phylogeny of the group by suggesting that size differences may have generated allometric structures that present reproductive barriers (see REMARKS under *diminutiva*).

Genitalic features of the females are less well marked than in the males. *B. similans* is highly distinctive in lacking a normal median spermatheca (correlated with the overly long and apically modified median penis filament in the male) but the number of these organs remains three in all the other forms. Of use primarily are the following characters although even these all seem to be subject to such variation as to make identification of isolated or atypical specimens often impossible: (1) number and distribution of macrochaetae on the VIIIth sternite lobes, (2) shape of the median fold, especially the median basal sclerotization thereof, (3) sclerotizations of the spermathecal ducts.

An additional fairly definitive and constant character is the shape of an organ which

I interpret from gross morphology as the accessory gland. Unfortunately it is sometimes difficult to discern in slide mounts, but when evident its outline takes a variety of consistent forms.

### PROCEDURE

All statistics given are means with the range in parentheses. Unless otherwise noted, the sample size for each set of measurements was normally 10 for wings and legs, 2-5 for head structures. Wherever the sample was less than 10 (e. g. *diminutiva*), ranges are not given in the descriptions. Because of the small series available from specific localities, it was usually necessary to take data from mixed populations. Body length of larvae was measured only on prepupal individuals (pupal branchiae visible). Measurements in text and on the figures are in millimeters.

Proportions of leg segments are given as "progressive proportions" meaning that each segment is taken relative to that proximal rather than to one standard segment. This makes comparisons easier and more accurate since the segments are progressively shorter to a small degree or nearly equal in length; greatly differing and disjunct lengths need not be compared to one another.

In the case of antennal segment proportions, the basal flagellar segment is used as the standard since it is more conveniently and accurately measured than either the scape or pedicel which are both globular and difficult to orient consistently.

Material is listed separately for the stages. That for the larvae includes pupae which accompanied the specimens when collected but which were insufficiently mature to make an adult determination. Pupae containing pharate adults are treated as adult records and recorded in their section of the species accounts.

Some new morphological terms have been introduced. They appear in bold-face when first used in the text and their application explained in the following figures: female genitalia (Fig. 27); head capsule (Figs. 14-15); larva (Figs. 1-2, 30).

### TAXONOMY-ADULTS

#### *BLEPHARICERA, TENUIPES GROUP*

#### DIAGNOSIS

**COLORATION:** *General.*—Integument well sclerotized, generally gray-brown or deep red-brown with dull gray (plumbeous) overtones. Membranes and appendages pale yellow to medium brown. All major sclerite surfaces opalescent; head sclerite surfaces also finely pruinose. *Head.*—Face, occiput and basal portion of clypeus gray, pruinose. **Suprafrontal carina** and distal portion of clypeus dull orange to brown. **Callis oculi** shiny black. *Antenna.*—Scape brownish yellow, pedicel and flagellum dark brown. Mouthparts generally orange to yellow, palpus grading to brown apicad. *Thorax.*—Anterior pronotum, mesoscutum and scutellum gray to gray brown; posterior pronotum, posterolateral corners of scutum usually, and prescutellar area of

scutum often, contrasting pale brown or yellow. No other well-defined lines or patterns on scutum. Preepisternum, episternum and meron similar to scutum but lighter and sometimes with reddish-brown tints; remainder of pleuron light brown to yellow. *Legs*.—Brownish-yellow basad, grading to dark brown distad. *Wing*.—Hyaline in both sexes; veins brown. *Haltere*.—Stem yellow or light brown basad; knob dark brown. *Abdomen*.—Tergites and sternites similar to scutum. Pleural membranes yellow to brown. Genitalia yellow orange to dark brown.

*SIZE*: Generally medium to small Blephariceridae. Wing length, range 3.2 - 9.5 mm.

*HEAD: Structure*.—General structure as usually found in family. Antennal fossae approximate, mesofrons very narrow.

Female. Clypeus length/width 2.0-2.2. **Suprafrons** narrow, suprafrontal carina strongly convex. **Parietal sclerite** broad (0.7 times width of **infrafrons**), trapezoidal in shape. Ocellar lobes joined to form a sessile tubercle; lenses inserted on lobes apically. *Eyes*.—Approximate at level immediately anterior to ocelli, interocular distance equal to diameter of one ommatidium; upper division well differentiated from lower; callis oculi broad, anterior portion striate. Size of upper division about equal to lower in area, 13-16 rows of ommatidia along maximum dorsal arc of upper division; upper ommatidia 1.4-2.5 times diameter of lower. *Proboscis*.—Short, about 0.7 times head width. Mandibles present.

Male. Clypeus length/width ratio slightly greater than female, 2.4-3.6. **Suprafrons** broad, slightly convex mesally. Parietal sclerite broad, but narrower than in female (0.2-0.4 times width of **infrafrons**), rectangular in shape. Ocellar lobes distinct; lenses inserted on lobes apically. *Eyes*.—Disjunct at level immediately anterior to ocelli, interocular distance equal to diameters of 3-5 upper ommatidia; upper division well differentiated from lower; callis oculi absent except for narrow anterior portion. Size of upper division one-fourth to one-half of lower in area, 8-16 rows of ommatidia as in female. *Proboscis*.—Short, about 0.6 times head width. Mandibles absent. Palpal segments five, proportions constant, segment 1 small and fused at base to rostrum, 3 and 4 about equal and each slightly longer than 2, 5 three to four times length of 2, about equal to 2-3 combined. *Chaetotaxy*.—Similar in sexes, except parietal bristles usually absent in male. Major setal groups present as follows: clypeal, variably sparse over most of surface; parietal, few to numerous bristles; vertical, few short bristles; postvertical, numerous short bristles over dorsal arc of occipital foramen; occipital, numerous long bristles; postgenal, numerous long bristles. Ocular bristles short.

*ANTENNA. Structure*.—Moderately long, about 1.5 times head width, 15-segmented. Scape subspherical, pedicel conopiform, flagellomeres elongate-cylindrical in female, stouter and compressed in male. *Chaetotaxy*.—Scape with group of numerous long slender bristles mesoventrally. Pedicel with small dorsal and ventral groups of short bristles. Flagellomeres with dense vestiture of macrotrichia (these more numerous on male) and scattered placoid sensilla on apical segments (confined to apex of terminal segment in male).

*THORAX: Chaetotaxy*.—Setal patterns incompletely studied. Scutellar bristles dense laterally, incomplete or absent mesally. *Wing*.—Venation typical for genus.

Dorsal macrotrichia on veins  $R_5$  and  $M_3$  complete,  $M_{1+2}$  and  $M_4$  apically only. *Legs*.—Segments simple, tarsal segments 5 all unmodified. Tibial spurs absent from fore and mid legs, 1 or 2 on hind leg. Claws simple, similar and not enlarged.

**FEMALE GENITALIA:** VIIIth sternite lobes broadly rounded, with or without setae. Oviscapt subquadrate, base slightly wider than apex, inner piece poorly developed. Spermathecae three (rarely two) in number, generally ovoid in shape with no or poorly developed necks.

**MALE GENITALIA:** Segments VIII and IX not specially modified; IXth tergite lobes prominent, subquadrate in form, posterior margin with a small acute projection. Basistyle short and broad, slightly longer than outer dististyle. Latter a simple, elongate lobe, slightly depressed on inner surface apically. Inner dististyle a narrow curved spatulate lobe. Phallosome vesica small, spherical; apodeme a simple, vertical flange. Parameres and penis filaments varied in form.

## KEY TO SPECIES

### ADULT MALES

1. Median penis filament distinctly longer than laterals and with asymmetrical, hooked apex. Wing length 4.1 mm (3.4-4.65). Apex of paramere an incurved, asymmetrically bifurcate finger. IXth tergite lobe shape as in figure 22.  
..... *similans*  
Median penis filament about same length as laterals, apex unmodified or only slightly enlarged. Apex of paramere and IXth tergite lobe varied in shape but not as above. Wing length 3.2-6.6 mm ..... 2
2. Posterior margin of tegmen deeply incised on either side of midline. Apex of paramere a dorso-mesally directed hook. IXth tergite lobe as in figures 24 or 26. Wing length 5.4 mm (4.4-6.2) ..... *tenuipes*  
Posterior margin of tegmen entire. Other characters varied but not as above ... 3
3. Inner margin of IXth tergite lobe greatly expanded mesad (posteromesal corner obliterated). Larger species, wing length 4.8 mm or greater ..... 4  
Inner margin of IXth tergite lobe straight from posteromesal corner to base, not greatly expanded (posteromesal corner angulate). Smaller species, wing length 4.8 or less ..... 5
4. Inner wall of apex of paramere an incurved, acute process extending well beyond aperture. IXth tergite lobe shape as in fig. 28. Wing length 5.6 mm (4.9-6.6)  
..... *williamsae*  
Inner wall of apex of paramere very slightly produced, truncate; aperture terminal. IXth tergite lobe shape as in figure 16. Wing length 5.1 mm (4.8-5.3)  
..... *capitata*
5. Posterior margin of IXth tergite lobe with submesal projection, general shape as in figure 18. Wing length 4.4 mm (4.0-4.8) ..... *cherokea*  
Posterior margin of IXth tergite lobe straight, oblique, general shape as in figure 20. Wing length 3.8 mm (definitive range undetermined) ..... *diminutiva*

## ADULT FEMALES

1. Two spermathecae, median reduced to a cylindrical rod. Wing length 6.0 mm (5.4-7.3) ..... *similans*  
Three spermathecae. Wing length varied ..... 2
2. Ducts of lateral spermathecae sclerotized for a short length before genital aperture. Wing length 5.95 mm (5.2-6.4) ..... *capitata*  
Ducts of spermathecae membranous throughout. Wing length varied ..... 3
3. A large species, wing length 8.1 mm (6.75-9.5). Thoracic scutum with a contrasting light brown quadrate area anterior to scutellum. VIIIth sternite lobe of genitalia devoid of setae ..... *williamsae*  
Smaller species, wing length 7.1 mm or less. Thoracic scutum generally unicolorous. VIIIth sternite lobe of genitalia usually with at least one major seta ... 4
4. VIIIth sternite lobes contiguous, median fold V-shaped. Very small species, wing length 5.1 mm (definitive range undetermined) ..... *diminutiva*  
VIIIth sternite lobes disjunct, median fold U-shaped. Larger species, wing length usually greater than 6.0 mm (5.5-7.1) ..... 5
5. Mesoscutum reddish-brown. Accessory gland a straight tube with irregular anterior sclerotizations. Wing length 6.0 mm (5.5-6.5) ..... *cherokea*  
Mesoscutum dull gray (plumbeous). Accessory gland triangular, very broad posteriorly, membranous anteriorly; wing length 6.6 mm (6.0-7.1) ..... *tenuipes*

*BLEPHARICERA CAPITATA* (LOEW)

*Blepharoptera capitata* Loew 1863:298-299. LECTOTYPE by present designation, female, District of Columbia, Washington, 1866, C. R. Osten Sacken, (MCZ, No. 16124).

*Blepharocera capitata*, Osten Sacken 1895:161. Kellogg 1903 (partim).

*Blepharocera tenuipes*, Aldrich 1905:172 (original synonymy; attributed to Osten Sacken). Kellogg 1907:12. Alexander 1963:56.

*Blepharicera capitata*, Stone 1965:99.

*Blepharocera separata* Alexander 1963:54-55. NEW SYNONYMY.

## DESCRIPTIONS

**Adult female** (Figs. 9, 17)

SIZE: A medium-sized *Blepharicera*; measurements as follows: Wing length 5.95 (5.2-6.4), width 1.90 (1.60-2.10). Head width 1.06. Labrum length 0.31. Palpal segments 2-5, lengths: 0.10, 0.13, 0.145, 0.33. Leg segment lengths as below:

	fore	mid	hind
femur	3.6 (3.2-3.95)	3.6 (3.15-4.0)	4.85 (4.25-5.4)
tibia	3.1 (2.75-3.35)	3.05 (2.3-3.3)	4.45 (3.95-4.9)
tarsus 1	1.41 (1.25-1.64)	1.46 (1.30-1.60)	1.78 (1.64-1.91)
2	0.79 (0.68-0.88)	0.78 (0.66-0.85)	0.64 (0.58-0.71)
3	0.52 (0.44-0.55)	0.53 (0.48-0.56)	0.39 (0.34-0.43)
4	0.30 (0.28-0.34)	0.31 (0.25-0.39)	0.26 (0.20-0.30)
5	0.30 (0.25-0.34)	0.31 (0.25-0.36)	0.29 (0.24-0.33)

**THORACIC COLORATION:** Anterior pronotum, mesoscutum and scutellum reddish-brown with slight gray overtone especially mesad; preepisternum, episternum and meron like mesoscutum but lighter; remainder of pleuron pale yellow.

**HEAD (Fig. 9):** Parietal sclerite with few (1-8) setae, restricted to lower half of sclerite. Distal four palpal segment proportions: 1.0, 1.4, 1.1, 2.3. Antennal segment proportions: 0.87, 0.87, **1.0**, 0.70, 0.79, 0.77, 0.75, 0.75, 0.77, 0.78, 0.76, 0.76, 0.73, 0.74, 1.31; ultimate segment 1.70 length of penultimate.

**LEGS:** Tibial spur formula 0-0-2 (lesser very small). Progressive proportions of leg segment lengths as below:

foreleg: 1.00, 0.86, 0.46, 0.56, 0.66, 0.58, 1.01

midleg: 1.00, 0.85, 0.48, 0.53, 0.67, 0.59, 1.01

hindleg: 1.00, 0.92, 0.40, 0.36, 0.61, 0.68, 1.09

**GENITALIA (Fig. 17):** VIIIth sternite lobes broadly rounded, median fold U-shaped, very shallow; lobe with 0-4 (usually 1) macro setae, in posterolateral region. Spermathecae 3 in number, equal in size and oval in shape; necks absent; ducts variably sclerotized, usually with posterior-most sections of two lateral ducts narrowed, smoothly sclerotized and pigmented. Accessory gland broad, anterior portion sharply expanded spherically or semi-rectangularly.

**Adult male (Figs. 3, 16)**

**GENERAL:** Character states as given for female except as follows:

**SIZE:** Smaller than female; measurements as follows: Wing length 5.1 (4.8-5.3), width 1.68 (1.60-1.80). Head width 0.86 (0.82-0.89). Labrum length 0.22 (0.20-0.24). Palpal segments 2-5, lengths: 0.10, 0.13, 0.14, 0.38. Leg segment lengths as below:

	fore	mid	hind
femur	3.1 (2.8-3.4)	3.6 (3.1-5.85)	4.35 (3.9-4.7)
tibia	2.8 (2.65-3.05)	2.8 (2.65-3.00)	4.0 (3.65-4.4)
tarsus 1	1.48 (1.38-1.63)	1.47 (1.31-1.61)	1.53 (1.31-1.75)
2	0.78 (0.69-0.88)	0.73 (0.64-0.82)	0.52 (0.44-0.61)
3	0.54 (0.60-0.48)	0.52 (0.45-0.58)	0.34 (0.25-0.38)
4	0.29 (0.26-0.31)	0.29 (0.25-0.31)	0.24 (0.20-0.29)
5	0.27 (0.25-0.31)	0.28 (0.23-0.30)	0.25 (0.21-0.26)

**HEAD (Fig. 3):** Parietal sclerite without setae. Distal four palpal segment proportions: 1.0, 1.4, 1.6, 4.2. Antennal segment proportions: 0.70, 0.71, **1.0**, 0.97, 1.02, 1.05, 0.95, 0.98, 0.96, 1.0, 0.94, 0.94, 0.88, 0.85, 1.06; ultimate segment 1.2 length of penultimate.

**LEGS:** Tibial spur formula 0-0-1. Progressive proportions of leg segments as below:

foreleg: 1.00, 0.91, 0.52, 0.53, 0.70, 0.53, 0.94

midleg: 1.00, 0.78, 0.52, 0.50, 0.70, 0.55, 0.96

hindleg: 1.00, 0.92, 0.38, 0.34, 0.64, 0.72, 1.02

**GENITALIA (Fig. 16):** IXth tergite lobes prominent, parallel; lobe shape irregular, outer corner a rounded right angle, posterior margin projecting beyond outer angle

as a broadly rounded lobe which gradually curves into inner margin to base of lobe; bristles numerous and regular over entire dorsal surface. Paramere broad basally, gradually tapering apically and curving outwardly; apex truncate (inner margin slightly produced); aperture terminal. Penis filaments 3 in number, simple truncate rods, median slightly longer and stouter than laterals and with small apical collar or cap, all shorter than parameres.

#### VARIATION

Some females fail to exhibit the typical pigmented, sclerotized sections of the posterior extremes of both of the lateral spermathecal ducts. Neither duct may be so modified, but in any case this region of the duct is always narrowed and smooth walled in contrast to the wholly membranous tubules found in other species.

Males occur in which the median penis filament is scarcely stouter than the laterals, and the inner margin of the IXth tergite lobe is expanded. This character state conforms to that of the holotype of *Blepharicera separata* Alexander. Since these specimens are identical in all other ways with the presumed male of *capitata*, I choose to interpret these differences as minor and therefore synonymize Alexander's form.

#### REMARKS

Some authors have synonymized *capitata* with *tenuipes*, but apparently without basing their decision on a thorough examination of the types of *capitata*. I have assembled five specimens which appear to be from the original series (collected by Osten Sacken) including two females labelled "type" in the collection of MCZ. No males are among these although indicated in Loew's description. Believing Loew to be in error in citing the sex of his material, I have selected one of the latter two females as a lectotype.

Superficially these females are indistinguishable from typical *tenuipes*. However, the genitalia are distinct and define a separate species to which I assign equally distinct males found at the type locality where no other species are known to occur.

#### DISTRIBUTION (Fig. 37)

This species is found along the entire Appalachian chain and beyond to the north into New Brunswick. The form named *separata* by Alexander may appear anywhere in this range and apparently is no more than an occasional variant.

#### MATERIAL

*Adults*: DISTRICT OF COLUMBIA, Washington, 1866, C. R. Osten Sacken (1 ♀ LECTOTYPE: MCZ No. 16124; 4 ♀ PARALECTOTYPES: MCZ No. 16124, AMNH, USNM). GEORGIA, *Rabun County*. Pine Mountain, 1400 feet, 15 May 1957, W. R. M. Mason (21 ♂, 6 ♀: CNC). *Towns County*. Hiawassee, 16 June 1945, P. W. Fattig (1 ♂: USNM). MARYLAND, *Cecil County*. Octorora Canyon, 17 June 1939, E. G. Fisher (1 ♀: ANSP). *Prince George's County*. Beltsville, 28 May 1916, W. L. McAtee (2 ♀: USNM). NEW HAMPSHIRE, *Grafton County*. Franconia, Mrs. Slosson (1 ♂: USNM). PENNSYLVANIA, *Monroe County*. Delaware Water Gap, 15 June 1934, C. P. Alexander (1 ♂: USNM). VIRGINIA, *Fairfax County*. Great Falls, 21 June 1931, A. L. Melander (1 ♀: USNM); Trammel's Landing, Potomac River, [above Great Falls, now Riverbend County Park] 26, 28 May 1935, A. Stone (1 ♂, 2 ♀: USNM). VERMONT, *Chittenden County*. Smuggler's Notch, 18 June 1927, C. P. Alexander (♀: USNM).

Atypical (*separata* form).—MAINE, *Somerset County*. Bingham, along the Kennebec River, 17 July 1937, C. P. Alexander (3♂ PARATYPES: CPA). NEW BRUNSWICK, *Northumberland County*. Boiestown, 13 July 1931, J. M. Aldrich (1♂:USNM). NORTH CAROLINA, *Madison County*. Hot Springs (1♂:AMNH). *Swain County*. Soco Valley, Cherokee, 20 June 1954, J. W. Green (1♀:CAS). NEW YORK, *Fulton County*. Sport Island, Sacandaga River, 18 June 1914, C. P. Alexander (2♀:USNM). PENNSYLVANIA, *Lebanon County*. Ono, 7 June 1940, A. L. Melander (1♀:USNM). VERMONT, *Windham County*. Dummerston, 14 July 1908 (1♀:USNM).

### *BLEPHARICERA CHEROKEA* NEW SPECIES

#### DIAGNOSIS

##### Adults

*Blepharicera cherokea* is well defined only by characters found in the male genitalia, principally the shapes of the IXth tergite lobes and apex of the paramere. The former resembles that of *tenuipes*, but the small median lobe on the hind margin is decidedly more mesal and the outer corner less pronounced. The latter presents a complex appearance in *tenuipes*, being a dorso-mesally directed, asymmetrical hook, formed by elaboration of the inner wall, while in *cherokea* both inner and outer walls terminate almost equally, giving the structure an oblique, truncate apex.

Female specimens with the anterior portion of the accessory gland irregularly sclerotized are tentatively assigned to this species. There is little else to separate them from *tenuipes*, the most closely related entity.

#### ETYMOLOGY

This species is named in honor of the Cherokee Indian Nation, in whose homeland it resides.

#### DESCRIPTIONS

##### Adult female (Figs. 10, 19)

SIZE: A moderately-small *Blepharicera*; measurements as follows: wing length 6.0 (5.5-6.5), width 1.96 (1.85-2.15). Head width 1.10. Labrum length 0.32. Palpal segments 2-5, lengths: 0.10, 0.14, 0.15, 0.49. Leg segment lengths as below:

	fore	mid	hind
femur	3.7 (3.35-4.1)	3.6 (3.15-4.0)	4.8 (4.35-5.1)
tibia	3.1 (2.7-3.4)	2.9 (2.55-3.05)	4.4 (3.9-4.6)
tarsus 1	1.44 (1.31-1.53)	1.48 (1.24-1.61)	1.90 (1.63-2.06)
2	0.75 (0.63-0.85)	0.72 (0.60-0.81)	0.66 (0.63-0.75)
3	0.46 (0.38-0.55)	0.45 (0.38-0.54)	0.38 (0.29-0.43)
4	0.28 (0.23-0.34)	0.27 (0.23-0.29)	0.26 (0.23-0.28)
5	0.29 (0.25-0.35)	0.29 (0.25-0.33)	0.29 (0.26-0.31)

THORACIC COLORATION: Anterior pronotum, mesoscutum and scutellum reddish-brown with gray overtone, especially mesally; lateral corners of anterior and posterior

pronota yellow; preepisternum, episternum and meron like mesoscutum but lighter; remainder of pleuron pale yellow.

**HEAD** (Fig. 10): Parietal sclerite with numerous (20-30) setae over entire median portion. Distal four palpal segment proportions: 1.0, 1.4, 1.5, 4.9. Antennal segment proportions: 0.85, 0.85, **1.0**, 0.69, 0.77, 0.85, 0.77, 0.77, 0.75, 0.77, 0.69, 0.69, 0.62, 0.69, 1.08; ultimate segment 1.56 length of penultimate.

**LEGS**: Tibial spur formula 0-0-2, (lesser spur of hind leg about one-half the size of greater). Progressive proportions of leg segments as below:

foreleg: 1.00, 0.82, 0.47, 0.52, 0.61, 0.61, 1.04

midleg: 1.00, 0.82, 0.51, 0.49, 0.63, 0.60, 1.07

hindleg: 1.00, 0.92, 0.43, 0.35, 0.58, 0.68, 1.12

**GENITALIA** (Fig. 19): VIIIth sternite lobes wide-set, median fold shallowly U-shaped; each lobe with few to numerous setae. Spermathecae 3 in number, equal in size and ovoid in shape; necks short. Accessory gland a straight tube with irregular anterior sclerotizations.

#### **Adult male** (Figs. 4, 18)

**GENERAL**: Character states as given for female except as follows:

**SIZE**: Smaller than female; measurements as follows: Wing length 4.4 (4.0-4.8), width 1.48 (1.35-1.70). Head width 0.67. Labrum length 0.19. Palpal segments 2-5, lengths 0.10, 0.14, 0.14, 0.39. Leg segment lengths as below:

	fore	mid	hind
femur	2.8 (2.55-3.1)	2.9 (2.6-3.55)	3.75 (3.4-4.3)
tibia	2.6 (2.35-2.9)	2.5 (2.25-2.8)	3.5 (3.2-3.9)
tarsus 1	1.46 (1.33-1.63)	1.39 (1.26-1.50)	1.35 (1.23-1.48)
2	0.73 (0.64-0.81)	0.69 (0.60-0.78)	0.45 (0.40-0.50)
3	0.51 (0.44-0.58)	0.49 (0.41-0.54)	0.28 (0.25-0.31)
4	0.25 (0.23-0.28)	0.25 (0.21-0.26)	0.18 (0.16-0.23)
5	0.23 (0.20-0.25)	0.23 (0.20-0.25)	0.20 (0.18-0.25)

**HEAD** (Fig. 4): Parietal sclerite without setae. Distal four palpal segment proportions: 1.0, 1.4, 1.4, 4.0. Antennal segment proportions: 0.63, 0.63, **1.0**, 0.94, 1.16, 1.18, 1.10, 1.10, 1.10, 1.18, 1.18, 1.18, 1.10, 1.18, 1.26; ultimate segment 1.06 length of penultimate.

**LEGS**: Tibial spur formula 0-0-1. Progressive proportions of leg segments as below:

foreleg: 1.00, 0.92, 0.50, 0.50, 0.70, 0.49, 0.92

midleg: 1.00, 0.86, 0.55, 0.50, 0.70, 0.50, 0.94

hindleg: 1.00, 0.93, 0.39, 0.33, 0.62, 0.65, 1.13

**GENITALIA** (Fig. 18): IXth tergite lobes prominent, parallel; lobe shape subquadrate, outer posterior corner a rounded right angle, not prominent; pointed lobe projecting from hind margin displaced mesad; bristles numerous and regular over entire dorsal surface. Tegmen entire, with a slight apico-median carina. Paramere broad basally, tapering regularly and gradually to apex; apex simple, obliquely truncate (inner wall only very slightly longer than outer); aperture terminal. Penis filaments

3 in number, equal in length, shorter than parameres, all simple truncate rods, the median slightly stouter than laterals.

#### VARIATION

The number of setae on the VIIIth sternite lobe of the female varies from 3 to 8. This indicates possible heterogeneity in the small sample available to me. Associated material is definitely needed to confirm the identity of the females of this species.

#### REMARKS

Association of the sexes is in some doubt because no females are available from the type locality. Collecting from populations containing known males should easily resolve the question.

#### DISTRIBUTION (Fig. 39)

This species is known only from the type locality and collections near the southern end of the Appalachians (Georgia and North Carolina).

#### MATERIAL

*Types*.—HOLOTYPE ♂ (genitalia on slide no. CLH 75-166; head on slide no. CLH 75-239; NORTH CAROLINA, *Macon County*. Highlands, Clear Creek, 3200 feet, 1-2 July 1958, J. G. Franclemont. 25 PARATYPE ♂: same data as holotype. All deposited at CU.

*Additional specimens*. GEORGIA, *Dawson County*. Amicalola Falls No. 5, 14 June 1960, G. W. Byers (19♀:KU). NORTH CAROLINA, *Swain County*. Bryson City, 3-5000 feet, May 1936, R. C. Shannon (1♂:USNM); Cherokee, Soco Valley, 20 June 1954, J. W. Green (1♀:CAS); Cherokee, 2000 feet, 24 May 1957, W. R. M. Mason (1♀:CNC). TENNESSEE, *Sevier County*. Greenbrier Cove, 2000 feet, Great Smoky Mountains National Park, 18 May 1957, J. R. Vockeroth (2 ♂:CNC).

### *BLEPHARICERA DIMINUTIVA* NEW SPECIES

#### DIAGNOSIS

##### Adults

Although this is the smallest species of *Blepharicera* it is set apart from the other members of its group primarily by unique features of the male genitalia: a simple, subquadrate IXth tergite lobe rather than the complex and marginally expanded shapes of all the other species, and the paramere apex with merely a thin, truncate extension of the shaft in place of being forked or spined in various ways. The females are difficult to distinguish because the most reliable character (shape of the accessory gland) is often obscure. This structure is an indefinite, membranous tube in this species whereas in the other species it assumes a variety of forms as a result of sclerotization. Also characteristic, but ill-defined, are the close-set VIIIth tergite lobes, meeting with a V-shaped median fold between; in all the other species the median fold is much broader, U-shaped and often with angular basal corners.

#### ETYMOLOGY

The name is derived from the Latin adjective *diminutivus*, meaning tiny, in reference to the species' small size.

## DESCRIPTIONS

**Adult female** (Figs. 11, 21)

SIZE: A very small *Blepharicera*; measurements as follows: Wing length 5.1, width 1.63. Head width 0.97. Labrum length 0.32. Palpal segments 2-5, lengths: 0.09, 0.12, 0.13, 0.44. Leg segment lengths as below:

	fore	mid	hind
femur	3.3	3.1	4.2
tibia	2.7	2.55	3.9
tarsus 1	1.25	1.2	1.6
2	0.595	0.545	0.52
3	0.39	0.34	0.33
4	0.215	0.215	0.21
5	0.23	0.23	0.22

THORACIC COLORATION: Anterior pronotum and mesoscutum generally brownish-gray; scutellum brownish-yellow; corner of posterior pronotum yellow; preepisternum, episternum and meron like mesoscutum but lighter; remainder of pleuron brownish-yellow.

HEAD (Fig. 11): Parietal sclerite with numerous setae over entire median portion. Distal four palpal segment proportions: 1.0, 1.3, 1.4, 4.9. Antennal segment proportions: 0.85, 0.77, 1.0, 0.85, 0.92, 0.77, 0.77, 0.77, 0.77, 0.69, 0.69, 0.69, 0.54, 0.54, 1.0; ultimate segment 1.85 length of penultimate.

LEGS: Tibial spur formula 0-0-2 (lesser spur of hind leg minute). Progressive proportions of leg segment lengths as below:

foreleg: 1.00, 0.82, 0.47, 0.48, 0.66, 0.55, 1.07

midleg: 1.00, 0.82, 0.46, 0.46, 0.62, 0.63, 1.07

hindleg: 1.00, 0.92, 0.42, 0.32, 0.64, 0.64, 1.05

GENITALIA (Fig. 21): VIIIth sternite lobes close-set, median fold V-shaped; each lobe with a few (4-6) macro setae. Spermathecae 3 in number, equal in size and ovoid in shape; necks short to nearly absent; ducts membranous throughout. Accessory gland a simple membranous tube, without definite shape.

**Adult male** (Figs. 5, 20)

GENERAL: Character states as given for female except as follows:

SIZE: Smaller than female; measurements as follows: Wing length 3.8, width 1.29. Head width 0.65. Labrum length 0.17. Palpal segments 2-5, lengths: 0.09, 0.09, 0.10, 0.35. Leg segment lengths as below:

	fore	mid	hind
femur	2.3	2.4	3.2
tibia	2.1	2.05	2.95
tarsus 1	1.13	1.07	1.17
2	0.51	0.50	0.35
3	0.35	0.35	0.22
4	0.19	0.19	0.145
5	0.17	0.18	0.17

HEAD (Fig. 5): Parietal sclerite without setae. Distal four palpal segment proportions: 1.0, 1.0, 1.1, 3.9. Antennal segment proportions: 0.90, 0.70, 1.0, 0.80, 0.90, 1.0, 0.90, 0.90, 0.80, 0.90, 0.80, 0.90, 0.80, 0.90, 0.80, 0.90, 1.10; ultimate segment 1.2 length of penultimate.

LEGS: Tibial spur formula 0-0-1. Progressive proportions of leg segment lengths as below:

foreleg: 1.00, 0.91, 0.54, 0.45, 0.69, 0.54, 0.89

midleg: 1.00, 0.85, 0.52, 0.46, 0.70, 0.54, 0.94

hindleg: 1.00, 0.91, 0.40, 0.30, 0.63, 0.66, 1.15

GENITALIA (Fig. 20): IXth tergite lobes prominent, slightly divergent; lobe shape subquadrate, a slight lobe projecting from midposterior margin, inner margin straight; bristles numerous and regular over entire dorsal surface. Tegmen entire. Paramere with a broad base, straight and gradually tapering shaft; apex a short, truncate, thin extension, with a slightly produced inner margin; aperture terminal. Penis filaments 3 in number, equal in length, shorter than parameres; all simple, similar, capitate rods.

#### REMARKS

The simplicity of several characters in both sexes (shape of the male IXth tergite lobe, V-shaped female median fold) of this species, its overall smallness and its rarity raise the possibility that it may actually constitute the negative allomorphic variant of another, sympatric form, perhaps *cherokea*. However, until this can be positively demonstrated, I think the entity should be recognized as a species.

#### DISTRIBUTION (Fig. 38)

This species has the most restricted range of the eastern *Blepharicera*. It is known only from localities clustered in the southernmost sector of the Blue Ridge Mountains located at the junction of the states of Georgia, South Carolina and North Carolina.

#### MATERIAL

*Types*.—HOLOTYPE ♂ (genitalia on slide no. CLH 75-177; wing on slide no. CLH 75-243); NORTH CAROLINA, *Macon County*. Highlands, Clear Creek, 3200 feet, 1 July 1958, J. G. Franclemont; ALLOTYPE ♀ (genitalia on slide no. CLH 75-155; mid and hind legs on slide no. CLH 75-248); 1 PARATYPE ♂ and 1 PARATYPE ♀: same data as holotype. All deposited at CU.

*Additional specimens*.—NORTH CAROLINA, *Transylvania County*. Lake Toxaway, 12 July 1957, J. G. Chillcott (1 ♂:CNC). GEORGIA, *Rabun County*. Addie Branch, east fork of Chattooga River, 2400 feet, 1 August 1957, J. G. Chillcott (1 ♀:CNC); Rabun Bald, 3000 feet, 14 July 1957, J. G. Chillcott (1 ♀:CNC); Tallulah Falls, 10 June 1910 (1 ♀:CU); Satalah, 2000 feet, 1 July 1957, J. R. Vockeroth (2♂:CNC).

#### *BLEPHARICERA SIMILANS* (JOHANNSEN)

*Blepharocera similans* Johannsen 1929: 123-124. Type locality, Massachusetts, Hampshire County, Orient Springs, near Amherst. Holotype male, CU.

*Blepharocera similans*, Johannsen 1934:50. Alexander 1963:55.

*Blepharicera similans*, Stone 1965:99.

## DESCRIPTIONS

**Adult female** (Figs. 12, 23)

SIZE: A medium-sized *Blepharicera*; measurements as follows: Wing length 6.0 (5.4-7.3), width 2.05 (1.69-2.75). Head width 1.08. Labrum length 0.37. Palpal segments 2-5, lengths: 0.11, 0.14, 0.14, 0.45. Leg segment lengths as below:

	fore	mid	hind
femur	3.5 (2.3-4.25)	3.76 (3.25-6.65)	4.8 (4.25-5.65)
tibia	3.0 (2.75-3.55)	2.9 (2.6-3.25)	4.3 (3.7-5.05)
tarsus 1	1.44 (1.26-1.68)	1.30 (1.15-1.44)	1.70 (1.41-2.0)
2	0.71 (0.57-0.81)	0.67 (0.54-0.76)	0.60 (0.46-0.73)
3	0.41 (0.26-0.50)	0.41 (0.30-0.46)	0.36 (0.28-0.41)
4	0.30 (0.29-0.33)	0.26 (0.21-0.30)	0.26 (0.21-0.30)
5	0.34 (0.28-0.43)	0.33 (0.30-0.40)	0.34 (0.31-0.39)

THORACIC COLORATION: Anterior pronotum and mesoscutum generally dark gray-brown; scutellum distinctly lighter than mesoscutum, brown, darker laterally; preepisternum, episternum and meron reddish brown; remainder of pleuron light-brown.

HEAD (Fig. 12): Parietal sclerite with numerous setae (15-20) on lateral half of surface. Distal four palpal segment proportions: 1.0, 1.25, 1.2, 4.0. Antennal segment proportions: 0.60, 0.80, **1.0**, 0.78, 0.71, 0.75, 0.66, 0.63, 0.63, 0.60, 0.59, 0.59, 0.59, 0.54, 0.93; ultimate segment 1.72 length of penultimate.

LEGS: Tibial spur formula 0-0-1. Progressive proportions of leg segment lengths as below:

foreleg: 1.00, 0.86, 0.47, 0.49, 0.58, 0.75, 1.12

midleg: 1.00, 0.77, 0.44, 0.51, 0.61, 0.63, 1.28

hindleg: 1.00, 0.89, 0.40, 0.35, 0.60, 0.72, 1.32

GENITALIA (Fig. 23): VIIIth sternite lobes broadly rounded, median fold deep, U-shaped, basal corners angular; lobe without setae. Spermathecae 2 in number, the median one reduced to a vestigial, sclerotized bar; laterals ovoid, equal in size and in shape; necks very short; ducts membranous throughout. Accessory gland cylindrical with a slightly inflated median zone.

**Adult male** (Figs. 6, 22)

GENERAL: Character states as given for female except as follows:

SIZE: Smaller than female; measurements as follows: Wing length 4.1 (3.4-4.65), width 1.32 (1.20-1.50). Head width 0.73 (0.69-0.82). Labrum length 0.21 (0.18-0.24). Palpal segments 2-5, lengths 0.08, 0.12, 0.12, 0.42. Leg segment lengths as below:

	fore	mid	hind
femur	2.6 (2.2-3.05)	2.7 (2.2-3.2)	3.55 (2.9-4.25)
tibia	2.4 (1.9-2.9)	2.3 (2.0-2.7)	3.3 (2.7-3.85)
tarsus 1	1.31 (0.85-1.56)	1.26 (0.98-1.48)	1.23 (0.98-1.45)
2	0.62 (0.44-0.75)	0.60 (0.49-0.74)	0.39 (0.33-0.48)

	fore	mid	hind
3	0.42 (0.28-0.61)	0.41 (0.33-0.48)	0.23 (0.16-0.30)
4	0.22 (0.13-0.28)	0.22 (0.16-0.28)	0.16 (0.13-0.19)
5	0.22 (0.16-0.28)	0.22 (0.16-0.28)	0.20 (0.13-0.24)

HEAD (Fig. 6): Parietal sclerite without setae. Distal four palpal segment proportions: 1.0, 1.3, 1.4, 4.1. Antennal segment proportions: 0.77, 0.68, **1.0**, 0.79, 0.82, 0.86, 0.79, 0.76, 0.72, 0.74, 0.75, 0.81, 0.80, 0.83, 1.11; ultimate segment 1.3 length of penultimate.

LEGS: Tibial spur formula 0-0-1. Progressive proportions of leg segments as below:

foreleg: 1.00, 0.93, 0.55, 0.47, 0.68, 0.51, 1.02

midleg: 1.00, 0.86, 0.54, 0.47, 0.68, 0.54, 1.00

hindleg: 1.00, 0.94, 0.37, 0.32, 0.59, 0.70, 1.25

GENITALIA (Fig. 22): IXth tergite lobes prominent, parallel; lobe shape irregular, outer corner a rounded right angle, posterior margin projecting posteriorly as an acute prominence, inner margin evenly and shallowly curved to the slightly constricted base; bristles numerous and regular over entire dorsal surface. Tegmen entire. Paramere broad basally, tapering gradually to two-thirds, then abruptly narrowing ectally to point where ental wall terminates, apex extended beyond aperture as a gradually incurved, asymmetrically bifurcate finger. Penis filaments 3 in number, all shorter than paramere but median heavier and longer than laterals and with a hooked apex.

#### VARIATION

No notable variations were observed in this species, which is the most constant and distinctive member of the *Tenuipes* Group.

#### REMARKS

The female of this species is unique in the genus in the absence of the median spermatheca. The organ is replaced by an elongate structure apparently modified especially to receive the male's extra long, hooked, median penis filament. The functional significance of this adaptation is unknown.

#### DISTRIBUTION (Fig. 40)

There are collections of *similans* from localities along the entire Appalachian chain from Maine to South Carolina and Tennessee. The species is sympatric with all the other members of its group, but would appear to be the least likely one to hybridize because of the genitalic peculiarities mentioned above. This also, perhaps, explains its lack of variability.

#### MATERIAL

*Adults*.—CANADA. NOVA SCOTIA, *Colchester County*. Truro, 4 July 1913, R. Matheson (3 ♂:CU). QUEBEC, *Gatineau County*. Wakefield, 9 July 1946, G. E. Shewell (2 ♂:CNC); 18 September 1928, 25 July 1926, F. P. Ide (1 ♂, 1 ♀:ROM); 21 July 1926, G. S. Walley (1 ♂, 1 ♀:CNC); 1 July 1959, J. R. Vockeroth (1 ♂, 1 ♀:CNC). *Huntingdon County*. Covey Hill, 8 July 1924, G. S. Walley (1 ♂:CNC). *Laprarie County*. Laprarie, 8 July 1924, G. S. Walley (1 ♂:CNC). UNITED STATES. GEORGIA, *Dawson County*. Amicalola Falls No. 5,

14 June 1960, G. W. Byers (1 ♀:KU). *Rabun County*. Satalah, 2000 feet, 1 July 1957, J. R. Vockeroth (5 ♂:CNC). Warwoman Creek, 1500 feet, 31 July 1957, J. G. Chillcott (2 ♂, 1 ♀:CNC). MASSACHUSETTS, *Hampshire County*. Amherst, 25 June 1927 (1 ♂:BMNH), Orient Springs, 375 feet, 30 May 1926, C. P. Alexander (1 ♀:CPA). NEW HAMPSHIRE, *Coos County*. Gorham, 18 July 1929, G. S. Walley (5 ♂:CNC). Moose Creek, Gorham, 19 July 1929, J. McDunnough (1 ♀:CNC). Dolly Copp, White Mountains, 29 August 1937, A. L. Melander (1 ♂, 5 ♀:USNM). *County Unknown*. White Mountains, Morrison (2♂:USNM). NEW YORK, *Essex County*. Wilmington, Adirondacks, 31 July 1929, A. L. Melander (4 ♂, 6 ♀:USNM). High Falls, Ausable River, 5 July 1938, C. P. Alexander (2 ♂:USNM). Lake Placid, 28 July 1929, A. L. Melander (5 ♂:USNM); 1 July 1922, J. M. Aldrich (3 ♂:USNM); 19 July 1962, J. R. Vockeroth (3 ♀:CNC). NORTH CAROLINA, *Avery County*. Linville, 3200 feet, 21 June 1939, C. P. Alexander (3 ♀:CPA). *Macon County*. Clear Creek, Highlands, 3200 feet, 1-2 July 1958, J. G. Franclemont (18 ♂:CU). Wayah Bald, 3500 feet, 6 July 1957, J. R. Vockeroth (1 ♀:CNC). Wayah Gap, 3500 feet, 10 August 1957, J. G. Chillcott (2 ♀:CNC). *Swain County*. Smokemount, 2 July 1941, A. L. Melander (1 ♂:USNM). Bryson City, 3-5000 feet, May 1936, R. C. Shannon (1 ♂:USNM). *Wilkes County*. Stone Mountain State Park, 10 July 1973, G. K. Pratt (2 ♂, 2 ♀:HDP). TENNESSEE, *Sevier County*. Chimneys, Great Smoky Mountains National Park, 8 July 1941, A. L. Melander (1 ♂:USNM). Smoky Mountains, 23 October 1938, I. Williams (1 ♀:CPA). VIRGINIA, *Page County*. Luray, 24 June 1933, A. L. Melander (2 ♂:USNM).

*Pupae* (pharate adults dissected).—UNITED STATES. NEW YORK, *Jefferson County*. Watertown, 30 November 1881, J. Q. Adams, No. 2213 (8 ♀, 3 pupae, 20 larvae:USNM). *Ulster County*. Vermooy Kill, 3/4 mi NW Wawarsing, 28 July 1974, P. & B. Wygodzinsky (26 pupae, 8 larvae:AMNH). NORTH CAROLINA, *Swain County*. Noland Creek, Great Smoky Mountains National Park, 16 August 1973, 24 May 1974, R. L. Green (1 pupa :LACM). TENNESSEE, *Sevier County*. Greenbrier Cove, Smoky Mountains National Park, 22 May, 10 September (?) 1938, A. C. Cole (34 pupae:UT). VIRGINIA, *Giles County*. Stoney Creek, 1800, 2000 feet, 26 May 1962, J. R. Vockeroth (18 pupae, 48 larvae:CNC). *County Unknown*. Dark Hollow Falls, Shenandoah National Park, 30 July 1949, E. A. Chapin (15 pupae:USNM).

### *BLEPHARICERA TENUIPES* (WALKER)

*Asindulum tenuipes* Walker 1848:86. Type locality, CANADA, Ontario, Albany River, holotype female, BMNH.

*Blepharocera capitata*, Kellogg 1900:1903 (partim). Johannsen 1903:333-336.

*Blepharocera tenuipes*, Comstock & Comstock 1895:432-436. Aldrich 1905:172. Kellogg 1907:12. Johannsen 1934:54. Alexander 1963:56.

*Blepharicera tenuipes*, Stone 1965:99.

### DESCRIPTIONS

#### Adult female (Figs. 14-15, 27)

SIZE: A medium-sized *Blepharicera*; measurements as follows: Wing length 6.6 (6.0-7.1), width 2.1 (1.78-2.4). Head width 1.08 (1.01-1.44). Labrum length 0.38. Palpal segments 2-5, lengths: 0.11, 0.15, 0.17, 0.46. Leg segment lengths as below:

	fore		mid		hind	
femur	3.9	(3.4-4.3)	3.8	(3.35-4.2)	5.4	(4.9-5.8)
tibia	3.3	(3.0-3.6)	3.2	(2.9-3.45)	4.9	(4.3-5.3)
tarsus 1	1.57	(1.30-1.79)	1.31	(0.89-1.65)	2.10	(1.84-2.21)
2	0.82	(0.68-0.94)	0.77	(0.56-0.94)	0.75	(0.68-0.84)
3	0.52	(0.45-0.60)	0.49	(0.41-0.59)	0.44	(0.40-0.49)
4	0.32	(0.24-0.37)	0.33	(0.27-0.40)	0.33	(0.28-0.37)
5	0.39	(0.33-0.46)	0.40	(0.33-0.46)	0.36	(0.28-0.43)

**THORACIC COLORATION:** Anterior pronotum and mesoscutum generally dull gray (plumbeous), corner of posterior pronotum and scutellum contrasting light brown, latter darker laterad; preepisternum, episternum and meron similar to scutum but paler and with reddish-brown cast; remainder of pleuron brownish-yellow.

**HEAD** (Figs. 14-15): Parietal sclerite with numerous setae (22-32) over entire median surface. Distal four palpal segment proportions: 1.0, 1.4, 1.1, 2.7. Antennal segment proportions: 0.92, 1.00, **1.0**, 0.85, 0.85, 0.85, 0.77, 0.77, 0.81, 0.85, 0.77, 0.77, 0.69, 0.62, 0.92; ultimate segment 1.50 length of penultimate.

**LEGS:** Tibial spur formula 0-0-2 (spurs subequal). Progressive proportions of leg segment lengths as below:

foreleg: 1.00, 0.84, 0.47, 0.52, 0.63, 0.62, 1.22  
 midleg: 1.00, 0.85, 0.40, 0.59, 0.64, 0.67, 1.21  
 hindleg: 1.00, 0.90, 0.43, 0.36, 0.59, 0.75, 1.09

**GENITALIA** (Fig. 27): VIIIth sternite lobes broadly rounded, median fold shallow and wide at base; lobe with a few (usually 6-7) macro setae. Spermathecae 3 in number, equal in size and ovoid in shape; necks very short; ducts membranous throughout. Accessory gland triangular, very broad posteriorly, tapering strongly anteriorly.

**Adult male** (Figs. 7, 24-26)

**GENERAL:** Character states as given for female except as follows:

**SIZE:** Smaller than female; measurements as follows: Wing length 5.4 (4.4-6.2), width 1.83 (1.56-2.16). Head width 0.86 (0.81-0.94). Labrum length 0.25 (0.22-0.29). Palpal segments 2-5, lengths 0.12, 0.15, 0.16, 0.44. Leg segment lengths as below:

	fore		mid		hind	
femur	3.3	(2.9-3.7)	3.5	(3.0-3.9)	4.7	(4.1-5.0)
tibia	3.1	(2.7-3.4)	2.95	(2.6-3.3)	4.3	(3.8-4.6)
tarsus 1	1.60	(1.24-1.85)	1.53	(1.28-1.76)	1.68	(1.38-1.87)
2	0.82	(0.71-0.92)	0.77	(0.67-0.89)	0.56	(0.46-0.68)
3	0.55	(0.39-0.70)	0.53	(0.41-0.63)	0.38	(0.33-0.57)
4	0.31	(0.27-0.35)	0.31	(0.26-0.35)	0.25	(0.21-0.35)
5	0.31	(0.24-0.41)	0.29	(0.26-0.33)	0.27	(0.23-0.33)

**HEAD** (Fig. 7): Parietal sclerite without setae. Distal four palpal segment proportions: 1.0, 1.25, 1.1, 2.75. Antennal segment proportions: 0.63, 0.63, **1.0**, 0.69, 0.81, 0.81, 0.78, 0.81, 0.81, 0.81, 0.78, 0.80, 0.78, 0.76, 0.91; ultimate segment 1.2 length of penultimate.

**LEGS:** Tibial spur formula 0-0-1. Progressive proportions of leg segments as below:

foreleg: 1.00, 0.92, 0.52, 0.51, 0.67, 0.56, 1.00  
 midleg: 1.00, 0.85, 0.52, 0.50, 0.69, 0.58, 0.94  
 hindleg: 1.00, 0.92, 0.39, 0.33, 0.68, 0.66, 1.08

**GENITALIA** (Figs. 24-26): IXth tergite lobes prominent, parallel; lobe shape irregular, generally quadrate, outer corner pronounced, rounded, posterior margin horizontal, with a mesally directed lobe near the middle; inner corner right angulate, the margin continuing straight to base; bristles numerous and regular over entire dorsal

surface. Tegmen deeply emarginate on either side of strong, median, vertical carina. Paramere broad basally, only slightly tapering apically and nearly straight; both inner and outer walls complete to apex; apex complex, a dorso-mesally directed, asymmetrical hook; aperture subterminal. Penis filaments 3 in number, simple truncate rods, of equal diameter, all shorter than paramere.

#### VARIATION

The southernmost record for typical *tenuipes* is Stoney Creek, Giles County, Virginia. All specimens from localities further south exhibit certain states approaching those found in *cherokea*. The most common involves the shape of the IXth tergite lobe of the male genitalia in which the small mesal projection of the posterior margin is displaced strongly mesad (Fig. 24) as in *cherokea* (Fig. 18). In other specimens, the posterolateral corner of this same structure is abnormally pronounced, a condition also reminiscent of *cherokea* or *williamsae* (Figs. 18, 28). The tegmen in some of these same specimens has very shallow excisions on either side of the postero-median carina. In all the other species the posterior margin of the tegmen is entire and without a carina except in *cherokea*. All variants preserve the typical *tenuipes* form of the apex of the paramere although there are a few *cherokea* specimens in which the normally simple apex is slightly extended and contorted in a fashion similar to the complexities found here in *tenuipes*. The existence of these intermediates suggests close genetic ties between *cherokea* and *tenuipes*. Although the possibility of hybridization exists present material is inadequate to reveal the real nature of these relationships.

Variations in the female genitalia are less well defined and so far involve only three specimens in which the number of macro setae on the VIIIth sternite lobes and configuration of the median fold are unusual.

#### REMARKS

This is the most common species of *Blepharicera* in Eastern North America. Since it is the oldest named regional form, the other similar species, especially *capitata*, have been confused with it. These two are indistinguishable externally, and the genitalic characters cited in the key must be used to separate them.

#### DISTRIBUTION (Fig. 41)

A map plot of the records below shows *tenuipes* to be the most widespread species in the group. It is mainly northern, although atypical specimens, tentatively assigned to this taxon, appear through the southernmost portions of the range of the genus in Tennessee, North Carolina and Georgia (see VARIATION above).

There are no records over a large area north of the Great Lakes, but widely disjunct collections, to the west at the Albany River, Ontario and eastern Minnesota, and abundant suitable habitats are cause to believe that the Great Lakes region is also populated with *tenuipes*. It is the only species found in the vicinity of Ithaca, New York where it has long been well known to entomologists and students at Cornell University.

#### MATERIAL

*Adults*.—CANADA. NOVA SCOTIA, *Kings County*. Kentville, 13 July 1924, R. P. Gorham (1 ♀:CNC). *Victoria County*. Baddeck, 27 June, 1 July 1936, J. McDunnough (3

♀:CNC). ONTARIO, *Carleton County*. Ottawa, 19 July 1924, G. S. Walley (1 ♀:CNC); 22-23 June 1943, G. S. Walley (4 ♀:CNC); 24 June 1943, A. Brooks (9 ♀:CNC); 15 June 1951, J. F. McAlpine (1 ♂, 5 ♀:CNC); 13 July 1956, J. R. Vockeroth (13 ♀:CNC). Shirley Bay, Ottawa, 23 June 1961, J. A. Downes (4 ♂, 4 ♀:CNC); Britannia, Ottawa, 15 June 1938, G. E. Shewell (1 ♂:CNC). Remic Rapids, Ottawa River, 18-21 June 1949, G. E. Shewell (2 ♂:CNC). *Wentworth County*. Dundas, 29 May 1960, Taylor and Wood (1 ♂, 1 ♀:MMU). QUEBEC, *Brome County*. Glensutton, 17 June 1936, G. S. Walley (1 ♀:CNC). Knowlton, 8 July 1929, L. J. Milne (1 ♀:CNC); 13 June 1930, G. S. Walley (1 ♂:CNC). *Gatineau County*. Aylmer, 10 June 1924, 26 June 1938, C. H. Curran (33 ♀:AMNH). Chelsea, 20-25 June 1916 (2 ♀:CU). Hull, 26 June 1920, 8 July 1923, Miss. Cramp, C. H. Curran (1 ♂, 1 ♀:CNC). Old Chelsea, 22 July 1956, J. R. Vockeroth (3 ♀:CNC). Royal Ottawa Golf Club, Ottawa, 14, 31 July 1924, 27 June 1932, F. P. Ide, G. S. Walley (5 ♀:CNC, ROM). Wakefield, 21 August 1925, 21, 26 July 1926, G. S. Walley (1 ♂, 3 ♀:CNC); 14 June 1926, 28 July 1926, 4 June 1935, 18 September 1928, 9 July 1946, F. P. Ide (12 ♂, 5 ♀:CNC, ROM); 1 July 1959, J. R. Vockeroth (1 ♂:CNC). *Huntingdon County*. Covey Hill, 11, 28 June, 4 July 1924, 15, 18 June 1927, G. S. Walley (2 ♂, 2 ♀:CNC). *Kamouraska County*. Parke Reserve, 9 July 1957, G. E. Shewell (1 ♂:CNC); 8 August 1957, W. R. M. Mason (2 ♀:CNC). *La Prairie County*. La Prairie, 8 July 1924, G. S. Walley (8 ♀:CNC). *Rouville County*. Richelieu, 5 July 1927, G. S. Walley (1 ♀:CNC). *Stanstead County*. Mount Orford, 14 July 1936, G. E. Shewell (1 ♀:CNC). UNITED STATES. CONNECTICUT, *Fairfield County*. Redding, 11 June 1929, A. L. Melander (1 ♀:USNM). MAINE, *Hancock County*. Bar Harbor, 4 June 1913, C. W. Johnson (1 ♀:USNM). MINNESOTA, *Cook County*. Minnesota "F. S.", Hovland, 23 June 1968, E. F. Cook, N.J. mosquito trap (1 ♂:USNM). NEW JERSEY, *Morris County*. Brookside, July, A. J. Weidt (3 ♀:AMNH, USNM). NEW HAMPSHIRE, *Coos County*. Bretton Woods, 1 July 1936, A. L. Melander (2 ♂:USNM); Gorham, 18, 20 July 1929, J. McDunnough (2 ♀:CNC); Jefferson (black light trap), 10 July 1964 (1 ♀:UNH). *Grafton County*. Benton, 6 July 1931, A. L. Melander (5 ♀:USNM); Franconia, A. T. Slosson (7 ♂, 2 ♀:USNM, AMNH); Noxon Camp, 2000 feet, North Haverhill, 7 July 1931, J. M. Aldrich (3 ♀:USNM). *County unknown*. White Mountains, July (1 ♂:USNM). NEW YORK, *Erie County*. Colden, 9 July 1922, 23 July 1916, M. C. Van Duzee (2 ♀:CAS). *Essex County*. Lake Placid, 1 July 1922 (5 ♂:USNM); 28 July 1929, A. L. Melander (1 ♂:USNM). Wilmington Notch, Adirondacks, 2 July, J. M. Aldrich (2 ♀:USNM). *Fulton County*. Sacandaga, 15 June 1928, C.P. Alexander (2 ♂, 1 ♀:USNM). *Lewis County*. Gomer Hill, 21 June 1963, W. W. Wirth (21 ♂, 3 ♀:USNM). Singing Waters Picnic Area, 21 June 1963, W. W. Wirth (3 ♂, 1 ♀:USNM). *Jefferson County*. Watertown, J. Q. Adams (1 ♀:USNM). *Saint Lawrence County*. Raquette River, Colton, 24 June 1963, W. W. Wirth, (1 ♂:USNM). *Tompkins County*. Coy Glen, 18 June 1894, 18 June 1895, 12 June 1920, J. M. Aldrich (part) (4 ♂, 4 ♀:LACM, USNM, CU). Fall Creek, Ithaca, 10-11 June 1920 (8 ♀:CU). Ithaca: 23 June 1885, O. E. Pearce (1 ♀:CU); 24 June 1901, J. M. Aldrich (21 ♀:USNM, AMNH); 21 June-7 July 1901 (2 ♂, 8 ♀:BMNH). 12, 27-28 June 1901 (20 ♀:UCR, CU); 14 June 1907 (1 ♀:CU); July 1908 (4 ♀:ANSP); 31 May 1914 (13 ♂, 3 ♀:USNM); 14 June 1914, 12-13, 17, 24 June 1915 (6 ♀:CU); 1, 10, 17, 21, 25 June 1916 (3 ♂, 17 ♀:KU, USNM, PSU, KS, CU); 13 June 1917, O. A. Johannsen (8 ♀:PSU, CU); 14 June 1920 (1 ♀:CU); 10 June 1925 (1 ♀:CU); 3 June 1967, R. Silberglied (1 ♀:CU); 1-7 July, N. Banks (1 ♀:OS); (3 ♀:USNM); May (6 ♂:USNM); no dates: (1 ♂, 2 ♀: USNM, CU); (1 ♀:CU); Forest Home, Ithaca, 30 May 1940, A. Stone (3 ♂:USNM). Taghanic, Ithaca, 26 June 1920, M. D. Leonard (3 ♀:CU). PENNSYLVANIA, *Adams County*. Arendtsville, 27 May, 10 June 1920, S. W. Frost (3 ♀:CU). *County unknown*. Castle Rock, 19 June 1910 (1 ♀:USNM). VIRGINIA, *Fairfax County*. Great Falls, 19 June 1910, 24 May 1914, 23 May 1918, 21 June 1931, 30 May 1939, F. K. Knab, W. L. McAtee, A. L. Melander, C. T. Greene (7 ♂, 14 ♀:USNM). *Giles County*. No. 5, Mountain Lake Biological Station, 1800 feet, 18 June 1965, G. W. Byers (2 ♀:KU). Stoney Creek, 2000 feet, 26 May 1962, J. G. Chillcott (9 ♂, 5 ♀:CNC). VERMONT, *Addison County*. East Middlebury, 14 June 1929, Bishop No. 8435 (1 ♂:USNM). *Bennington County*. Peru, 15 July 1931, A. L. Melander (1 ♀:USNM). *Windham County*. Halifax Gorge, 8 June 1973, H. D. Pratt (11 ♂:HDP, CPA). LOCALITY UNKNOWN. (1 ♀:INHS).

*Atypical adults*.—GEORGIA, *Walker County*. Cloudland Canyon State Park, 8 May 1952, G. S. Walley et al. (20 ♂, 7 ♀:CNC). NORTH CAROLINA, *Macon County*. Highlands, 3-5000 feet, May 1936, R. C. Shannon (3 ♂:USNM). Same locality, 3200 feet, 2 July 1958, J. G. Franclemont (2 ♀:CU). *Swain County*. Deep Creek at Deep Creek Campground, Great Smoky Mountains National Park, Bryson City, 21 May 1970, Wiggins and Yamamoto, 700365 (2 ♂:ROM). TENNESSEE, *Sevier County*. Great Smoky Mountains National Park, 18 May 1957, J. R. Vockeroth (1 ♂:CNC); Greenbrier Cove, 2000 feet, 22 May 1938, I. Williams (1 ♂:USNM). VIRGINIA, *Bath County*. Blowing Springs Camp, 8 mi W Warm Springs, 18-20 May 1963, Field and Flint (2 ♂, 1 ♀:USNM). *Page County*. Luray, 21-24 June 1933, R. L. Melander (2 ♂, 3 ♀:USNM).

*Pupae* (pharate adults dissected).—CANADA. ONTARIO, *Wentworth County*. Spencer Creek, 27 May 1960, D. M. Wood (1 ♂, 6 ♀, 25 pupae, 4 larvae:CNC). QUEBEC, *Brome County*. Sutton Mountain Creek, 11 July 1929, G. S. Walley (16 pupae:CNC). UNITED STATES. MAINE, *Somerset County*. Pleasant Pond Stream, Caratunk, 24 June 1966, R. & D. Koss (21 pupae:JH). MASSACHUSETTS, *Worcester County*. Fitchburg, 27 May 1871 (44 pupae:USNM). NEW YORK, *Lewis County*. Gomer Hill, 21 June 1963, W. W. Wirth (19 ♂, 44 pupae, 15 larvae:USNM).

*Pupae* (atypical pharate adults dissected).—UNITED STATES. MARYLAND, *Frederick County*. Little Catocin Creek, 1 mi N Harmony, 30 May 1958, P. H. Freytag (2 pupae, 1 larva:OSU). Little Hunting Creek, 4, 17, 25 May 1958, P. H. Freytag (5 pupae, 24 larvae:OSU). Stream 1/2 mi E Yellow Springs, 31 May 1958, P. H. Freytag (8 pupae:OSU). NORTH CAROLINA, *Swain County*. Deep Creek Campground, Great Smoky Mountains National Park, Bryson City, 21 May 1970, Wiggins & Yamamoto #700365 (4 pupae, 2 larvae:ROM). Noland Creek, Great Smoky Mountains National Park, 24 May 1974, R. L. Green (1 pupa:LACM). VIRGINIA, *Giles County*. Stoney Creek, 1800, 2000 feet, 25 May 1962, J. R. Vockeroth (33 pupae, 1 larva:CNC). *Madison County*. White Oak Creek, Shenandoah National Park, 24 June 1959, B. D. Burks (5 pupae, 4 larvae:USNM).

#### *BLEPHARICERA WILLIAMSIAE* ALEXANDER

*Blepharocera williamsiae* Alexander 1953:43, Type locality Tennessee, Sevier County, above Greenbrier Cove, Mount Leconte, Great Smoky Mountains, 4200 feet elevation. Holotype female and allotype male in Alexander collection.

*Blepharocera williamsiae*, Alexander 1963:57. Redescription.

*Blepharicera williamsiae*, Stone 1965:99.

#### DESCRIPTIONS

##### Adult female (Figs. 13, 29)

SIZE: A medium-sized *Blepharicera*: measurements as follows: Wing length 8.1 (6.75-9.5), width 2.57 (2.1-2.9). Head width 1.27. Labrum length 0.48. Palpal segments 2-5, lengths: 0.16, 0.19, 0.18, 0.58. Leg segment lengths as below:

	fore	mid	hind
femur	4.2 (4.1-5.4)	4.45 (3.85-5.1)	6.2 (5.4-7.1)
tibia	3.5 (3.3-4.55)	3.6 (3.1-4.15)	5.5 (4.85-6.1)
tarsus 1	1.84 (1.56-2.09)	1.61 (1.36-1.80)	2.25 (1.96-2.46)
2	0.89 (0.81-1.08)	0.81 (0.65-0.99)	0.77 (0.66-0.88)
3	0.55 (0.41-0.64)	0.50 (0.38-0.59)	0.47 (0.40-0.54)
4	0.36 (0.30-0.44)	0.34 (0.30-0.41)	0.33 (0.28-0.39)
5	0.46 (0.40-0.60)	0.43 (0.35-0.58)	0.40 (0.34-0.50)

**THORACIC COLORATION:** Anterior pronotum and mesoscutum generally reddish-brown with slight gray overtone especially mesad; corner of posterior pronotum, posteromesal quadrate area of scutum and scutellum markedly lighter than mesoscutum, pale yellowish-brown; outer corners of scutellum darker; remainder of pleuron brownish-yellow.

**HEAD** (Fig. 13): Parietal sclerite with numerous (35-50) setae over entire median surface of sclerite. Distal four palpal segment proportions: 1.0, 1.2, 1.1, 3.6. Antennal segment proportions: 0.77, 0.78, **1.0**, 0.77, 0.80, 0.80, 0.80, 0.80, 0.80, 0.80, 0.74, 0.74, 0.68, 0.62, 0.99; ultimate segment 1.60 length of penultimate.

**LEGS:** Tibial spur formula 0-0-2 (spurs subequal). Progressive proportions of leg segment lengths as below:

foreleg: 1.00, 0.82, 0.53, 0.48, 0.62, 0.66, 1.26

midleg: 1.00, 0.81, 0.45, 0.50, 0.62, 0.67, 1.27

hindleg: 1.00, 0.89, 0.33, 0.34, 0.61, 0.63, 1.18

**GENITALIA** (Fig. 29): VIIIth sternite lobes disjunct, broadly rounded, median fold U-shaped, the basal corners angular; lobe without macro setae, a pair of micro setae on either side of midline on bridge between lobes. Spermathecae 3 in number, equal in size and ovoid in shape; necks very short; ducts membranous throughout. Accessory gland a slightly inflated, elongate tube.

**Adult male** (Figs. 8, 28)

**GENERAL:** Character states as given for female except as follows:

**SIZE:** Smaller than female; measurements as follows: Wing length 5.6 (4.9-6.6), width 1.85 (1.65-2.05). Head width 0.85. Labrum length 0.25. Palpal segments 2-5, lengths: 0.10, 0.14, 0.14, 0.52. Leg segment lengths as below:

	fore	mid	hind
femur	3.4 (2.75-4.0)	3.7 (3.45-4.2)	4.8 (4.5-5.5)
tibia	3.3 (3.1-3.7)	3.1 (2.85-3.55)	4.5 (4.1-5.3)
tarsus 1	1.78 (1.60-2.09)	1.61 (1.45-1.89)	1.70 (1.48-2.00)
2	0.83 (0.68-0.96)	0.78 (0.67-0.90)	0.56 (0.49-0.63)
3	0.58 (0.52-0.65)	0.55 (0.47-0.63)	0.37 (0.31-0.57)
4	0.31 (0.29-0.35)	0.30 (0.28-0.34)	0.25 (0.21-0.31)
5	0.30 (0.25-0.34)	0.29 (0.26-0.31)	0.27 (0.25-0.30)

**HEAD** (Fig. 8): Parietal sclerite with 6-7 setae in dorsolateral portion of sclerite. Distal four palpal segment proportions: 1.0, 1.4, 1.4, 5.6. Antennal segment proportions: 0.70, 0.72, **1.0**, 0.76, 0.97, 1.01, 0.94, 0.96, 0.96, 0.99, 0.96, 0.98, 0.96, 0.88, 1.11; ultimate segment 1.3 length of penultimate.

**LEGS:** Tibial spur formula 0-0-1. Progressive proportions of leg segment lengths as below:

foreleg: 1.00, 0.96, 0.54, 0.42, 0.70, 0.55, 0.95

midleg: 1.00, 0.81, 0.52, 0.49, 0.70, 0.55, 0.94

hindleg: 1.00, 0.93, 0.38, 0.33, 0.66, 0.68, 1.06

**GENITALIA** (Fig. 28): IXth tergite lobes very prominent, slightly convergent; lobe shape irregular, outer corner acutely rounded, posterior margin oblique, projecting

posteriorly as an angulate lobe, inner margin strongly inflated mesally, i.e. strongly curved to a narrowed base; bristles numerous and regular over entire dorsal surface. Tegmen entire. Paramere broad basally, tapering to distal four-fifths where abruptly narrowed (outer wall terminating); apex acute and incurved; aperture subapical, at termination of outer wall. Penis filaments 3 in number, equal in length, shorter than parameres, all simple, truncate rods, median much heavier basally than laterals.

#### REMARKS

This is the largest species of the *Tenuipes* Group, although of average size for the genus. In addition to diagnostic characteristics found in the genitalia of both sexes (see keys), the adults appear distinctive, even to the naked eye, because of the light brown prescutellar quadrate area of the scutum. The scuta of all the other species are more or less unicolorous.

#### DISTRIBUTION (Fig. 42)

*B. williamsae* is known only from the extreme southern portion of the Appalachians at the confluence of Georgia, Tennessee and the Carolinas.

#### MATERIAL

*Adults*.—GEORGIA, *Lumpkin County*. De Soto Falls State Park, upper falls, 28 April 1973, H. D. Pratt (5 ♂:HDP). NORTH CAROLINA, *Macon County*. Highlands, 3-5000 feet, April-May 1936, R. C. Shannon (18 ♂, 17 ♀, 4 pupae:USNM). Clear Creek, Highlands, 3200 feet, 1-2 July 1958, J. G. Franclemont (19 ♀:CU). *County unknown*. Bubbling Spring Creek, 5100 feet, 17 July 1957, J. G. Chillcott (1 ♀:CNC). TENNESSEE, *Sevier County*. Great Smoky Mountains National Park, Greenbrier Cove, 2000 feet, 18 May 1957, W. R. M. Mason (2 ♀:CNC); same locality, 2-2500 feet, 22 April 1939, 15 May 1938, I. W. Williams (♂ ALLOTYPES, 2 ♂, 3 ♀ PARATYPES:USNM); upper Greenbrier Cove, slopes Mount Leconte, 4200 feet, 5 June 1939, C. P. Alexander (♀ HOLOTYPE:CPA).

*Pupae* (pharate adults dissected).—UNITED STATES. TENNESSEE, *Sevier County*. Greenbrier Cove, Great Smoky Mountains National Park, 22 May 1938, A. C. Cole (14 pupae:UT). Oconaluftee River near Alum Cave Bluffs, Great Smoky Mountains National Park, 8 July 1974, D. & M. Davis (10 pupae:USNM).

#### TAXONOMY-PUPAE

The difficulties of distinguishing pupae because of their similarity among all the species (excepting species F) was mentioned earlier. Size may be used when there is reason to believe the sample contains disparate forms. Otherwise, since length-width ratios are constant and length is a continuum from the smallest males to the largest females, one must dissect the pharate adults to identify pupae. (Size data on samples of known species are given in Table I).

#### DESCRIPTION

**GENERAL**.—Typical in basic structure for genus *Blepharicera*. Outline shape ovate, cross section hemi-oval. *Size*.—♂ 3.6-4.7; ♀ 4.7-5.7 mm. *Color* (in life).—Upper surface evenly black; lower surface white. *Structure*.—Dorsal cuticle of metascutal, scutellar and abdominal sclerites, as well as small area immediately an-

TABLE I

<i>Blepharicera</i> , <i>Tenuipes</i> Group. Size of pupae (mean lengths in mm). N.a. = not available.		
	♂	♀
<i>B. capitata</i>	n.a.	n.a.
<i>B. cherokea</i>	n.a.	n.a.
<i>B. diminutiva</i>	n.a.	n.a.
<i>B. similans</i>	3.62	4.70
<i>B. tenuipes</i>	4.37	5.04
<i>B. williamsae</i>	4.74	5.65
<i>B. species F</i>	n.a.	4.7

terior to branchial lamellae on branchial sclerite, finely and densely papillate; remainder of dorsum smooth or weakly wrinkled. Branchiae parallel, widely separated; posture erect, composed of 4 elongate, apically rounded, rigid plates; all plates of equal length; internal pair more weakly sclerotized than external. Antennal cases of both sexes extending to less than half the length of wing cases.

The material for this project includes one specimen which deviates from all the others in the form of the tergites of abdominal segments I-V. These sclerites, instead of forming a flat arch across the midline, possess a low, cone-shaped prominence anteromedially; a similar, but lower and broader prominence arises from the scutellar sclerite. The processes are presumed homologous to those on the mid dorsum of "Larva F."

#### TAXONOMY-LARVAE

Six types of larvae are distinguishable in the material assembled for this study. Because none could be definitely associated with adults, their identities are tentative and in 3 cases still so uncertain that they can only be guessed.

#### DESCRIPTION

**GENERAL.**—Typical in basic structure for genus *Blepharicera*. **Size.**—Body length (prepupal) 5-7 mm. Width of head capsule 1.2-1.5 mm. **Color.**—Pigmentation usually pale, yellowish, sometimes medium brown. Sclerotized structures medium to dark brown. **Structure.**—Intercalary segments present. Head capsule with complete incision in lateralia. Antennae very short and with two sclerotized rings. Dorsal pseudopods absent. No dorsal spines, sclerotized plates or processes of any kind present (one species with middorsal coniform swellings). Ventrolateral gills with 7 filaments (6 occasionally on terminal division). **Chaetotaxy.**—Integument dorsally set with numerous secondary, coniform or claviform sensilla, primary sensilla recognizable as follows: tp M-T, members of pairs disjunct; ss P-T, that of P out of line laterad with those of M-T; st, inner tp, and dpod I-VII.

LARVA A  
(TENTATIVELY *B. tenuipes*)

## DESCRIPTION

*Fourth instar larva* (Fig. 30): Body length 6.9 mm; head width 1.48 mm. Secondary dorsal sensilla short, elongate-claviform; arranged in two irregular transverse rows on trunk divisions and abdomen I; a single row on each thoracic segment; rows confluent and sensilla general laterally, some setiform sensilla mixed. Recognizable primary sensilla all setiform except t P-M which are subchaetiform.

## MATERIAL (Fig. 41)

*Larvae* (and accompanying immature pupae).—*CANADA*. NEWFOUNDLAND. Baie Verte River, 23 June 1971, S. W. Frost (4 larvae:CNC). ONTARIO, *Carleton County*. Cunningham and Riopelle Islands, Remic Rapids, 18 May, 6 June 1949 (3 pupae, 14 larvae:CNC). *Renfrew County*. Petawawa, rapids below Highway 17 bridge, 28 April 1959, G. E. Shewell (5 pupae, 3 larvae:CNC). *Timiskaming County*. Kelly Creek, Highway 101, 28.8 mi W Timmins, 23 May 1972, ROM field party No. 720183 (14 larvae:ROM). *Wentworth County*. Spencer Creek, below falls, Ontario Railway Station, Dundas, 13 May 1954 (2 pupae, 6 larvae:USNM). QUEBEC, *Saguenay County*. Baie-Comeau, 11 June 1963, H. C. Connell (15 larvae:CNC). STATE and COUNTY UNKNOWN. Bug River Rapids, 21 June 1951 (8 pupae, 5 larvae:USNM). UNITED STATES. MARYLAND, *Frederick County*. Catoctin Creek, 1 mi N Little Catoctin, Harmony, 30 May 1958, P. H. Freytag (1 larva:OSU). *Garrett County*. Savage River at Big Run Campground, 17 April 1968, Yamamoto & Odum (1 larva:ROM).

## REMARKS

Determination of this larva seems fairly certain because of its wide occurrence in areas occupied exclusively by *tenuipes*. A significant locality in this respect is Ithaca, New York, where the numerous collections of all stages have never contained any deviant forms.

LARVA B  
(TENTATIVELY *B. similans*)

## DESCRIPTION

*Fourth instar larva* (Fig. 33): Body length 5.1 mm; head width 1.22 mm. Secondary dorsal sensilla short, extremely capitate (almost spherical in some), the largest apically dentate; arranged in two irregular transverse rows on trunk divisions and abdomen I; a single row on each thoracic segment; rows confluent laterally and where sensilla setiform mixed and general. Usually one conspicuously large, secondary claviform sensillum in dorsolateral area. Recognizable primary sensilla all setiform.

## MATERIAL (Fig. 40)

*Larvae* (and accompanying immature pupae).—*CANADA*. QUEBEC, *Brome County*. Sutton Mountain Creek, 11 July 1929, G. S. Walley (19 larvae:CNC). UNITED STATES. MAINE, *Somerset County*. Pleasant Pond Stream, Caratunk, 24 June 1966, R. & D. Koss (78 larvae:JH). MARYLAND, *Garrett County*. "CCXXXIV falls, muddy creek", 25 August 1965, J. Glime (1 larva:USNM). MASSACHUSETTS, *Berkshire County*. Bashbish Creek, 6 July 1950, A. Stone (4 pupae, 12 larvae:USNM). NEW HAMPSHIRE, *Coos County*. Creek on way to Glen

House, 18 July 1929, G. S. Walley (1 pupa, 3 larvae:CNC). NORTH CAROLINA, *Jackson County*. 3 mi E Balsam, 3400 feet, 11 July 1974, D. & M. Davis (12 larvae:USNM). *Swain County*. Deep Creek at Deep Creek Campground, Great Smoky Mountains National Park, Bryson City, 21 May 1970, Wiggins & Yamamoto No. 700365 (10 larvae:ROM). TENNESSEE, *Sevier County*. Gatlinburg, fork Little Pigeon River, 27 May 1934, T. H. Frison (3 larvae:INHS). Greenbrier Cove, Great Smoky Mountains National Park, 18 May 1952, H. B. Reed (53 larvae:UT). VIRGINIA, *Giles County*. Big Stony Creek, Kimballton, 26 May 1962, C. V. Covell (1 pupa, 3 larvae:UL). Sinking Creek, 29 May 1941, A. Stone No. 111 (6 pupae, 10 larvae:USNM). *Highland County*. Cowpasture River, 3 mi N Williamsville, 27 July 1974, M. M. Davis (1 pupa, 11 larvae:USNM). *Madison County*. White Oak Creek, Shenandoah National Park, 24 June 1951, B. O. Burks (8 larvae:USNM).

#### REMARKS

Identification of this form is fairly certain and based upon several widely spaced collections of larvae accompanying pupae with clearly recognizable pharate adults (see MATERIAL under account of *similans*).

#### LARVA C (SPECIES UNDETERMINED)

#### DESCRIPTION

*Fourth instar larva* (Fig. 35): Body length 6.4 mm; head width 1.33 mm. Secondary dorsal sensilla long, attenuo-claviform; arranged generally over each division but tending to form transverse rows especially on thoracic segments; also fewer across trunk segments slightly posterior to a mid-transverse line; laterally mixed with setiform sensilla. Recognizable primary sensilla all setiform.

#### MATERIAL (Fig. 43)

*Larvae* (and accompanying immature pupae).—UNITED STATES, GEORGIA, *Lumpkin County*. Hightower River, 11 April 1941, A. Stone No. 21 (5 larvae:USNM). *Union County*. Vogel State Park, 11 April 1941, A. Stone No. 18 (9 larvae:USNM). MARYLAND, *Frederick County*. Cunningham Falls State Park, 15 April 1973, P. & P. Spangler (23 larvae:USNM). *Garrett County*. Ginsend Run, 4 May 1965, J. Glime (2 larvae:MSU). Sang Run Crossing, Sang Run Road, 17 April 1968, Yamamoto & Odum (6 larvae:ROM). VIRGINIA, *Alleghany County*. Tributary Jackson River beside Route 220 just N Covington, 18 April 1968, Yamamoto & Odum (1 larva:ROM). Potts Creek, 3 mi SW Jordan Mines, 18 April 1968, Yamamoto & Odum (9 larvae:ROM). *Amherst County*. Tributary of James River beside Blue Ridge Parkway near junction with Route 501, 19 April 1968, Yamamoto & Odum (3 larvae:ROM). *Bath County*. Stream in Blowing Springs Recreation Area on Route 39, 18 April 1968, Yamamoto & Odum (6 larvae:ROM). *Floyd County*. Little Indian Creek, Copper Valley, 24 April 1966, P. & B. Wygodzinsky (6 larvae:AMNH). *Giles County*. Big Stony Creek, Kimballton, Station 2, 14 April, 5 May 1962, C. V. Covell (4 pupae, 25 larvae:UL). Sinking Creek, 29 May 1941, A. Stone No. 111 (1 larva:USNM). *Green County*. Swift Run, 5 mi W Standardville, Highway Route 33, 17 May 1970, R. W. Koss (10 pupae, 15 larvae:JH). Lydia, 20 April 1938, R. Burks (3 larvae:INHS). *Madison County*. Oak Creek, Shenandoah National Park, 6 May 1951, B. D. Burks (5 larvae:USNM). White Oak Canyon, Skyline Drive, 6 May 1951, Burks & Sommerman (2 larvae:USNM). *Rappahannock County*. Thornton River, Shenandoah National Park, 15, 20, 26 April 1961, O. & R. Flint (1 pupa, 29 larvae:USNM). *Shenandoah County*. Passage Creek, Camp Roosevelt, 21 May 1973, S. Fiance (3 larvae:USNM). STATE and *County UNKNOWN*. Treasler Run, Aitkin Farms, 29 April 1951, S. W. Frost (9 larvae:PSU).

## REMARKS

The distribution of this form coincides approximately with that of the atypical type of *tenuipes* (see VARIATION under that species) and may represent its larva. If this proves to be the case, its distinctiveness and constancy detract from the hypothesis of hybrid origin for that type and suggest that a separate species or subspecies is present.

LARVA D  
(TENTATIVELY *B. WILLIAMSÆ*)

## DESCRIPTION

*Fourth instar larva* (Fig. 31).—Body length 6.7 mm; head width 1.43 mm. Secondary dorsal sensilla short, lanceolate; arranged generally over each division but tending to form transverse rows on thoracic segments; mixed with chaetiform sensilla only near lateral margin. Recognizable primary sensilla all setiform except t P-I and st V-VI which are cylindrical. Specimens are often more darkly pigmented dorsomesally than laterally and present a longitudinally banded appearance.

## MATERIAL (Fig. 42)

*Larvae* (and accompanying immature pupae).—UNITED STATES. GEORGIA, *Dawson County*. Amicalola Falls, 11 April 1941, A. Stone (2 larvae:USNM). *Gilmer County*. Little Turnip Town Creek, Walnut Mountain Development, 13 March 1974, H. D. Pratt (6 pupae, 6 larvae:HDP). *Rabun County*. Tallulah River at Tallulah River Campground, S Tate City, 17 May 1970, Wiggins & Yamamoto (1 larva:ROM). *Union County*. Chestatee River, 11 April 1941, A. Stone (1 larva:USNM). NORTH CAROLINA, *McDowell County*. Woodlawn, 23 March 1940, Frison, Mohr & Hawkins (3 larvae:INHS). *Swain County*. New Found Gap, 3560 feet, 28 May 1934, T. H. Frison (6 pupae, 6 larvae:INHS). SOUTH CAROLINA, *Oconee County*. Howard Creek, 6 February 1976, R. L. Green & D. A. Braatz (5 larvae:LACM). TENNESSEE, *Sevier County*. Campground near Chimneys, Great Smoky Mountains National Park, 11 May 1944, Frison & Ross (16 larvae:INHS). Stream 10.2 mi E Gatlinburg entrance on Route 441, 20 May 1970, Wiggins & Yamamoto No. 700361 (10 larvae:ROM). Greenbrier Cove, Great Smoky Mountains National Park, 13 February 1938, A. C. Cole (47 larvae:UT); 18 March 1939, A. C. Cole (2 larvae:INHS). Small stream 0.8 mi W New Found Gap on Route 441, 20 May 1970, Wiggins & Yamamoto No. 700359 (2 larvae:ROM).

## REMARKS

Coincidence of large size and larval collections with the adults of *williamsæ* strongly suggest the identity of that species with this form.

LARVA E  
(SPECIES UNDETERMINED)

## DESCRIPTION

*Fourth instar larva* (Fig. 32).—Body length 5.9 mm; head width 1.64 mm. Secondary dorsal sensilla all setiform (except for occasional claviform shapes on thoracic segments in some specimens); arranged in two irregular rows on trunk divisions and abdomen I; a single row on each thoracic segment; rows confluent and sensilla general

laterally. Recognizable primary sensilla all setiform and similar to secondary sensilla except for larger size.

#### MATERIAL (Fig. 44)

*Larvae*.—*CANADA*, ONTARIO, *Parry Sound County*. Cashman Creek crossing Highway 518 at Sand Lake, 1 June 1972, ROM field party, No. 720212 (1 larva:ROM). *UNITED STATES*, MINNESOTA, *Lake County*. Split Rock Creek, 2 mi W Lake Superior, 16 May 1952, J. Gerberich (6 larvae:OSU). VIRGINIA, *Giles County*. Big Stony Creek, Station 2, Kimballton, 5 May 1962, C. V. Covell (1 larva:UL). STATE and *County* UNKNOWN. Stillwater Creek, 13 June 1961 (1 larva:USNM).

#### REMARKS

I have no idea of the identity of this form. It is sympatric only with *tenuipes*, but since the larva of that species is known, larva E would appear to belong to an unknown entity.

#### LARVA F (SPECIES UNDETERMINED)

#### DESCRIPTION

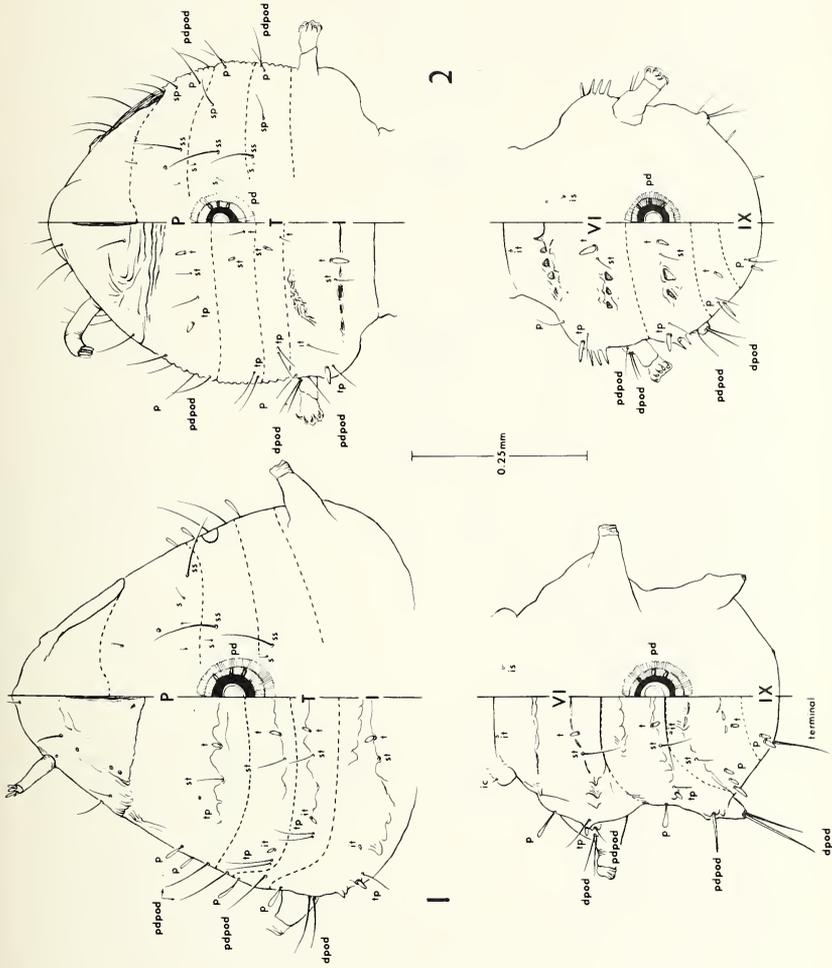
*Fourth instar larva* (Figs. 34, 36).—Body length 5.8 mm; head width 1.25 mm. A conspicuous median conical protuberance on each trunk division and abdomen I. Posterolateral lobes of terminal division poorly developed, terminal incision very shallow. Secondary dorsal sensilla claviform; arranged generally on all divisions except for 4-6 larger sensilla grouped tightly at apex of each coniform process; lateral sensilla mostly setiform. Recognizable primary sensilla well marked, all setiform except for t P-T and t V-VI which are cylindrical.

#### MATERIAL (Fig. 44)

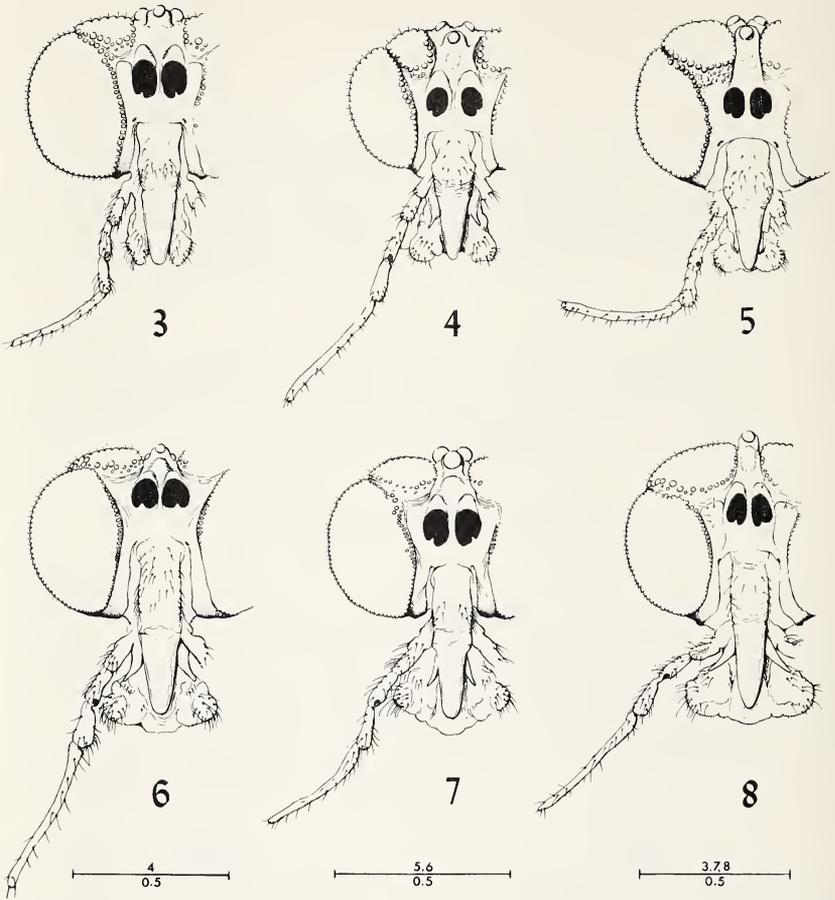
*Larvae* (and accompanying immature pupa).—*CANADA*, NEW BRUNSWICK, *Charlotte County*. Saint Stephen, 27 June 1965, G. E. Shewell (1 pupa, 2 larvae:CNC). *UNITED STATES*, GEORGIA, *Lumpkin County*. Hightower River, 11 April 1941, A. Stone No. 21 (11 larvae:USNM). MAINE, *Somerset County*. Pleasant Pond Stream, Caratunk, 24 June 1966, R. & D. Koss (1 larva:JH). NORTH CAROLINA, *Avery County*. Linville River at Linville Falls Campground, Blue Ridge Parkway, 22 May 1970, Wiggins & Yamamoto No. 700369 (11 larvae:ROM). *Swain County*. Deep Creek at Deep Creek Campground, Great Smoky Mountains National Park, Bryson City, 21 May 1970, Wiggins & Yamamoto No. 700365 (2 larvae:ROM). Noland Creek, Great Smoky Mountains National Park, 24 May 1974, R. L. Green (1 larva:LACM). VIRGINIA, *Bath County*. Stream in Blowing Springs Recreation Area on Route 39, 18 April 1968, Yamamoto & Odum (1 larva:ROM).

#### REMARKS

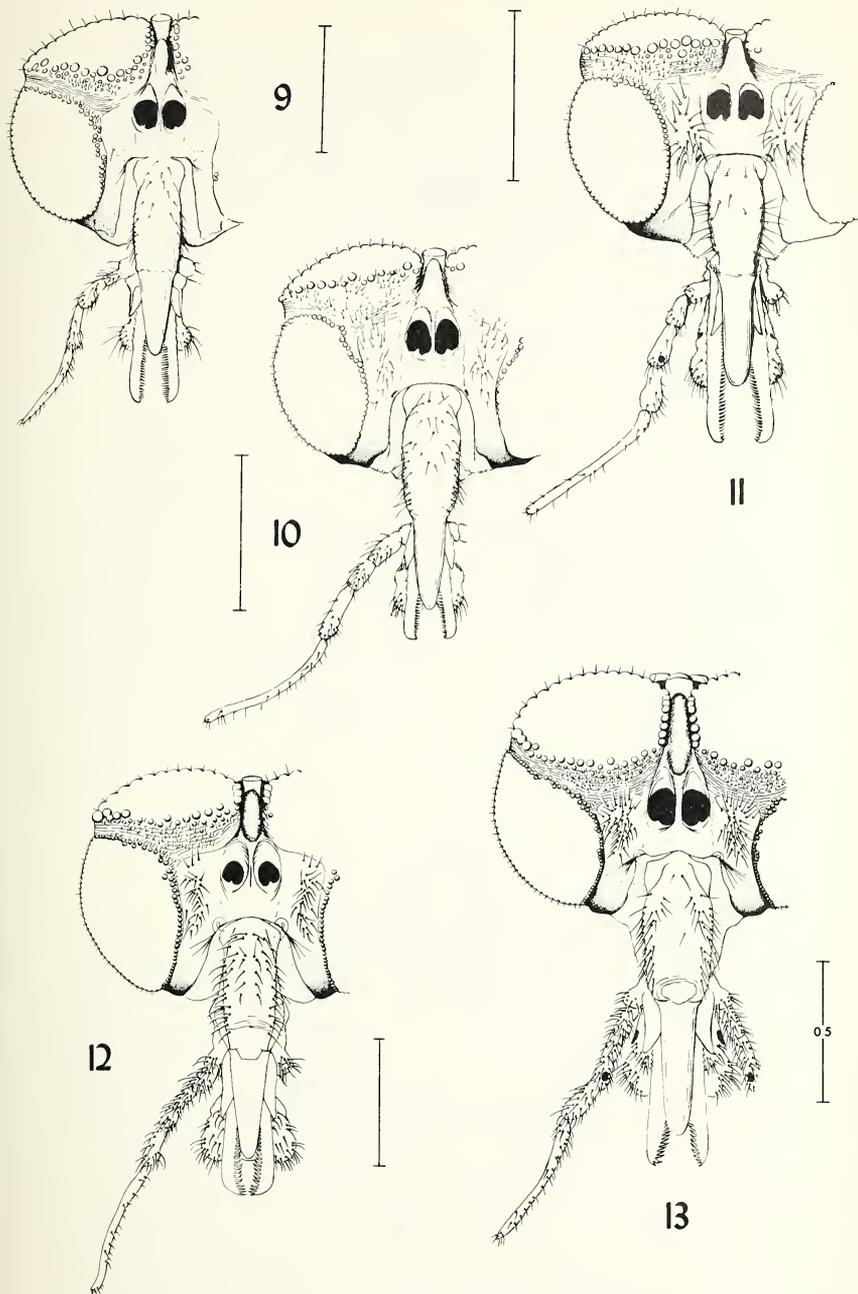
Unfortunately the female dissected from the single pupa available of this form was immature and not identifiable. Because of its great latitudinal range it seems unlikely that it belongs to either *capitata*, *cheroke* or *diminutiva*, all species now known to have restricted distribution. Possibly another new species is indicated.



FIGURES 1-2: Chaetotaxy of first instar larvae: 1. *Agathon comstocki*. 2. *Neocurpira chiltoni*. See section on TAXONOMIC CHARACTERS for explanation of abbreviations.

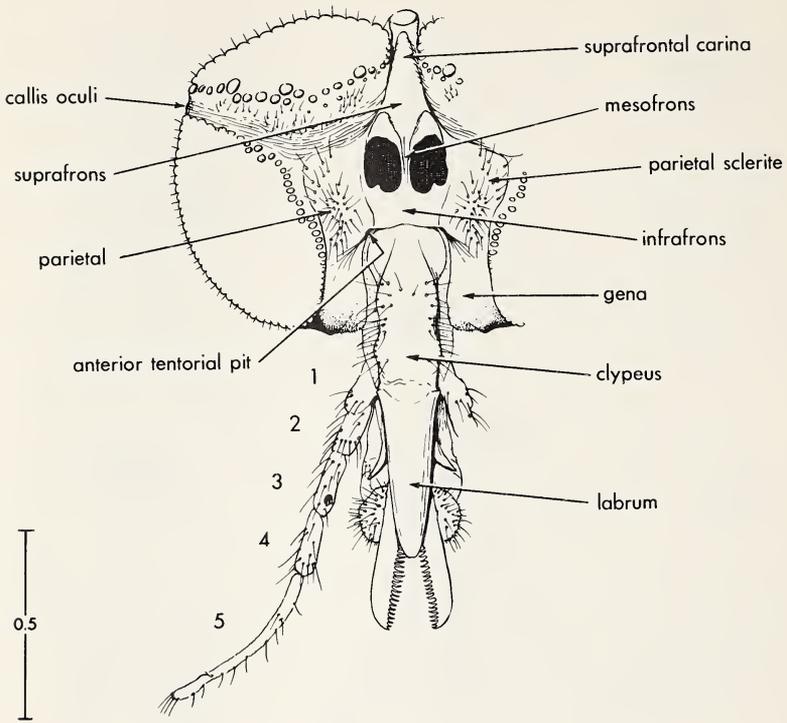


FIGURES 3-8: Anterior view of head capsules of male *Blepharicera*: 3. *B. capitata*. 4. *B. cherokea*. 5. *B. diminutiva*. 6. *B. similans*. 7. *B. tenuipes*. 8. *B. williamsae*.

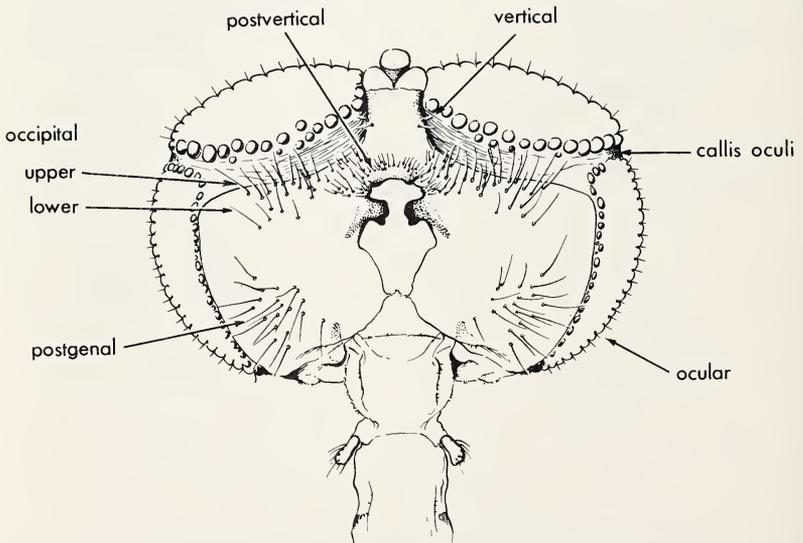


FIGURES 9-13: Anterior view of head capsule of female *Blepharicera*: 9. *B. capitata*. 10. *B. cherokeea*. 11. *B. diminutiva*. 12. *B. similans*. 13. *B. williamsae*.

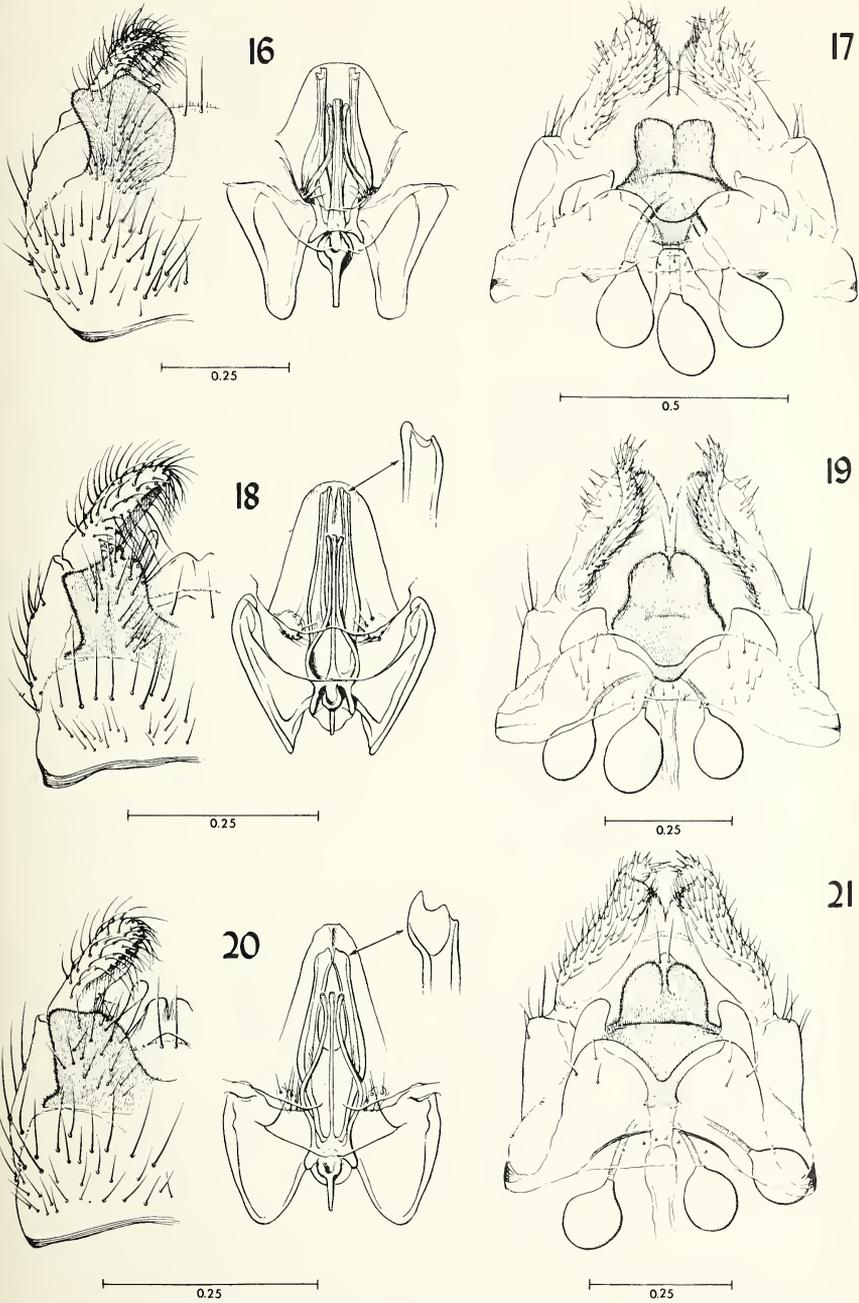
14



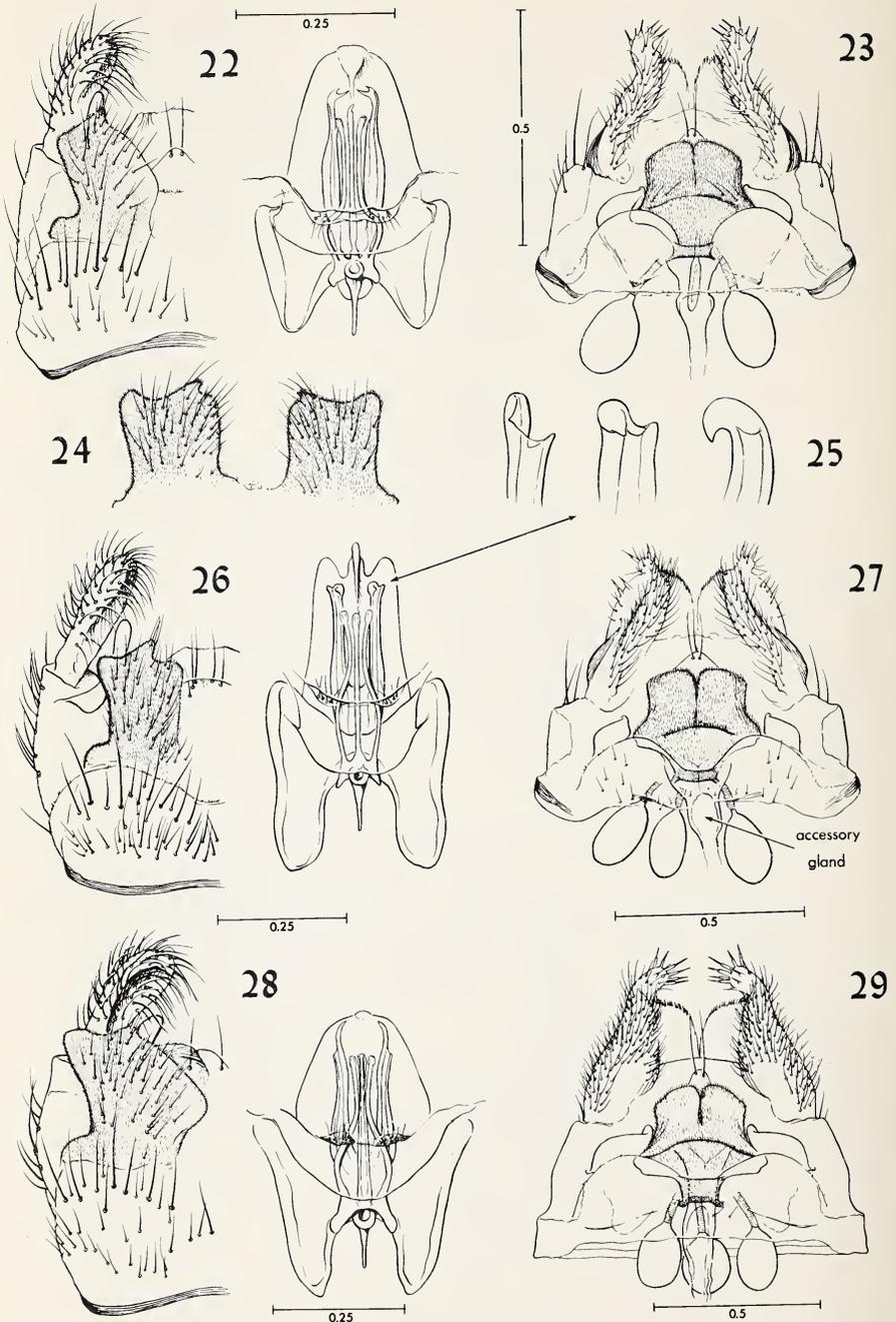
15



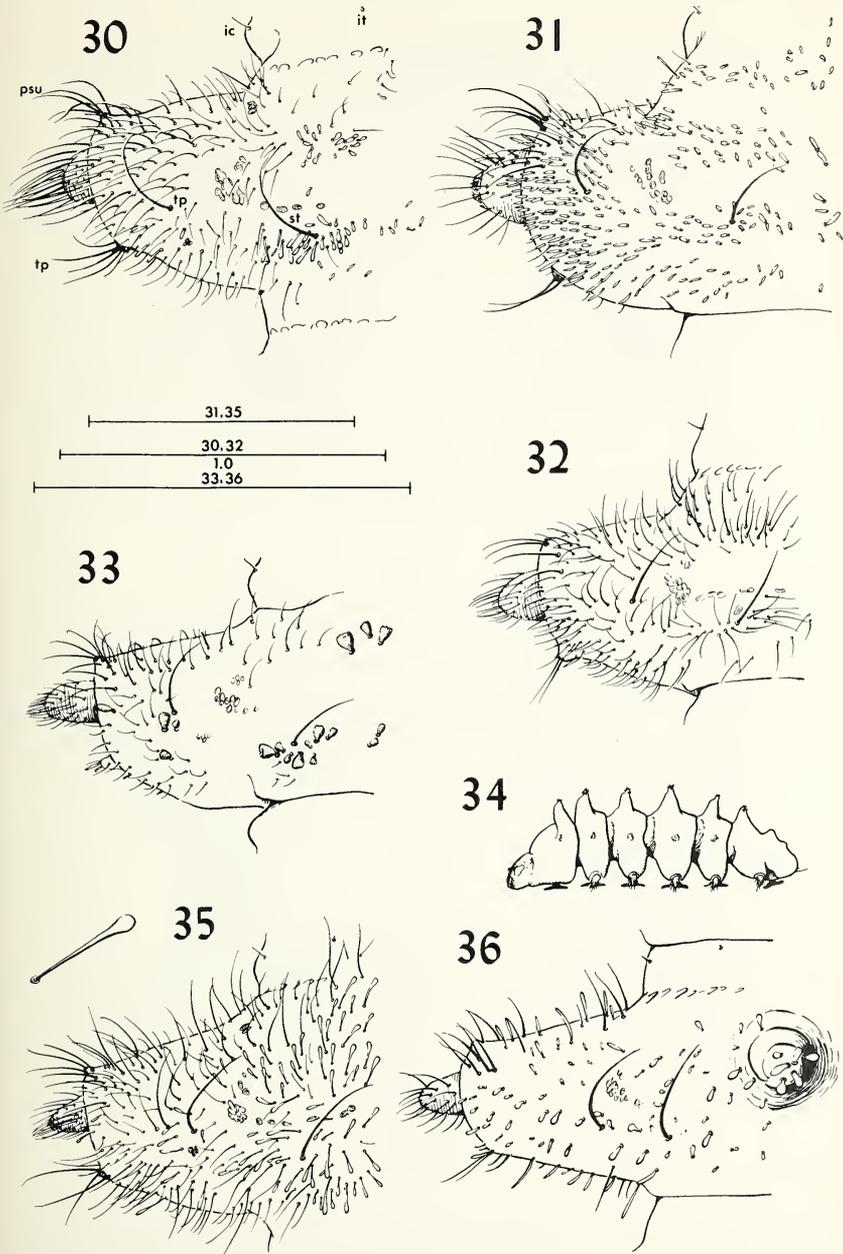
FIGURES 14-15: Terminology of head capsule, *Blepharicera tenuipes*, female: 14. Anterior view. 15. Posterior view, mouthparts omitted.



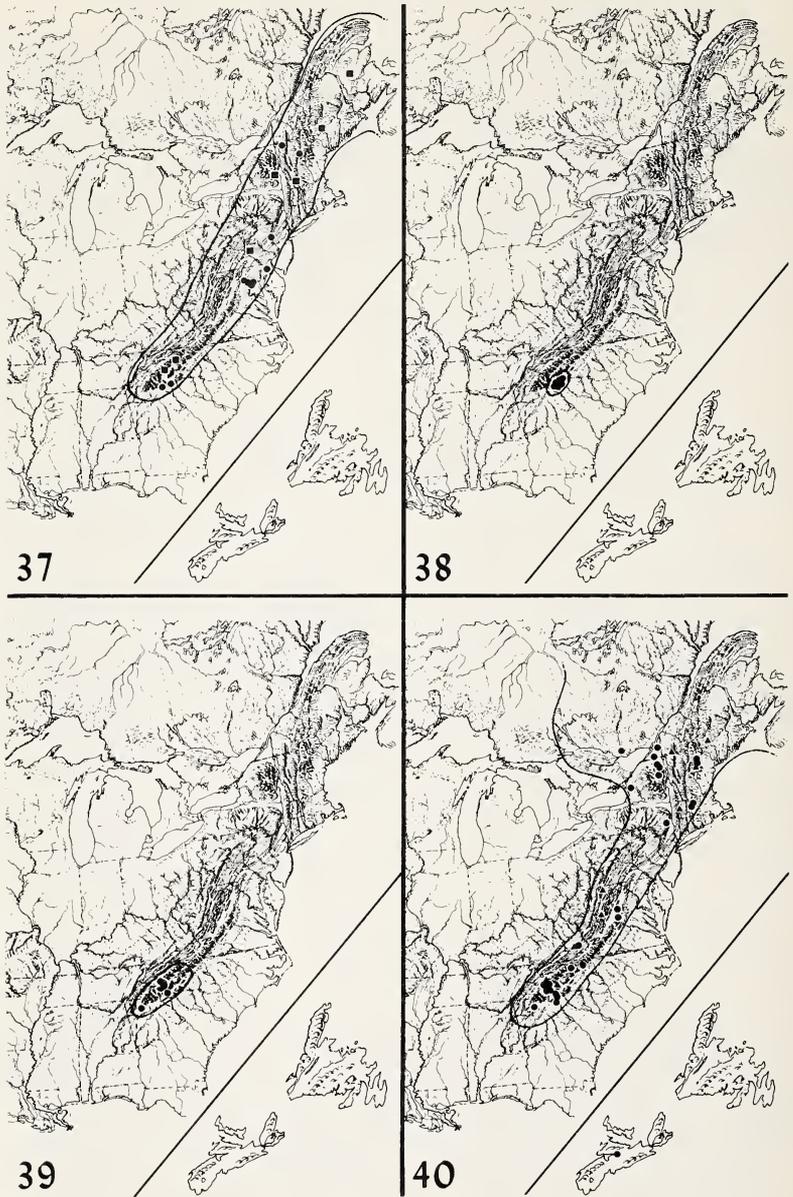
FIGURES 16-21: Male (left) and female (right) genitalia of *Blepharicera*: 16-17. *B. capitata*. 18-19. *B. cherokeea*. 20-21. *B. diminutiva*.



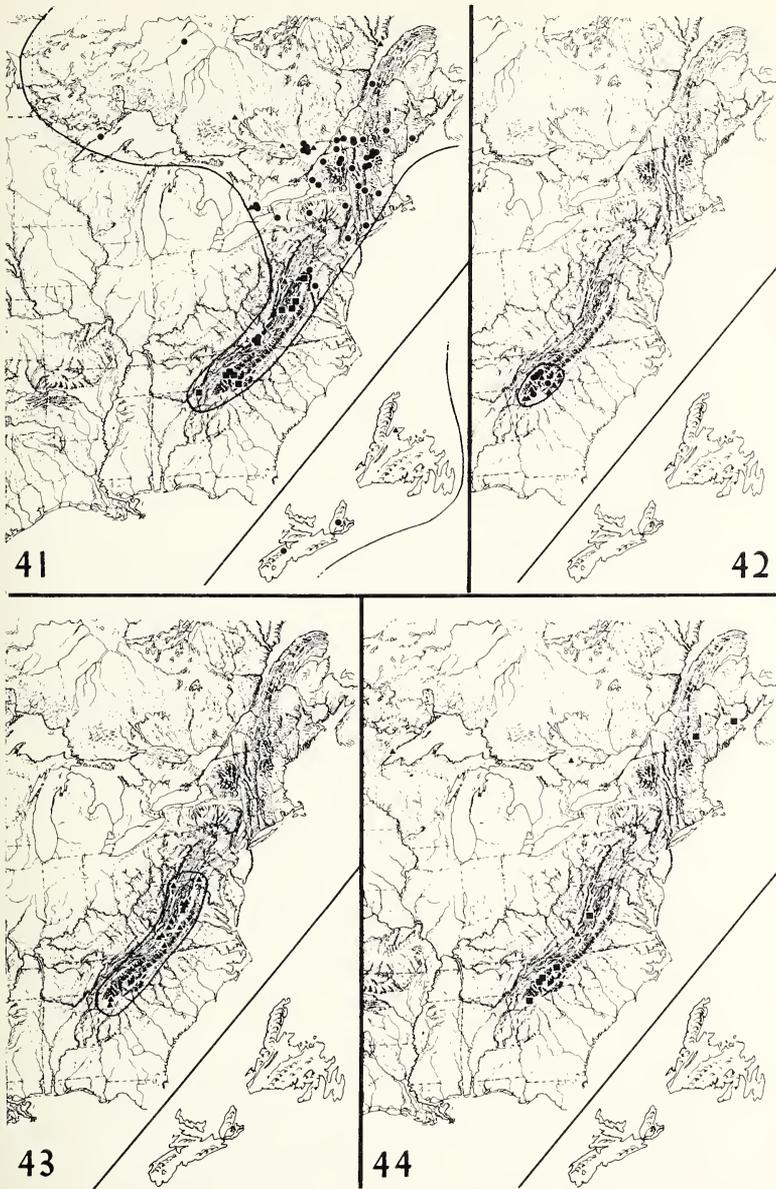
FIGURES 22-29: Male (left) and female (right) genitalia of *Blepharicera* (continued): 22-23. *B. similans*. 24-27. *B. tenuipes* (24. Ninth tergite lobes of "southern type"; 25. Three views of apex of paramere of male genitalia). 28-29. *B. williamsae*.



FIGURES 30-36: Fourth instar larvae of *Blepharicera*, 34. lateral view of Larva F (species undetermined), remainder dorsal view of left side of third abdominal segment showing details of chaetotaxy. 30. Larva A (probably *tenuipes*). 31. *B. williamsae*. 32. Larva E (species undetermined). 33. Larva B (probably *similans*). 35. Larva C (species undetermined). 36. Larva F (species undetermined).



FIGURES 37-40. Distribution of *Blepharicera* in eastern North America. Points indicate loci of collections, line encloses probable total range. 37. Typical *B. capitata* (dots) and "separata" type (squares). 38. *B. diminutiva*. 39. *B. cherokea*. 40. *B. similans* adults (dots) and larvae (triangles).



FIGURES 41-44. Distribution of *Blepharicera* in eastern North America (continued). Points indicate loci of collections, line encloses probable total range. 41. Typical *B. tenuipes* adults (dots), southern type (squares) and larvae (triangles). 42. *B. williamsae* adults (dots) and larvae (triangles). 43. Larva C. 44. Larva E (triangles and larva F (squares).

## ACKNOWLEDGMENTS

This study is based on 1869 specimens (773 adults, 1096 larvae and pupae). For the use of this material I wish to acknowledge the following repositories (listed alphabetically by the acronym used in citing specimens in the text above) and thank their respective curators who kindly arranged loans and provided much information:

- AMNH - American Museum of Natural History, Pedro Wygodzinsky.
- ANSP - Academy of Natural Sciences of Philadelphia, Harold Grant (deceased).
- BMNH - British Museum, Natural History, Paul Freeman.
- CAS - California Academy of Sciences, Paul H. Arnaud.
- CNC - Canadian National Collection, B. V. Peterson.
- CPA - Private collection of Charles P. Alexander, Amherst, Massachusetts.
- CU - Cornell University, L. L. Pechuman.
- DPC - Duke Power Company, Environmental Laboratories. R. Lynn Green.
- HDP - Private collection of Harry D. Pratt, Atlanta, Georgia.
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- KS - Kansas State University, Norman Marston.
- KU - University of Kansas, Snow Entomological Museum, George W. Byers.
- LACM - Natural History Museum of Los Angeles County.
- MCZ - Harvard University, Museum of Comparative Zoology, Philip J. Darlington.
- MMU - McMaster University.
- MSU - Michigan State University, Roland L. Fischer and Frederick W. Stehr.
- OS - Oregon State University, J. D. Lattin.
- OSU - Ohio State University, Paul Freytag.
- PSU - Pennsylvania State University.
- ROM - Royal Ontario Museum, Glenn B. Wiggins.
- UCR - University of California, Riverside, Saul Frommer.
- UL - University of Louisville, Charles V. Covell, Jr.
- USNM - U.S. National Museum of Natural History Collection, Alan Stone, F. Christian Thompson, and W. W. Wirth, Agricultural Research Service, United States Department of Agriculture.
- UNH - University of New Hampshire, J. G. Conklin.
- UT - University of Tennessee, Arthur C. Cole, Jr.

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NEW SPECIES AND RECORDS OF TROPICAL WEST AMERICAN  
MARGINELLIDAE (MOLLUSCA: NEOGASTROPODA)

By BARRY ROTH

NATURAL HISTORY MUSEUM OF LOS ANGELES COUNTY

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NEW SPECIES AND RECORDS OF TROPICAL WEST AMERICAN  
MARGINELLIDAE  
(MOLLUSCA: NEOGASTROPODA)<sup>1</sup>

By BARRY ROTH<sup>2</sup>

ABSTRACT: Six new species of Marginellidae are described: *Prunum* (*Prunum*) *gorgonense* from off Gorgona Island, Colombia; *Prunum* (*Prunum*) *macleani* from Ecuador; *Prunum* (*Microspira*) *aletes* and *Dentimargo zetetes* from localities on the Pacific coast of Costa Rica; *Dentimargo epacrodonta* from the Republic of Panama; and *Volvarina innexa* from the Galapagos Islands. *Prunum* (*Microspira*) *aletes* is similar to several Caribbean species and Neogene species from Florida. *Prunum* (*Prunum*) *curtum* (Sowerby) ranges into temperate waters south of the Panamic province; records from the Gulf of Panama need confirmation. The radula of *Prunum* (*Prunum*) *woodbridgei* (Hertlein and Strong) is illustrated and compared to that of *Prunum storerium* (Couthouy). *Dentimargo anticlea* (Dall) is tentatively recognized from several Galapagos localities.

INTRODUCTION

Recent accounts of the members of the Marginellidae known from the Panamic faunal province of tropical western America (Coan and Roth *in* Keen 1971; Roth and Coan 1971) cite 20 named species and subspecies. The extensive molluscan collections of the Section of Malacology of the Natural History Museum of Los Angeles County (LACM), and the gastropod collections of the Allan Hancock Foundation, currently on loan to that section, have furnished material for the description of the following new species and additional information concerning species previously described.

I acknowledge the courtesy of James H. McLean, Curator of Invertebrate Zoology, LACM, in making these collections available for study and aiding in the preparation of this paper. For assistance of various kinds during this investigation I am indebted to Emily H. Vokes, Eugene V. Coan, Antonio J. Ferreira, and Patrick LaFollette. An earlier draft of part of the manuscript was read critically by J. Wyatt Durham. Joseph Rosewater, Thomas R. Waller, and Frederick J. Collier lent comparative material from the National Museum of Natural History. Phillip W. Clover supplied information on type material studied by him in European museums.

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

WILLIAM K. EMERSON

JAMES H. MCLEAN

JOSEPH ROSEWATER

<sup>2</sup>Department of Geology, California Academy of Sciences, San Francisco, California 94118.

## FAMILY MARGINELLIDAE FLEMING

GENUS *PRUNUM* HERRMANNSEN 1852

Type species, by monotypy and tautonymy, *Voluta prunum* Gmelin 1791; Recent, Caribbean region.

As stated by Woodring (1970), *Prunum* is the proper generic allocation for a large number of fossil and Recent species. *Prunum* in the broad sense includes ovate to elongate shells with medium to low spire, aperture narrow or wide but not flaring anteriorly, outer lip more or less thickened and smooth or denticulate, and some development of callus around the aperture.

SUBGENUS *PRUNUM* SENSU STRICTO

Outer lip not greatly thickened, smooth within; anterior canal shallow; callousing around aperture generally limited to small patch on parietal wall; color pattern, when present, generally of indistinct banding.

*Prunum (Prunum) gorgonense* NEW SPECIES

## Figure 1

*Diagnosis:* A small, elongate *Prunum* differing from other west American species in the relatively high spire, narrow body whorl, and short aperture, colored pale pinkish tan with interior of aperture yellow.

*Description of holotype:* Shell rather small for the genus, elongate-ovate, narrower anteriorly, highly polished, solid. Color pale pinkish tan with two very faint, narrow, darker spiral bands dividing the body whorl into thirds, and a narrow zone of apricot-orange immediately below the suture. Apex translucent, apricot-orange; outer lip white; interior of aperture golden yellow. Spire elevated, apical angle about 60°, covered by a transparent glaze, which leaves sutures visible but impalpable. Outer lip with simple convex curvature, sharply varicose externally, not denticulate. Aperture narrow, wider anteriorly, with a short posterior notch; anterior margin evenly rounded, without indentation. Parietal wall moderately convex, not calloused. Columella very slightly concave, with four oblique folds including fold at base of columella, the two most anterior folds close together and fusing distally into a low, white fasciole that proceeds around anterior end of shell to merge with outer lip callus. Length 16.2 mm, width 8.0 mm.

*Type locality:* AFH 221-34, off Gorgona Island, Colombia (3° 01' 25" N, 78° 10' W), in 37 m on rock and shell bottom. Collected by Allan Hancock Pacific Expedition of 1934, 12 February 1934. One specimen.

*Type material:* Holotype, LACM-AHF 1777.

*Referred material:* One immature specimen, AHF 228-34, between Gorgona and Gorgonilla Islands, Colombia (2° 56' 20" N, 78° 14' W), mud and sand bottom. Collected by Allan Hancock Pacific Expedition of 1934, 12 February 1934.

*Discussion:* *Prunum (Prunum) gorgonense* is smaller and much paler than *Prunum (Prunum) sapotilla* (Hinds 1844), which is grayish brown with a deep brown aperture, tinged with dull orange outside the outer lip. The new species has a proportionally higher spire, shorter aperture, and less inflated body whorl than *P. sapotilla*. The latter species appears to be confined to the region of the Gulf of Panama.

In shape *P. gorgonense* is closer to *Prunum (Prunum) godini* Olsson 1964, from the Esmeraldas Formation, Neogene of Ecuador, and may be a descendant of that species (Figs. 2, 3). *Prunum godini* is larger (holotype 21.8 mm long), broader at the shoulder, and has the columella markedly excavated anteriorly so that the two most anterior folds diverge, rather than converge as in *P. gorgonense*. The fossil species also has a raised vertical callus rim anteriorly, visible in left side view (Fig. 3), which is absent in *P. gorgonense*.

The columellar folds of *P. gorgonense* like those of other species of the subgenus are concave in profile, with the hollow surface directed posteriorly.

*Etymology:* *gorgonense*—from Gorgona Island, the type locality.

*Prunum (Prunum) curtum* (Sowerby 1832)

Figure 4

*Marginella curta* Sowerby 1832:105; Reeve 1864: pl. 6, figs. 23a, 23b.

*Marginella (Prunum) curta* Sowerby, Coan and Roth 1966:280, pl. 48, figs. 4-6.

*Prunum (Prunum) curtum* (Sowerby), Coan and Roth in Keen 1971:633, fig. 1398.

Although it was described from Iquique, Chile, and Paita, Peru, few collections



FIGURES 1-3. 1. *Prunum (Prunum) gorgonense* new species, holotype, LACM-AHF 1777, length 16.2 mm. 2-3. *Prunum (Prunum) godini* Olsson, holotype, USNM 643945, length 21.8 mm.

of this species have been made south of the Panamic province. Fresh beach shells were found in some numbers on an intertidal sandbar at Laguna Grande, Ica Province, Peru ( $14^{\circ} 08' S$ ,  $76^{\circ} 15' W$ ) by J. H. McLean and Victor Alamo, 31 March 1972. One specimen from that locality (LACM 72-77) is illustrated. An analogous situation in the Atlantic Ocean is the presence of *Prunum* species in temperate waters of Argentina (Carcelles 1944).

No verified type material of this species is known to exist (Coan and Roth 1966). The specimens from Laguna Grande agree with the original diagnosis and with Reeve's (1864) figure of a specimen from the Cuming collection. For purposes of comparison with *Prunum* (*Prunum*) *macleani*, I have considered the Laguna Grande material to represent typical *P. curtum*.

Coan and Roth *in* Keen (1971) cite this species as ranging north to Manta, Ecuador. Lots at LACM from the Gulf of Panama differ in several details from South American specimens and may represent other, unrecognized, species.

### *Prunum* (*Prunum*) *macleani* NEW SPECIES

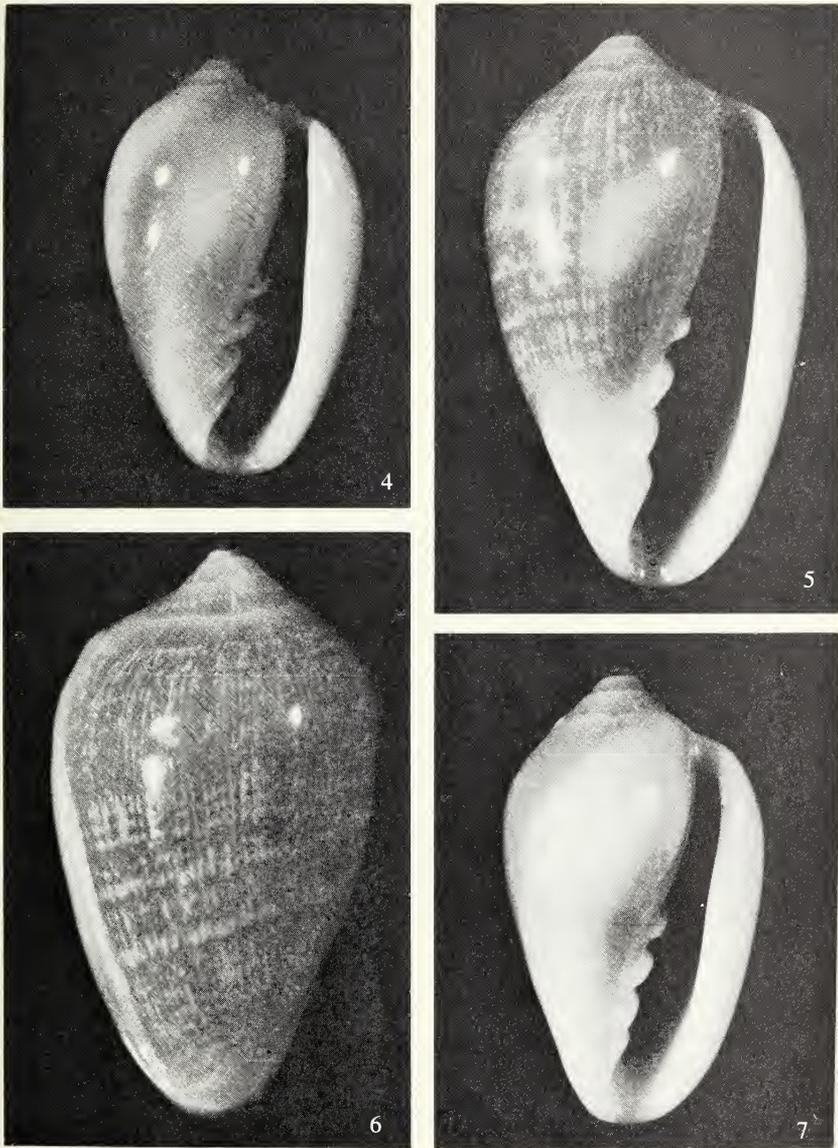
Figures 5-8

*Diagnosis:* A large *Prunum* with relatively low spire, differing from other west American species in the elongate-conic body whorl, wide aperture, and coloration: muted rose with white flecking in spiral bands, apertural callus edged with bright orange.

*Description of holotype:* Shell large for the genus, inflated, ovate-conic, narrower anteriorly, highly polished, solid. Color muted rose to rosy tan with a lighter, poorly defined, flesh color subsutural band and fine white flecking tending toward arrangement in spiral bands, most evident around middle of body whorl and near anterior end. Apex translucent, rosy brown; spire low, apical angle about  $80^{\circ}$ , light flesh color, covered by a transparent glaze which renders suture indistinct. Aperture moderately wide, wider anteriorly, rose color within, anterior margin somewhat effuse. Outer lip varicose, white on ventral surface, margined with brilliant orange externally, not denticulate. Parietal wall moderately convex with a patch of translucent, whitish callus. Columella concave, with four oblique, moderately diverging folds, including fold at base of columella; the two most anterior folds most oblique, nearly parallel, and closer together than posterior two folds, merging distally into a low, white fasciole with a bright orange external margin that proceeds around anterior end of shell to merge with outer lip callus. Length 36.6 mm, width 21.2 mm.

*Type locality:* Station 778, *Anton Bruun* Cruise 18B (LACM 66-198), west of Cabo Pasado, Ecuador ( $0^{\circ} 21' S$ ,  $80^{\circ} 41' W$ ), in 19 m, collected 12 September 1966. Twelve specimens.

*Type material:* Holotype, USNM 749065. One paratype, USNM 749066. Nine paratypes (shells) and one paratype radula slide, LACM 1778. One paratype, California Academy of Sciences, Geology Type Collection 55607. The paratypes differ slightly from the holotype in height of spire, posterior extent of outer lip, degree of development of parietal callus, and depth of ground color. In the lowest-spined ex-



FIGURES 4-7. 4. *Prunum (Prunum) curtum* (Sowerby), hypotype, CASG 54324, Laguna Grande, Ica Province, Peru, length 17.8 mm. 5-6. *Prunum (Prunum) macleani* new species, holotype, USNM 749065, length 36.6 mm. 7. *Prunum (Prunum) macleani* new species, hypotype, AHF 213-34, off La Plata Island, Ecuador, length 22.7 mm.

ample, the apical angle is about  $130^\circ$  and the outer lip extends nearly as far backward as the tip of the spire.

*Referred material:* Thirteen specimens, AHF 213-34, off La Plata Island, Ecuador ( $1^\circ 15' 25''$  S,  $81^\circ 05' 15''$  W), 13-18 m on rock bottom. Collected by Allan Hancock Pacific Expedition of 1934, 10 February 1934. Three specimens, AHF 212-34, off La Plata Island, Ecuador ( $1^\circ 15' 15''$  S,  $81^\circ 04' 15''$  W), 82-100 m on rock and mud. Collected by Allan Hancock Pacific Expedition of 1934, 10 February 1934. These specimens range from 15.4 to 23 mm in length and are more strongly calloused on the face of the body whorl (Fig. 7).

*Discussion:* This handsome species is the largest marginellid known from the eastern Pacific region and, in the form represented by the type lot, could not be confused with any other species. The referred material from off La Plata Island, however, is much smaller and superficially resembles *Prunum (Prunum) curtum*. These specimens are distinguished from *P. curtum* by their roseate color, more elongate-conic body whorl, and effuse anterior end of the aperture. *Prunum curtum* is usually grayish yellow or grayish brown with a variable amount of lighter flecking. Its body whorl is shorter and broader than that of *P. macleani*, with a characteristic gibbous angulation of the upper part. Its anterior end appears truncated in ventral view. The exterior of its outer lip callus is brownish orange, and this same color appears, often quite extensively, around the edge of the parietal callus (Fig. 4). The interior of the aperture is commonly brown.

The radula of *Prunum (Prunum) macleani* (Fig. 8) consists of broad, nearly straight, comblike rachidian teeth on which large and small cusps alternate. Each tooth of the figured specimen bears 29 cusps.

*Etymology:* The species is named for Dr. James H. McLean.

*Prunum (Prunum) woodbridgei* (Hertlein and Strong 1951)

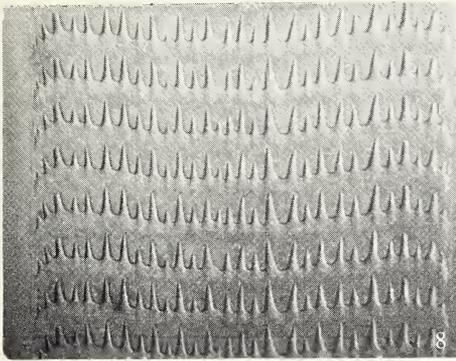
Figure 9

*Marginella woodbridgei* Hertlein and Strong 1951:80, pl. 26, figs. 3, 4.

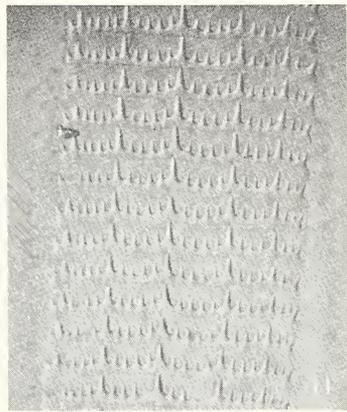
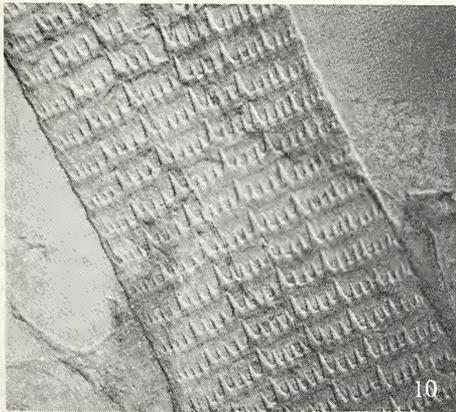
*Prunum (Prunum) woodbridgei* (Hertlein and Strong), Coan and Roth in Keen 1971:633, fig. 1400.

Figure 9 illustrates the radula of a specimen from AHF 930-39, off San Jose Light, Guatemala ( $13^\circ 52' 35''$  N,  $91^\circ 01' 02''$  W), 22-24 m on fine black sand, collected 23 March 1939. The radula consists of a single row of approximately 35 broad, straight, comblike rachidian teeth on which large cusps alternate with from 1-4 smaller cusps. A total of 24 cusps are present on each tooth of the figured specimen.

The radula is closely similar to that of *Prunum storerium* (Couthouy 1837) (Figs. 10, 11), a Caribbean species. The shell characters noted by Hertlein and Strong (1951) also suggest close relationship between the two species. The radula of *Prunum apicinum* (Menke 1828), suggested by Coan and Roth (1966) as another allied species, is less similar. *Prunum storerium* frequently is placed in the subgenus *Microspira* Conrad 1868, based on the extensive callousing around the aperture and on the face of the body whorl (*cf.* Woodring 1970:331-332); but this character evidently cuts



FIGURES 8-9. 8. *Prunum (Prunum) macleani* new species, radula of paratype, LACM 1778. 9. *Prunum (Prunum) woodbridgei* (Hertlein and Strong), radula, AHF 930-39, off San Jose Light, Guatemala.



FIGURES 10-11. Radulae of *Prunum storerium* (Couthouy), Margarita Island, Venezuela.

across phyletic lines based upon radular features, which are assumed to be more conservative.

#### SUBGENUS *MICROSPIRA* CONRAD 1868

Type species, by monotypy, *Volutella (Microspira) oviformis* Conrad 1868; Miocene, Virginia.

Outer lip thick, smooth to finely denticulate within; anterior canal shallow; spire low, sometimes depressed but not fully involuted, covered with a wash of callus; callousing generally extensive around aperture and on face of body whorl; color pattern, when present, of banding and/or irregular spotting.

Pending further studies, *Egouena* Jousseume 1875 (type species, *Egouena egouen* Jousseume = *Marginella amygdala* Kiener; Recent, west Africa), and *Lep-tegouana* Woodring 1929 (type species, *Voluta guttata* Dillwyn; Recent, West Indies), are here tentatively considered synonyms of *Microspira*, an interpretation suggested by Woodring (1970). The chief characters on which supraspecific taxa in the *Prunum* group are traditionally recognized pertain to development of callus on body whorl and spire and the degree of thickening of the outer lip—characters having limited phyletic significance, as discussed above under *Prunum* (*Prunum*) *woodbridgei*. With the exclusion of the generally less calloused species of *Prunum*, (SENSU STRICTO), *Microspira*, as broadly construed, contains the majority of recent and fossil species of the genus.

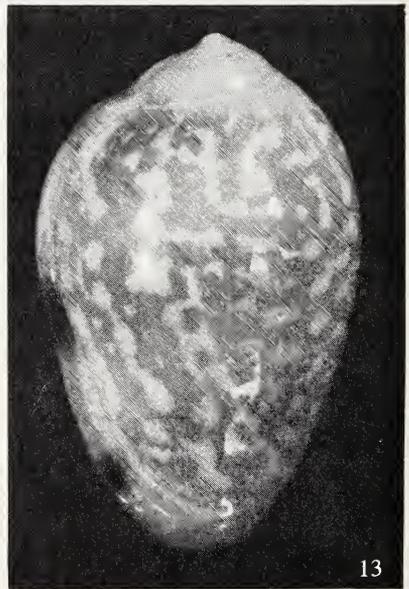
*Prunum* (*Microspira*) *aletes* NEW SPECIES

Figures 12-13

*Marginella* (*Prunum*) species, Coan and Roth 1966:280, pl. 48, figs. 7, 8.

*Prunum* (*Microspira*) species Coan and Roth, Woodring 1970:332.

*Diagnosis:* A pyriform marginellid distinguished from other west American species of *Prunum* by its ground color of orange-brown with indistinct darker brown



FIGURES 12-13. *Prunum* (*Microspira*) *aletes* new species, holotype, LACM 1779, length 15.2 mm.

spiral bands and an overall pattern of irregular white flecks, narrow, sinuous aperture, denticulate outer lip, and calloused parietal wall.

*Description of holotype:* Shell of medium size for the subgenus, solid, pyriform, inflated at shoulder, narrower anteriorly, with a shallow constriction across body whorl slightly anterior to middle. Entire shell somewhat dorsoventrally flattened. Surface highly polished, unsculptured. Color pale orange-brown with three darker, rather indistinct, purplish brown spiral bands, the first immediately below the suture, the second at the middle of the body whorl, and the third at the anterior one-fourth of body whorl. Shell completely overlain by a layer of clear enamel, rendering suture indistinct and, on the body whorl, bearing numerous white flecks of irregular shape, which tend to fall into ranks parallel to outer lip and into series oblique to axis of shell. Spire low, light apricot-orange; extreme apex white. Outer lip white, sharply varicose externally and bearing two brown spots aligned with the two lower color bands on body whorl; slightly constricted medially; finely denticulate along most of its length. Aperture narrow, even, shallowly S-curved, banded brown and apricot-orange inside; terminating posteriorly in a deep, straight sulcus. Parietal wall concave anteriorly, convex posteriorly, covered with translucent white callus that thickens to rim the posterior sulcus and continues up apertural side of spire nearly to apex. Center of parietal callus thickened into an acute, axially elongate node. Columella with four nearly equal, diverging folds, including one at base of columella, the two lowest folds terminating anteriorly in a weakly developed, white fasciole that is continuous with the varicose outer lip around anterior end of shell. Length 15.2 mm, width 10.0 mm.

*Type locality:* LACM locality 72-21, 3-11 m in cove between Isla San Jose and Isla Cocinero, Islas Murcielagos, Guanacaste Province, Costa Rica (10° 51' 50" N, 86° 55' 30" W), collected by P. LaFollette, D. Cadien, A. J. Ferreira, 17 February 1972 (R/V *Searcher* station 404-405). Four specimens.

*Type material:* Holotype, LACM 1779. Two paratypes, LACM 1780. One paratype, California Academy of Sciences, Geology Type Collection, 55608. The paratypes differ very slightly from the holotype in development of the white spotting on the body whorl and in extent of the parietal callus. Two are of paler ground color than the holotype, with light orange, rather than brown, transverse bands. The paratypes range from 13.7 to 16 mm in length.

*Referred material:* The species was taken by the R/V *Searcher* at eight other stations off Costa Rica: **392**, LACM 72-12, 1.6 km offshore between Bahia Elena and Juanillo Bay, Guanacaste Province (10° 57' 20" N, 85° 46' 08" W), in 53.0-26 m, 14 February 1972, 1 immature specimen; **403**, LACM 72-20, cove on west side of Isla Cocinero, Islas Murcielagos, Guanacaste Province (10° 51' 27" N, 86° 55' 15" W), in 12-18 m, 16 February 1972, one specimen; **409**, LACM 72-24, anchorage in cove, northeast side of Isla San Pedrita, Islas Murcielagos, Guanacaste Province (10° 51' 40" N, 86° 57' 54" W), in 18-24 m, 17 February 1972, two specimens; **415**, LACM 72-30, south tip of Punta Santa Elena, Guanacaste Province (10° 53' 35" N, 85° 57' 52" W), in 12-15 m, 18 February 1972, four specimens; **423**, LACM 72-37, between the two Vivadores Norte Islands, near Bahia Culebra, Guanacaste Province (10° 36' 42" N, 85° 43' 00" W), in 18-21 m, 19 February 1972, two specimens; **428**,

LACM 72-40, 1.6 km off beach, Bahia Brasilito, Guanacaste Province (10° 25' 57" N, 85° 49' 18" W), in 18 m, 20 February 1972, three specimens; **431-432**, LACM 72-42, 2.4 km east of Punta Ballena, Bahia Ballena, Puntarenas (9° 44' 15" N, 84° 33' 45" W), in 3-15 m, 21 and 22 February 1972, one specimen; **480-481**, LACM 72-67, off Isla del Caño, NW side, Puntarenas Province (8° 45' N, 84° 00' W), in 73-82 m, 16 March 1972, one specimen.

One specimen, AHF 245-34, off Pacora Island, off Bahia Honda, Panama (7° 44' 19" N, 81° 35' 23" W), 27-46 m on rock and shell bottom, collected 21 February 1934.

Two specimens, California Academy of Sciences, Geology Type Collection 12749, 12750, from CAS locality 27557, dredged off Puntarenas, Costa Rica, by the Templeton Crocker Expedition, 1 July 1932. These two worn specimens are the ones described by Coan and Roth (1966:280, pl. 48, figs. 7, 8) as "*Marginella (Prunum) sp.*"

*Discussion:* Placement of this species in the subgenus *Microspira* was first suggested by Woodring (1970), citing the Coan and Roth (1966) illustrations. This is the first verified record of the subgenus in west American waters. (*Marginella albuminosa* Dall 1919, probably a *Microspira*, is now thought to have been reported from west Mexico in error; cf. Keen 1971:907.)

The color pattern of *Prunum (Microspira) aletes* distinguishes it from all other known eastern Pacific Marginellidae. Its pyriform shape, narrow, S-curved aperture, and dorsoventral flattening of the shell are other diagnostic characters. *Prunum sapotilla* (Hinds), which may be sympatric with *P. aletes* in the region of Bahia Honda, Panama, sometimes has faint spiral bands, but it is much more elongate and lacks any trace of white spotting. Coan and Roth (1966: table 2) contrasted the new species to *Prunum curtum* (Sowerby) on several features, including the narrow aperture, the thick, finely toothed outer lip, and the outline of the shell. *Prunum woodbridgei* (Hertlein and Strong) is brownish gray, not spotted, and has an open, simply curved aperture.

The dark spiral bands of *P. aletes* are at least partially antecedent to the clear enamel with white spots that lies over them. An immature specimen (LACM 72-12) is plainly banded and has much sparser spotting than any of the adult specimens. Young specimens of the Caribbean *Prunum storerium* (Couthouy) are conspicuously banded with purple on a straw-colored ground, this pattern later being obscured by the predominantly gray enamel of mature shells.

Like many other tropical west American marginellids, *Prunum (Microspira) aletes* is most similar to species now living in the Caribbean region. The actual number of western Atlantic species remains to be determined. Probably closest to *P. aletes* is the species from Grand Cayman Island, British West Indies, figured by Abbott (1958:84, pl. 2, figs. j, k) as "*Prunum pruniosum* Hinds" (error for *Marginella pruinosa* Hinds 1844) with *Marginella nivea* C. B. Adams 1850, placed in synonymy. Abbott (1958:84) described the species thus: "Shell 8 to 12 mm. in length, resembling *guttatum*, but with its white spots half as small; with numerous, weak, uneven, denticulations on the inner [outer?] lip; with 3 weak, diffused spiral bands of yellowish brown (or absent); without color spots on the outer lip, and with a slightly raised spire

which is never covered by the labral callus." Some color variation among Grand Cayman populations was also specified. The narrow aperture is doubly curved, as in *P. aletes*.

Tryon (1882) united *Marginella pruinosa* and *Marginella nivosa* Hinds 1844, under the latter name; this synonymy was disputed by Abbott (1958). *Marginella nivea* C. B. Adams 1850, described from Jamaica, is also similar. The lectotype, figured by Clench and Turner (1950), is a worn, whitish shell 9 mm long, of the same general shape as Abbott's Grand Cayman species, with columellar folds more nearly parallel. Tryon (1882) cited *M. nivea* as another synonym of *M. nivosa*. Examination of large suites of Caribbean material may be necessary to settle the question of synonymy. Some workers consider the presence or absence of dark spots on the outer lip to be taxonomically significant.

*Prunum (Microspira) guttatum* (Dillwyn 1817) from Florida, the West Indies, and Panama, is another white-flecked species. It is larger than *P. aletes*, frequently reaching 20 mm or more in length, and more regularly ovate than the Pacific species. Its apertural callus may extend as far as, or even posterior to, the tip of its low spire. The outer lip is slightly constricted medially and bears a variable number of orange-brown blotches. The labral denticulation is very weak in all specimens examined. In form and color, *P. guttatum* is quite variable; notes on one variation were given by Bayer (1943).

The somewhat similar *Prunum (Microspira) roscidum* (Redfield 1860), living from New Jersey to eastern Florida, was contrasted to *P. guttatum* by Abbott (1957). In the synonymy of *P. roscidum*, Abbott included *Marginella eulima* Dall 1892, late Neogene of Shell Creek and Caloosahatchie beds, Florida, which was described as having opaque white flakes on translucent enamel and was itself a renaming of spotted specimens previously (Dall 1890) referred to *Marginella limatula* Conrad 1834. Dall (1892) suggested that *M. eulima* might be ancestral to *M. nivosa*. Spotted patterns, sometimes detectable under ultraviolet light, characterize a number of other small to medium-sized species from the Neogene of Florida.

*Prunum (Microspira) donovani* (Olsson 1967) of the Pinecrest beds, middle Pliocene of southern Florida (Akers 1974), more than twice the size of *P. aletes* and having five instead of four columellar folds, appears to be another relative. Under ultraviolet light it shows a pattern of spots in the superficial enamel and, beneath, transverse banding (Olsson 1967: pl. 8, figs. 9a-9c).

Throughout the later Tertiary, *Microspira* constitutes a prolific group in the American tropics. Discrimination of probable lineages is difficult. It seems certain, however, that several stocks of white-spotted species existed in the area prior to the closing of the Central American isthmus. On the west, one such stock has survived to the present day, represented by *P. aletes*.

*Etymology:* *aletes*—Gr., a wanderer.

#### GENUS *DENTIMARGO* COSSMANN 1899

Type species, by original designation, *Marginella dentifera* Lamarck 1803; Eocene, western Europe.

Small to minute, biconic, high-spired; anterior notch absent; outer lip smooth or denticulate within, commonly with a large posterior denticle.

*Eburnospira* Olsson & Harbison 1953 (type species, *Marginella eburneola* Conrad), *Longinella* Laseron 1957, non Gros and Lestage 1927 (type species, *Marginella maugeana* Hedley), and *Volvarinella* Habe 1951 (type species, *V. makiyamai* Habe), are regarded as synonyms of *Dentimargo*.

*Dentimargo anticlea* (Dall 1919)

*Marginella anticlea* Dall 1919:307. Coan and Roth 1966:289, pl. 51, fig. 61 (in synonymy of *Volvarinella eremus* [Dall]).

Coan and Roth (1966) synonymized this species with *Marginella eremus* Dall 1919, considering the type lot of *M. anticlea* to represent immature specimens of *M. eremus*. The lectotype of *anticlea* is smaller, less sharply biconic, and lacks the prominent labral denticle of *M. eremus*. Its nucleus is moderately large and blunt, and projects little from the succeeding whorls. The LACM-AHF collections contain material from the Galapagos Islands, from depths of approximately 80 to 110 meters, which seems at least tentatively referable to *Dentimargo anticlea*. Since these specimens show evidence of maturity—e.g., slight thickening and inturning of the outer lip and development of a low posterior denticle a short distance inside the aperture—at lengths of 2.7 to 3.5 mm, they call into question the premise that Dall's two nominal taxa represent growth stages of the same species.

These specimens share with the lectotype of *M. anticlea* a low, blunt nuclear shorl, a columella excavated so that the most posterior fold projects farthest into the aperture, and an acute posterior angle of the aperture.

*Referred material*: Two specimens, bottom sample AHF 406, Hancock Bank, northeast of Charles Island, Galapagos Islands, Ecuador (01° 03' 30" S, 90° 17' 30" W), 110 m. Collected by Allan Hancock Pacific Expedition of 1933, 5 February 1933. Five specimens, bottom sample AHF 415, north of Indefatigable Island, Galapagos Islands (0° 27' S, 90° 22' W), 100 m. Collected by Allan Hancock Pacific Expedition of 1933, 17 February 1933. One immature specimen, bottom sample AHF 411, north of Duncan Island, Galapagos Islands (approx. 0° 35' S, 90° 40' W), 82 m. Collected by Allan Hancock Pacific Expedition of 1933, 15 February 1933. Seven specimens (four juvenile), bottom sample AHF 417, north of Indefatigable Island, Galapagos Islands (0° 27' S, 90° 22' W), 100 m. Collected by Allan Hancock Pacific Expedition of 1933, 17 February 1933.

A lot of three specimens, bottom sample AHF 400, Gardner Bay, Hood Island, Galapagos Islands (approx. 01° 22' S, 89° 39' W), 31 m, collected by Allan Hancock Pacific Expedition of 1933, 25 January 1933, is distinctive in having a medium-sized, moderately elevated nucleus, higher and more conic spire, aperture 58% of total length of shell (compared to an average of 66% for specimens from bottom sample AHF 415), and slightly more shouldered body whorl, resulting in a more obtuse posterior angle of aperture. The largest specimen is 3.7 mm long. One additional, worn individual from bottom sample AHF 407, Albemarle Point, Albemarle Island, Galapagos

Islands (approx. 0° 12' N, 91° 21' W), 91 m, collected by Allan Hancock Pacific Expedition of 1933, 10 February 1933, is intermediate in spire height and projection of the nucleus. I believe the Hood Island specimens to be extreme members in a varying series of shallow water populations of *Dentimargo anticlea*.

Coan and Roth (1966: pl. 51, figs. 62, 63) illustrated as a hypotype of "*Volvarinella*" *eremus* (Dall) a high-spired shell with orange-brown bands around the body whorl; the same figure was reprinted by Keen (1971: fig. 1401). The figured specimen, from the Stanford University collection (SUPTC 9847), was labeled Albemarle Island, Galapagos Islands. It is extremely similar to specimens of *Dentimargo aureocincta* (Stearns 1873) from Cedar Key, Florida (Locality 852, California Academy of Sciences Department of Geology), particularly in size, disposition of the color bands, prominence of columellar folds, and arrangement of teeth along the convex and thickened outer lip. They also share a marked diagonal truncation of the outer lip anteriorly. Unless further collecting in the Galapagos turns up material to confirm the record, it appears probable that the Stanford specimen is a misallocated Atlantic shell. The only *Dentimargo* species in tropical west America definitely known to have brown banding is *D. zetetes*, described below.

#### *Dentimargo zetetes* NEW SPECIES

#### FIGURE 14

*Diagnosis:* A small, gracefully fusiform *Dentimargo* with whorls of spire only slightly convex, sutures scarcely impressed; distinguished from other west American species by the presence of orange-brown spiral banding which is composite in size and strength of the bands.

*Description of holotype:* Shell rather small for the genus, gracefully fusiform, somewhat inflated anteriorly. Surface highly polished, unsculptured. Translucent white, with four narrow, sharply defined, orange brown spiral bands on body whorl, the first band paler than the rest, just anterior to suture, the remaining three dividing the body whorl approximately into fourths; regions between second and third, and third and fourth bands lightly colored orange-brown, with faint indications of secondary banding; with a poorly defined orange-brown zone extending from anterior end of shell to just anterior of last narrow band. Nucleus small, rounded, moderately projecting. Spire high, of three whorls, flat-sided; suture indistinct, scarcely impressed; two posterior color bands showing on whorls of spire. Outer lip thick, convex, white with color bands continuing to its edge, with moderately broad, sloping shoulder behind aperture; interior with one major denticle posteriorly and three smaller, low, obscure denticles medially. Aperture moderately wide, whitish inside with color bands showing through, anterior margin slightly produced, posterior angle obtuse, posterior notch distinct. Parietal wall faintly convex, uncalloused. Columella shallowly concave, with four diverging, nearly equidistant folds including fold at base of columella; posterior three folds subequal in size, basal one smaller. Length 4.1 mm, width 2.0 mm, length of aperture 2.2 mm.

*Type locality:* LACM locality 72-7, 1-11 m, Punta Isla to 500 m south of point,

Bahia Elena, Guanacaste Province, Costa Rica (10° 56' 00" N, 85° 48' 55" W), collected by P. LaFollette & D. Cadien, 13 February, 1972 (R/V *Searcher* station 382-383). Two specimens.

*Type material:* Holotype, LACM 1781. Paratype, LACM 1782.

*Referred material:* Two specimens, AHF 472-35, Port Parker, Costa Rica (10° 57' 50" N, 85° 48' 45" W), 55 m on shell bottom. Collected by Allan Hancock Pacific Expedition of 1935, 9 February 1935. One specimen, AHF 470-35, Port Parker, Costa Rica (10° 57' 35" N, 85° 49' W), 9 m on sand and mud bottom. Collected by Allan Hancock Pacific Expedition of 1935, 9 February 1935. One specimen, bottom sample AHF 316, Gulfo Elena (Port Parker), Costa Rica (approx. 10° 55' N, 85° 49' W), 26 m. Collected by Allan Hancock Pacific Expedition of 1935, 8 February 1935. One specimen, LACM 70-65, Playas del Coco, Costa Rica (10° 33' N, 85° 43' W), intertidal. Collected by T. M. Spight, February-March 1970. Two specimens, LACM 72-30, south tip of Punta Santa Elena, Guanacaste Province, Costa Rica (10° 53' 35" N, 85° 57' 52" W), in 12-15 m, collected by P. LaFollette and D. Cadien, 18 February 1972 (R/V *Searcher* sta. 415). Ninety-five specimens, LACM 72-12, 1.6 km offshore between Bahia Elena and Juanillo Bay, Guanacaste Province, Costa Rica (10° 57' 20" N, 85° 46' 08" W), in 53-26 m, collected by P. LaFollette and D. Cadien, 14 February 1972 (R/V *Searcher* sta. 392).

*Discussion:* The paratype is banded similarly to the holotype, and the large lot from LACM locality 72-12 shows minor variations of the same pattern. The banding on a specimen from AHF 472-35 differs in having (starting below the suture) a very faint narrow band, followed by a distinct narrow band on the posterior third of the whorl, a broad band near the middle of the aperture, another narrow band, and a brown zone at the anterior end of the shell. Other specimens show banding faintly but are too worn to permit a detailed description of the pattern. The complex nature of the banding, in both size and strength, nevertheless appears to be a diagnostic character and helps to distinguish *D. zetetes* from the Caribbean *Dentimargo aureo-cincta* (Stearns 1873), which also differs in having a shorter aperture and denticles borne on the edge of the outer lip rather than a short distance inside the aperture.

*Dentimargo zetetes* appears to be the only eastern Pacific species with a color pattern, as mentioned above under *D. anticlea*. The latter species has, in most instances, a larger, flatter nucleus and more convex whorls of the spire. *Dentimargo erema* (Dall 1919) is unbanded, has denticles on the edge of the outer lip, and a larger, bulbous nucleus. *Dentimargo epacrodonta* is unbanded, and has a narrower aperture, narrower shoulder on body whorl, and well developed teeth inside the aperture.

*Etymology:* *zetetes*—Gr., a searcher.

#### *Dentimargo epacrodonta* NEW SPECIES

#### FIGURE 15

*Diagnosis:* A small, ivory-white *Dentimargo* distinguished from other west American species by its narrowly shouldered and anteriorly constricted body whorl and the presence of several subequal denticles a short distance inside aperture.

*Description of holotype:* Shell rather small for the genus, narrowly biconic, produced anteriorly. Surface highly polished, unsculptured. Translucent ivory-white. Body whorl constricted by a broad, shallow sulcus about one-third of the distance from anterior end. Nucleus small, hemispherical, moderately projecting. Spire high, of three convex whorls; suture appressed but distinct; "false suture" (internal trace of each whorl's junction with previous whorl) visible. Outer lip sharp at edge but thickened a short distance back, with narrow, steeply sloping shoulder behind aperture; straight along its medial portion; with seven distinct denticles a short distance inside aperture, of which the most posterior and the fourth are largest, the second and third from posterior are small and sharp, and the three most anterior are low and progressively less distinct. Aperture moderately narrow, produced anteriorly and somewhat effuse toward anterior end of outer lip; posterior angle acute; posterior notch indistinct (on paratype; holotype broken here). Parietal wall excavated, not calloused. Columella markedly concave, with four folds including fold at base of columella; posterior two folds subparallel, anterior two very oblique. Length 3.7 mm, width 1.7 mm, length of aperture 2.0 mm.

*Type locality:* Bottom sample AHF 308, off Bahia Honda, Republic of Panama (7° 44' N, 81° 35' W), 55-64 m. Collected by Allan Hancock Pacific Expedition of 1934, 21 February 1934. Three specimens.

*Type material:* Holotype, LACM-AHF 1783. Two paratypes, LACM-AHF 1784.

*Referred material:* One specimen, bottom sample AHF 312, Secas Islands, Republic of Panama (approx. 7° 57' N, 82° 02' W), 26 m. Collected by Allan Hancock Pacific Expedition of 1935, 4 February 1935. Three specimens, bottom sample AHF 307, off Secas Islands (approx. 7° 50' N, 82° 00' W), 73-146 meters. Collected by Allan Hancock Pacific Expedition of 1934, 22 February 1934.

*Discussion:* The ivory color, absence of banding, and narrower shoulder distinguish *D. epacrodonta* from *D. zetetes*, which in addition lacks the anterior constriction of the body whorl. No other west American species seems to have the array of apertural denticles shown by *D. epacrodonta*, but identification should not hinge on these characters since, as demonstrated in one paratype, the denticles may be incompletely developed. The dentition of *D. anticlea* (Dall), as far as seen, is dominated by a single strong posterior tooth. The nucleus of *D. anticlea* is proportionally larger and less projecting.

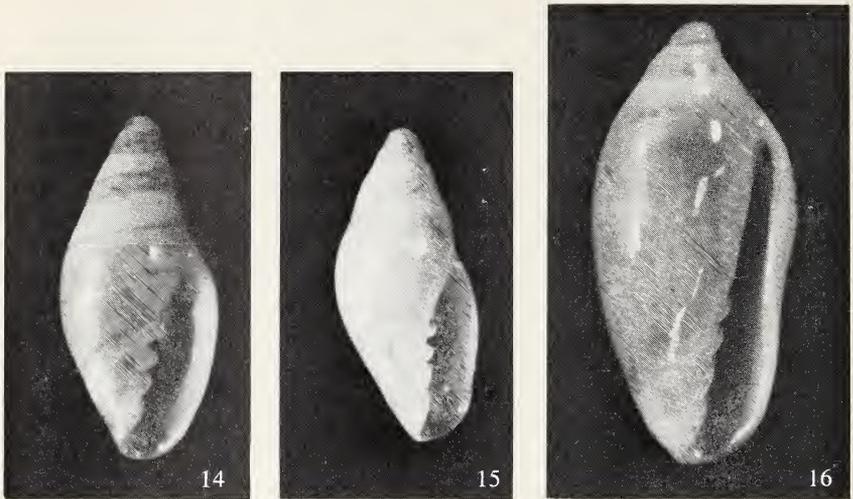
*Etymology:* Gr., *epakros*, pointed at the end + *odontos*, tooth; a noun.

#### GENUS *VOLVARINA* HINDS 1844

Type species, by subsequent designation, Redfield 1870, *Marginella nitida* Hinds 1844 (= *Voluta mitrella* Risso 1826); Recent, Mediterranean.

Small, cylindrical to conic; anterior notch absent; outer lip smooth or weakly denticulate within; spire low to moderately elevated.

The status of *Hyalina* Schumacher 1817 (type species, *H. pellucida* Schumacher; Recent, locality unknown), used by some workers for this group of species, is unresolved. Dodge (1955) identified *H. pellucida* with *Voluta pallida* Linnaeus 1767, and considered the latter a recognizable Caribbean species. Woodring (1970) regarded



FIGURES 14-16. 14. *Dentimargo zetetes* new species, holotype, LACM 1781, length 4.1 mm. 15. *Dentimargo epacrodonia* new species, holotype, LACM 1783, length 3.7 mm. 16. *Volvarina innexa* new species, holotype, LACM-AHF 1785, length 5.3 mm.

*H. pellucida* as unrecognizable and the genus as a *nomen dubium*. No type specimen of *H. pellucida* is extant (J. Knudsen, personal communication); designation of a neotype in conjunction with a revisionary study would resolve the question.<sup>3</sup>

#### *Volvarina innexa* NEW SPECIES

##### FIGURE 16

*Diagnosis:* A small *Volvarina* with relatively high spire, conic outline, and large nucleus, differing from other west American species by being white with two translucent spiral bands and having a narrow yellow band near the anterior end.

*Description of holotype:* Shell small for genus, elongate-conic, narrower anteriorly. Surface highly polished, unsculptured. Translucent white with two spiral zones of greater translucency, the first extending from shoulder of body whorl to just below suture, the second at middle of body whorl. Outer lip and extreme anterior end opaque white. Nucleus large; spire elevated, nearly transparent, with "false suture" (internal trace of each whorl's junction with previous whorl) visible; whorls of spire convex. Outer lip varicose externally, thickest posterior to middle, slightly constricted medially, not denticulate. Aperture narrow, evenly widening to anterior end; anterior mar-

<sup>3</sup>Coan and Roth (1976, Jour. Moll. Stud. 42:217-222) recently discussed this problem and designated a neotype.

gin evenly rounded, without indentation; posterior notch shallow. Parietal wall moderately convex, uncalloused. Columella very slightly concave, with four equidistant, nearly parallel folds including fold at base of columella, the folds terminating distally in a weakly defined white fasciole with a pale yellow spiral band along its posterior margin. Length 5.3 mm, width 2.2 mm.

*Type locality:* Station AHF 177-34, Sullivan Bay, James Island, Galapagos Islands, Ecuador (0° 16' 30" S, 90° 35' 15" W), 9-37 m on bottom of rock with sand patches. Collected by Allan Hancock Pacific Expedition of 1934, 23 January 1934. One specimen.

*Type material:* Holotype, LACM-AHF 1785.

*Discussion:* The high spire, prominent nucleus, and conic outline of *Volvarina innexa* distinguish it from other west American species of the genus, as does its singular color pattern. *Volvarina nysa* Roth and Coan 1971, from Pinta and Genovesa Islands, Galapagos Islands, has a much lower spire and bright orange-brown bands on the body whorl. *Volvarina taeniolata rosa* (Schwengel 1938) is larger, more ovate in outline, and bright pink in color; some specimens show brown banding like that of the nominate subspecies, which ranges from southern California to Central America. Some specimens from the Gulf of California, like those referred to *Volvarina taeniolata* by Coan and Roth (1966: pl. 50, figs. 54, 55), resemble *V. innexa* in their pale coloration and high spire. They do not however have the large nucleus of the new species. The columellar folds of *V. innexa* seem to be proportionally the largest of any west American *Volvarina* examined. I interpret *V. innexa* as an eastern Pacific representative of the group of high-spired Caribbean Marginellidae which includes *Volvarina veliei* (Pilsbry 1896) and *V. avenacea* (Deshayes 1844).

*Etymology:* *innexa*—L., joined.

## RESUMEN

Se describen seis nuevas especies de Marginellidae: *Prunum (Prunum) gorgonense* de la Isla Gorgona, Colombia; *Prunum (Prunum) macleani* de la República del Ecuador; *Prunum (Microspira) aletes* y *Dentimargo zetetes* de la costa Pacífica de Costa Rica; *Dentimargo epacrodonta* de la República de Panamá; y *Volvarina innexa* de las Islas Galápagos. *Prunum (Microspira) aletes* se parece a algunas especies Caribes y a especies Neogenos de Flórida. *Prunum (Prunum) curtum* (Sowerby) se extiende hasta aguas templados al sur de la provincia Panámica; su presencia en el Golfo de Panamá requiere confirmación. La radula de *Prunum (Prunum) woodbridgei* (Hertlein y Strong) se ilustra; concuerda bien con la radula de *Prunum storerium* (Couthouy). *Dentimargo anticlea* (Dall)—identificación tentativa—se encuentra en varias localidades en las Islas Galápagos.

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*MCCOSKERICHTHYS SANDAE,*  
A NEW AND UNUSUAL CHAENOPSID BLENNY  
FROM THE PACIFIC COAST OF PANAMA AND COSTA RICA

By RICHARD H. ROSENBLATT AND JOHN S. STEPHENS, JR.

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*MCCOSKERICHTHYS SANDAE*, A NEW AND UNUSUAL CHAENOPSID  
BLENNY  
FROM THE PACIFIC COAST OF PANAMA AND COSTA RICA<sup>1,2</sup>

by RICHARD H. ROSENBLATT<sup>3</sup> AND JOHN S. STEPHENS, JR.<sup>4</sup>

ABSTRACT: A new genus and species of chaenopsid blenny is described, based upon a series of 651 specimens. This new species occurs at depths ranging from 1 to 30 meters along the Pacific coast of Costa Rica and Panama. It is a tube dwelling blennioid fish, living along near-vertical rock faces or coral heads. This new chaenopsid is unique in having the following combination of characters: four circumorbital bones, ectopterygoid teeth, jaw with spatulate teeth on outer row but granular ones on inner row, five orbital cirri, a blunt head, 17-20 spines and 31-34 soft rays in dorsal fin, 2 spines and 32-36 soft rays in anal fin, and 54-57 vertebrae. The relationships of the new genus are discussed as they relate to the clinidlike blenny families (Clinidae, Chaenopsidae, Tripterygiidae). Osteological features are discussed and illustrated, and their interpretation as evidence of evolutionary significance is presented.

INTRODUCTION

In 1971 while on fellowship to the Smithsonian Tropical Research Institute in Panama, John E. McCosker collected and made observations on a new species of tube dwelling blennioid fish. Extensive series of this species were also taken by McCosker and Rosenblatt during the Janss Foundation expedition to Costa Rica on the R/V *SEARCHER*. The characteristics of this species are so distinctive that it cannot be assigned to any known genus, but its characteristics certainly ally it to the family Chaenopsidae.

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<sup>1</sup>REVIEW COMMITTEE FOR THIS CONTRIBUTION  
ROBERT J. LAVENBERG  
RICHARD ROBINS  
VICTOR G. SPRINGER

<sup>2</sup>Contribution from the Scripps Institution of Oceanography.

<sup>3</sup>Scripps Institution of Oceanography, University of California at San Diego, La Jolla, California 92093.

<sup>4</sup>Department of Biology, Occidental College, Los Angeles, California 90041.

**Mccoskerichthys** NEW GENUS

Figure 1

*Diagnosis:* A chaenopsid with the following unique combination of characters: four circumorbital bones, teeth on the ectopterygoid, outer row of jaw teeth spatulate, teeth of inner rows granular, 5 pairs of orbital cirri and a combination of blunt head and high dorsal, anal and vertebral counts. Other characters those of the single included species.

*Type species:* *Mccoskerichthys sandae* new species

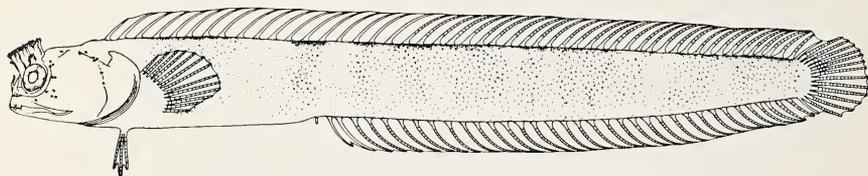
Derivation of name: Named for John E. McCosker, who discovered the species and has participated in the collection of all known specimens.

## RELATIONSHIPS

Böhlke and C. H. Robins (1974) in describing the new clinid genus *Haptoclinus* discussed certain characters of this monotypic genus that they regarded as breaking down the separation of the three often recognized clinidlike blenny families: the Clinidae, Chaenopsidae and Tripterygiidae. They recognized only the family Clinidae, admitting that the chaenopsids and tripterygiids represent lines of divergence within the family, but suggested that other equally distinct clinid subgroups may later be defined. However, the characters given for *Haptoclinus apectolophus* do not seem to indicate relationship to chaenopsids; in fact, all its characters are typically clinid. There is also very little evidence presented allying *Haptoclinus* to the tripterygiids. *Haptoclinus* represents a specialized clinid, perhaps allied to *Paraclinus*.

It may well be that uniting all clinidlike or clinid-derived fishes into a single family is the best way to treat these relationships but unfortunately the discussion by Böhlke and Robins (1974) is mostly irrelevant to this problem. We, therefore, will continue to treat clinids, chaenopsids and tripterygiids as separate blennioid families.

The morphological characters given in the diagnosis of *Mccoskerichthys* indicate its isolated position within the family Chaenopsidae. Any one of these characters distinguishes this genus from all other known chaenopsids, and the presence of ectopteryoid teeth is unique within the Blennioidei. If these special characters are ignored, *Mccoskerichthys* seems to be most closely related to the *Protemblemaria* to *Acanthemblemaria* line of chaenopsids in that the paired nasals have fused medially into

FIGURE 1. *Mccoskerichthys sandae*, Holotype

a single element and the frontals (parietal of Jollie 1962; Stephens 1963) are ridged and sculptured (Fig. 3). Further, there is a tendency toward modified dentition in this evolutionary line. The species of *Chaenopsis* agree with *Mccoskerichthys* in having a high number of vertebrae and dorsal and anal soft rays, as well as the correlated characters of a reduced number of caudal peduncle vertebrae and the absence of dorsal pterygiophores anterior to the first vertebra, but are otherwise very different.

Stephens (1963) listed 13 characters he considered to represent the primitive condition in chaenopsids. *Mccoskerichthys* exhibits the primitive condition in six characters (snout shape, orbital cirri, palatovomerine dentition, upper jaw length dimorphism, median fin height and circumorbital width). Although relatively slender circumorbitals were considered to be primitive by Stephens, this character needs clarification. The primitive condition is better described as a slender lachrymal and the advanced character a ventrally expanded lachrymal as in most *Coralliozetus* ( $\sigma$   $\delta$ ) and most species of *Acanthemblemaria* (Figs. 6-9). The other circumorbitals are relatively stout primitively (Stephens 1963, fig. 2A and B). The slender circumorbital ring is found in almost all species of the *Emblemariopsis* to *Chaenopsis* line, though several species of *Emblemaria* show a modified, stouter ring. The circumorbital ring of *Mccoskerichthys* is similar to that of *Neoclinus*, a clinid considered close to the ancestral chaenopsid lineage, in that there are four bones, the lachrymal is slender and

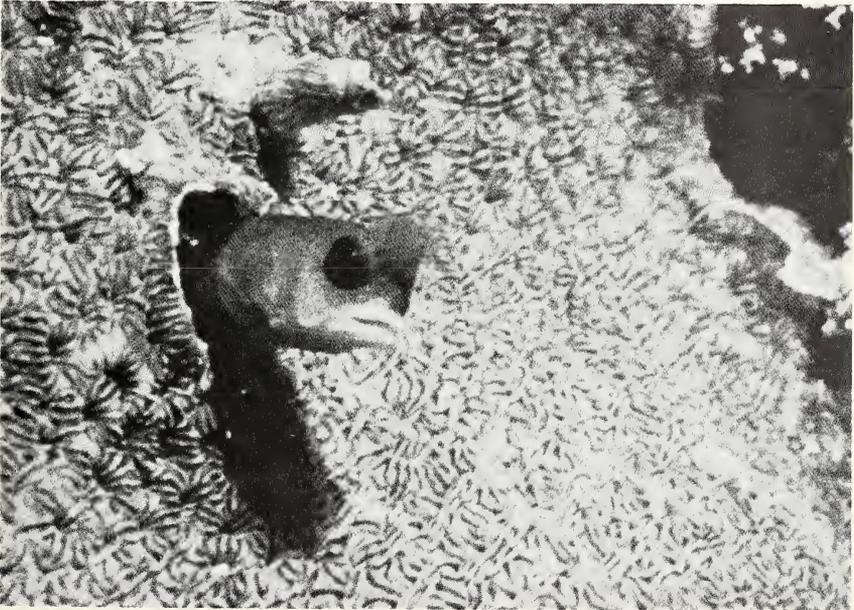


FIGURE 2. *Mccoskerichthys sandae*, a living individual in a tube in the coral panona. Photo taken by Edwin Janss at Isla del Caño Costa Rica in March, 1973.

the other three circumorbitals (postorbitals) relatively stout. *Neoclinus* has a distinct dermosphenotic not present in *Mccoskerichthys* or other chaenopsids.

The four circumorbitals, blunt snout and low nondimorphic dorsal fin impart a primitive facies to *Mccoskerichthys*. The strongly modified dentition, presence of teeth on the ectopterygoid, and the elongate body are specializations but do not argue against a primitive origin. If the presence of four circumorbital bones indeed represents the retention of a primitive character, then *Mccoskerichthys* must have evolved prior to the division of the chaenopsids into the *Protemblemaria* to *Acanthemblemaria* and *Emblemariopsis* to *Chaenopsis* lineages, as the circumorbitals are reduced in both. If *Mccoskerichthys* diverged this early, however, it is difficult to explain its numerous apomorphic characters shared with members of the *Protemblemaria* to *Acanthemblemaria* lineage, i.e. a single fused nasal, cranial sculpturing, specialized incisor and molariform dentition, as well as short and stout pelvic fins.

*Mccoskerichthys* is certainly not particularly clinidlike: the body is scaleless, and the lateral line absent, most of the head pores are simple, there is a single epural, and the fifth hypural (minimal hypural) is not identifiable nor are the dermosphenotic and median and lateral extrascapulars. All of these are chaenopsid characters. Typically there are two epurals and the fifth (minimal) hypural in the Clinidae and the dermosphenotic and one or more extrascapulars are present. It must be stressed, however, that the chaenopsid condition in these osteological characters is approximated by *Stathmonotus* and *Starksia* and in one or more characters by other clinids. An additional chaenopsid character, the presence of a well defined anteriorly projecting lateral process on the hyomandibular (Figs. 6, 7, and 9) has been examined by Springer (personal communication). This hook is certainly characteristic of most species but appears to be absent in *Coralliozetus* (Fig. 8) and those species of *Emblemariopsis* that we have examined. This process is at best rudimentary in *Mccoskerichthys* (Fig. 3).

It is difficult to evaluate the phyletic significance of the presence of four separate postorbital bones in *Mccoskerichthys*. It would be especially helpful to know whether there are three postorbital centers of ossification or only one in the rest of the chaenopsids. If there are three, joints could easily be regained; if one, it is likely that the separate bones of *Mccoskerichthys* represent a primitive condition. The fact that the postorbital of other chaenopsids anomalously may show separate elements suggests that several centers of ossification are present and that these normally fuse during development.

It is our interpretation, based on parsimony, that *Mccoskerichthys* evolved after the main chaenopsid features had appeared, and that it represents an offshoot of the *Protemblemaria* to *Acanthemblemaria* line close to *Eemblemaria* in the phylogenetic diagram given by Stephens (1970) but has lost the fusion of the postorbitals. This phyletic position eliminates the difficulty of interpreting the synapomorphies of the *Mccoskerichthys* and the *Protemblemaria* to *Acanthemblemaria* species.

*Mccoskerichthys* also agrees with the Chaenopsidae in another feature, which has not previously been noted. In chaenopsids the maxilla is not visible externally. Anteriorly it slips beneath the lower free margin and posterior projection of the lachrymal (the postorbital or second circumorbital usually forms the dorsal parts of the projec-

tion). Posteriorly, a free fold of skin extends from the posteroventral angle of the circumorbitals across the cheek forming a pocket covering the maxilla. This pocket is variously developed but present in all species. It is best developed in *Chaenopsis*, in which the maxilla extends far beyond the rear margin of the eye, and least developed in forms where the maxilla is short or the posterior expansion of the circumorbital ring is large. In *Mccoskerichthys* the posterior extension of the lachrymal and the second circumorbital cover all but the posterior tip of the maxilla and the free fold is rudimentary. *Emblemaria* has a reduced fold, but the maxilla is buried beneath the skin and there is a fold across its tip. This character is approximated in some genera of clinids including *Stathmonotus* and *Malacoctenus* but not *Haptoclinus*.

The effect of these structural chaenopsid modifications is to limit the lateral expansion of the jaws. Because of the limited protusibility of the premaxilla, the maxilla is but little rotated downward when the mouth is opened. Illustrations of throat display in which the mouth is opened widely in *Chaenopsis* and *Emblemaria* (Robins, Phillips and Phillips 1959, text fig. 1, Pl. 3, figs. 1 and 2; Wickler 1964) indicate that the maxilla remains closely applied to the cheek. The rigidly fused circumorbital ring of chaenopsids further limits lateral mobility of the maxilla.

It is possible that the early chaenopsids were omnivorous nibblers, and that the change to plankton-picking, characteristic of most members of the family (species of *Coralliozetus*, *Acanthemblemaris*, *Protemblemaria*, and *Emblemaria* examined, see also Stephens, Hobson and Johnson 1966; Hobson 1968) was correlated with increasing reliance on the tubiculous habit. *Chaenopsis* and *Lucayablennius* (Hobson 1968; Greenfield 1972) have become predators on relatively large food items, and the gape is proportionately long, but the basic chaenopsid jaw structure is otherwise little modified. The chisellike teeth of *Mccoskerichthys* hardly seem adapted to plankton feeding, yet observations and gut analyses suggest this mode of existence.

#### *Mccoskerichthys sandae* NEW SPECIES

#### Figures 1, 2

*Morphology:* Terminology is that of Stephens 1970. Counts and measurements of certain body parts are given in Tables 1 and 2. Body greatly elongated for a chaenopsid, approaching the species of *Chaenopsis* in this respect, body depth at dorsal origin 10-12 in standard length. Body strongly compressed; its dorsal and ventral outlines with little posterior taper. Head length 5.5-7.0 in standard length, head width slightly less than its depth. Snout short and rounded, lips projecting because of broad, projecting incisors; snout length from two-thirds of, to almost equal to, eye diameter, difficult to measure accurately, because of anterior excavation of orbit. Eyes directed anteriad as well as laterad, pupil round; diameter of eye 3.5-4.5 in head. Interorbital narrow, rim of orbit incised anteriorly to accommodate anteriorly directed eyes, and posteriorly to accommodate orbital cirri. Orbital cirri forming a bushy mass, which completely covers interorbital region. Cirral mass composed of five pairs of cirri; each cirrus with a stout base and at least two major branches, one medial and one lateral, each branch complexly multifid and with short lateral branches, imparting a ragged

TABLE 1  
Meristic variations in  
*Mccoskerichthys sandae*.

Total Dorsal Elements				
50	51	52	53	
8	19	14	6	
Dorsal Spines				
XVII	XVIII	XIX	XX	
4	12	26	5	
Dorsal Soft Rays				
31	32	33	34	
3	17	19	8	
Anal Soft Rays				
32	33	34	35	36
1	1	23	21	1
Pectoral Rays*				
12	13	14		
5	85	2		
Total Vertebrae				
54	55	56	57	
6	32	12	4	

\*2 damaged pectoral fins with 10 and 11 rays

appearance. Cirral mass extends from posterior edge of postorbital flange of frontal to anterior margin of eye at level of center of pupil; height of mass slightly less than eye diameter.

Top of head behind eyes with a series of transverse folds, which become longitudinal and converge toward dorsal commissural pore; folds originate anteriorly about at junction of frontals with circumorbitals and reflect underlying bony ridges. A crescentic fold at occiput, outlining anterior extent of body musculature. Fold reduced in females and absent in juveniles, although bony ridges may be seen.

Upper jaw horizontal, terminating behind eye, its length about 1.3-1.5 in post-orbital head length. Maxilla in males extending slightly beyond end of posteroventral expansion of circumorbitals, rather than ending beneath it as in females. Upper jaw with a pair of recurved incisors, one on either side of symphysis, followed by three enlarged, somewhat forward-directed, spatulate incisors; posterolateral to these a row

TABLE 2  
Measurements in millimeters of body parts of the holotype and  
ten paratypes of *Mccoskerichthys sandae*

	<i>Holotype</i>										
Standard length	62.5	63.5	65.0	69.5	62.6	59.9	62.5	62.0	69.1	65.7	65.0
Head Length	10.0	9.6	10.0	10.0	9.7	9.9	9.6	9.6	9.3	9.6	9.5
Head Depth	5.5	5.1	5.6	5.9	5.0	4.9	5.5	5.1	5.6	5.4	5.5
Head Width	5.4	5.3	5.7	5.5	5.0	5.1	5.9	5.4	5.8	5.4	5.1
Upper Jaw Length	4.9	4.3	4.5	4.5	4.5	4.9	4.9	4.0	5.0	4.6	4.4
Snout Length	1.9	1.7	1.9	2.0	1.6	1.6	1.9	1.9	1.9	1.9	1.5
Eye Diameter	2.1	2.3	2.1	2.0	2.0	2.3	2.1	2.1	2.0	2.3	2.1
Interorbit Width	.9	.9	.9	.9	.8	.7	.7	.6	.8	.6	.7
Predorsal Length	8.0	7.9	7.9	8.5	7.9	8.0	8.0	7.9	8.0	8.0	7.8
Preanal Length	25.5	25.0	26.1	27.8	24.6	24.5	25.0	25.4	26.0	27.0	25.6
Body Depth at Anus	5.7	4.8	5.3	5.2	4.9	4.8	5.5	5.6	5.6	5.0	5.5

of 7-10 smaller, downward directed, stout incisors. A patch of granular teeth anteriorly behind large incisors, continued as a single row behind small incisors. Dentition of lower jaw similar to that of upper except that there are no small symphyseal incisors, and there is a pair of stout, conical, almost caniniform teeth, one on each side of symphysis, behind patch of granular teeth. About 6 short, stout, teeth on vomer. Palate with a patch of teeth anteriorly on palatine, narrowing to two rows posteriorly; ectopterygoid with a zig-zag row of ten teeth. Anterior nostril just above upper lip, with a short tube bearing two tentacles on its rim, one anterior and one posterior. Posterior nostril just behind anterior. Cranial sensory pores mostly simple, except over postorbital bones; preoperculomandibular series with 1 commissural, 3 occipital, 1 lateral, and 1 temporal, 6-7 preopercular and 5 mandibular anterior to corner of mouth; postorbital series with 2 pores; supraorbital series with 4 pores. No pores on body posterior to upper corner of gill opening.

Gill membranes united, free from isthmus; branchiostegals 6. Gill rakers 4-5+11-12 on first arch in five specimens counted.

Total dorsal fin rays 50-53; XVII-XX, 31-34. Dorsal origin above upper anterior corner (formed by attachment of opercle membrane to body) of operculum. All rays evenly spaced, first spine short, two-thirds length of second, subsequent rays subequal, with middle of soft dorsal somewhat higher; longest soft rays  $1.5 \times$  first and last soft rays.

No notch between spinous and soft dorsal, last ray attached for its entire length by a membrane inserting on middle third of dorsalmost segmented caudal ray. Anal fin II, 32-36, all soft rays evenly spaced, spines slightly closer together. First spine short, one-half length of second, and one-third as long as first soft-ray. Soft-rays subequal, last ray attached as last dorsal ray but to ventralmost procurrent caudal ray. Caudal rounded, with 13 segmented rays and 3-6 procurrent rays; only one procurrent ray visible dorsally and one ventrally. Pectorals rounded, about 1.5 in head length, rays 12-14. Pelvics short, about two-thirds pectoral length, 1, 3, spine short, closely

applied to first soft-ray, soft-rays joined by membrane, middle ray longest. Male with a well-developed, fingerlike genital papilla, female with numerous short, flattened, fleshy processes around anus, and a short, broad genital papilla.

*Osteological characteristics:* The important cranial and caudal characters of *Mccoskerichthys sandae* are presented in figures 3-5. Comparative illustrations of *Protemblemaria* to *Acanthemblemaria* are presented in figures 6-14. Worthy of note for *Mccoskerichthys* are: the specialized anterior dentition, well-hidden maxillary, posteroventrally expanded circumorbital ring; 3 postorbital elements; fused nasals, sculptured frontals; single epural oriented almost vertically; absence of distinct minimal hypural; close association of last dorsal and anal pterygiophore to caudal (3 vertebrae between urostyle and last pterygiophore). Two additional osteological characteristics of this species that may be worthy of note are the presence of 3 anal pterygiophores anterior to the first haemal arch (typical of chaenopsids) and the lack of any dorsal pterygiophores anterior to the first vertebra (all chaenopsids except *Chaenopsis* have 2-3 pterygiophores anterior to the first vertebra).

*Color in alcohol:* Males are dark brown to tan with a series of darker marks on the sides. The dark markings vary from squarish or almost circular blotches to bars. When blotches are present there is usually a series of about 8 along the dorsal base and a series of 10-12 more or less centered on the midline. When bars are present there are usually about 10-12. The bars are irregular, and may be split by light centers. The head is notably lighter than the body, but there is much variability. In some individuals only the snout, jaws and lower surface of the head are much lighter than the sides. The cheeks and opercles are usually darker than the anterior and ventral parts of the head. The orbital cirri appear pale, but are dusted with melanophores. Often the light coloration of the head extends onto the body and there is a sharp line of demarcation extending from the pectoral base to the dorsal, between the third and fourth spines. The line of demarcation is accentuated by a dark bar behind the fourth dorsal spine. The belly is dusted with chromatophores and varies from lighter than the sides to almost as dark as them. The folds around the anus are outlined in black and the genital papilla is contrastingly white. There is much variability in coloration: in some individuals the body is light with the dark markings strongly contrasted, in others the body is dark brown and the markings difficult to discern. This variation in coloration is not correlated with size, but may be related to breeding condition.

The median fins are clear, except that the dorsal fin is marked with brown for the first 3-5 spines. The pectoral has a dusky area basally and the pelvics usually have a few melanophores on them, mostly basally.

Females are similar to males in coloration, but the head, orbital cirri and belly are paler, and a higher proportion have pale background color. However, dark females and light males do occur. In life the impression is of a dark red fish with the light areas light olive green. The dark body markings are vague, and all the fins are red.

*Ecology:* *M. sandae* occurs along near-vertical rock faces or coral heads, in areas of moderate surge, where they inhabit mollusc or worm tubes. The heads protrude from the tubes, and the fish make short darts forward, apparently snapping at plankton. Individuals were not seen to emerge completely from their tubes, but may come out

for one-half the body length or more. The elongated body of *M. sandae* allows the head to be thrust well away from the tube in feeding, with the tail still in contact with the substrate. Stephens et al. (1966) indicated that *Acanthemblemaria macrospilus*, a relatively short bodied species, may leave its tube in feeding.

Observations indicating that *M. sandae* feeds on plankton were confirmed by the examination of gut contents of several specimens. Most individuals contained fragments of copepods and amphipods, and occasional ostracods. Individuals from LACM 32551 contained numbers of tiny (.3-.5 mm) planktonic stages of pelecypods and gastropods.

*M. sandae* has been taken at depths ranging from 1m (3 ft) to almost 30 meters (100 ft). The shallowest records were from the Gulf of Chiriqui, Panama; at Isla del Caño, Costa Rica; individuals were not seen much shallower than 5 meters (15 ft).

There was a striking disparity in the numbers of males and females in the Costa Rica collections SIO75-404 (capture depth 5-10 m) contained 149 males and 76 females. LACM 32551 (capture depth 20-30 m) yielded 231 males and 154 females. The ratios of males to females deviate from 50:50 at  $p < .01$ . This unbalanced sex ratio in favor of males is difficult to explain. It almost certainly does not represent unisexual patchiness. The areas collected were large, and the tube-dwelling habit, small size and relatively poor swimming ability of the species makes it unlikely that the sexes could come together for breeding if they did not live in close proximity. It is possible that collecting bias toward the more obvious specimens could be involved, since males reach a larger size than females. This cannot be ruled out, but it is not likely that the great disparity in sex ratios can be attributed to it.

Otoliths were removed from three specimens before preservation (63.0, 66.0 and 69.5 mm). The otoliths were cleared in anise oil and examined by John E. McCosker. The largest and smallest specimens had three hyaline rings, the outer at the margin, indicating that they may have been entering their fourth year of growth. The 66.0 mm individual did not have differentiated areas in the otolith.

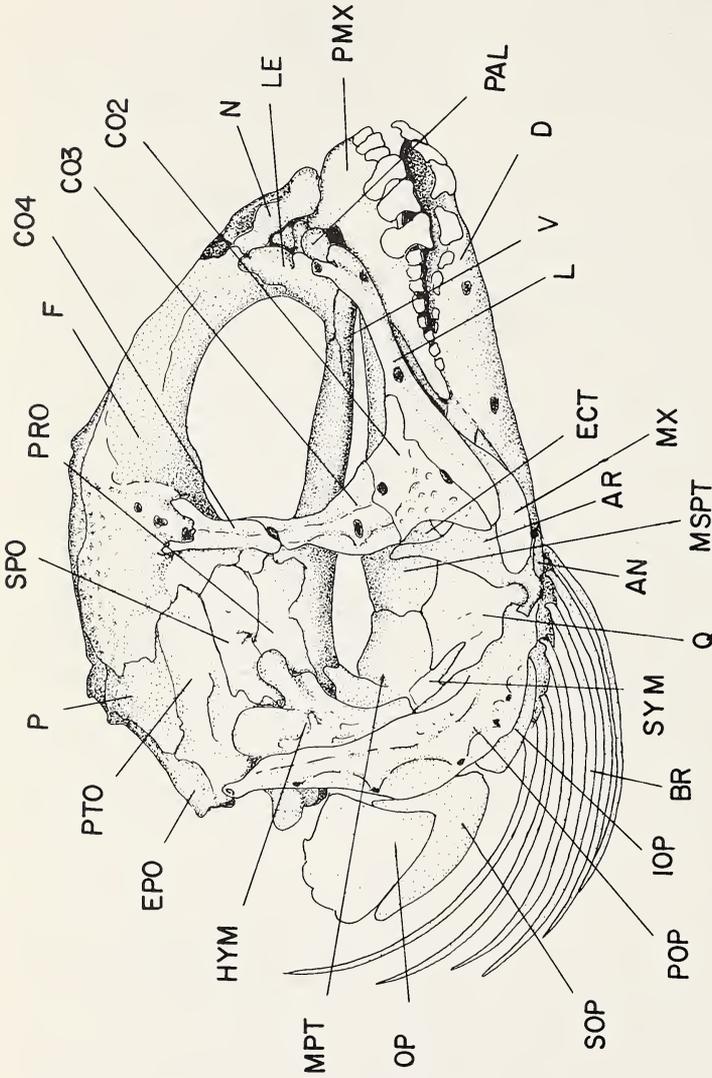
*Range:* Thus far known only from Isla del Caño, Costa Rica and the Golfo de Chiriqui, Panama.

*Derivation of name:* Named for Sandra McCosker, who participated in the first collection of the species.

#### MATERIAL EXAMINED

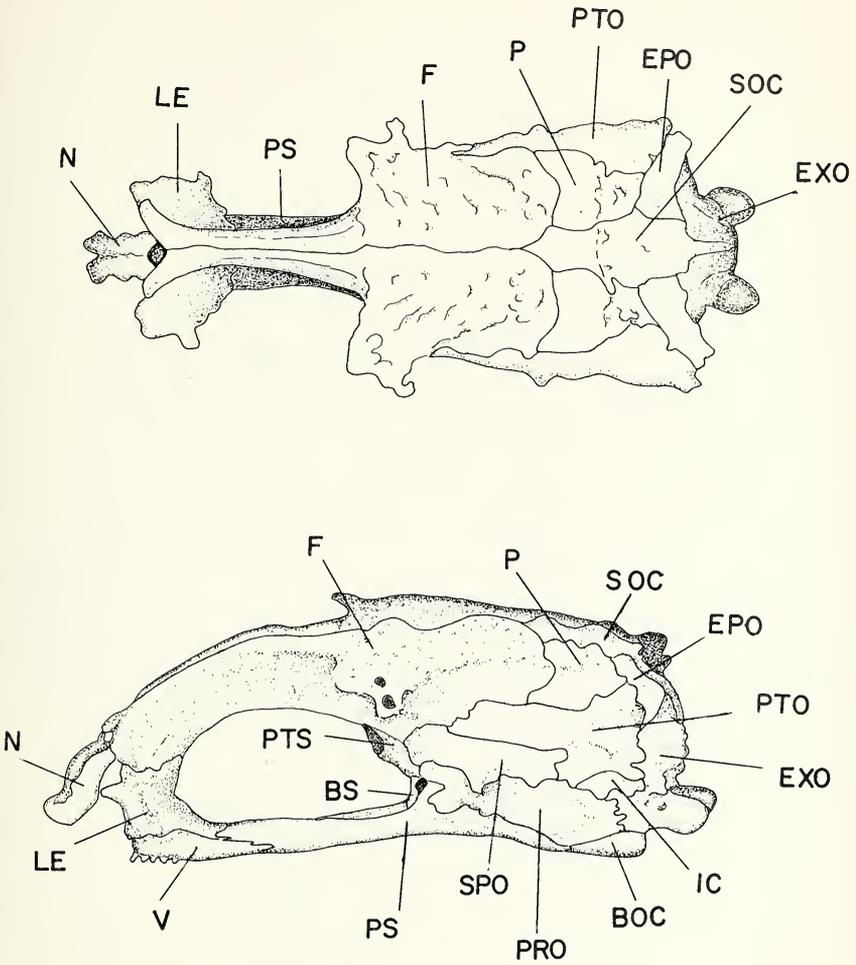
*Holotype:* LACM 32551-34, a 62.5 mm ♂ from an isolated rockpile 1.4 miles NW of Isla del Caño, Costa Rica. Taken with rotenone in 65'-75' (21-24 m) by William Bussing, John McCosker, James McLean, Manuel Murillo, Richard Rosenblatt and Richard Wheeler on 16 March 1972.

*Paratypes:* Costa Rica: LACM 32551-35, 403 (18-70 mm), bearing the same data as the holotype; USNM 214706, 10, bearing the same data as holotype; SIO-75-404, 255 (21.5-62), Isla del Caño. Panama: Golfo de Chiriqui; SIO70-358, 14 (22-65 mm), Isla Montuosa; SIO71-51, 6 (30-60 mm), SIO71-37, 2 (42-46 mm), Isla Uva; SIO71-54, 1 (38), Isla Canal de Afuera.



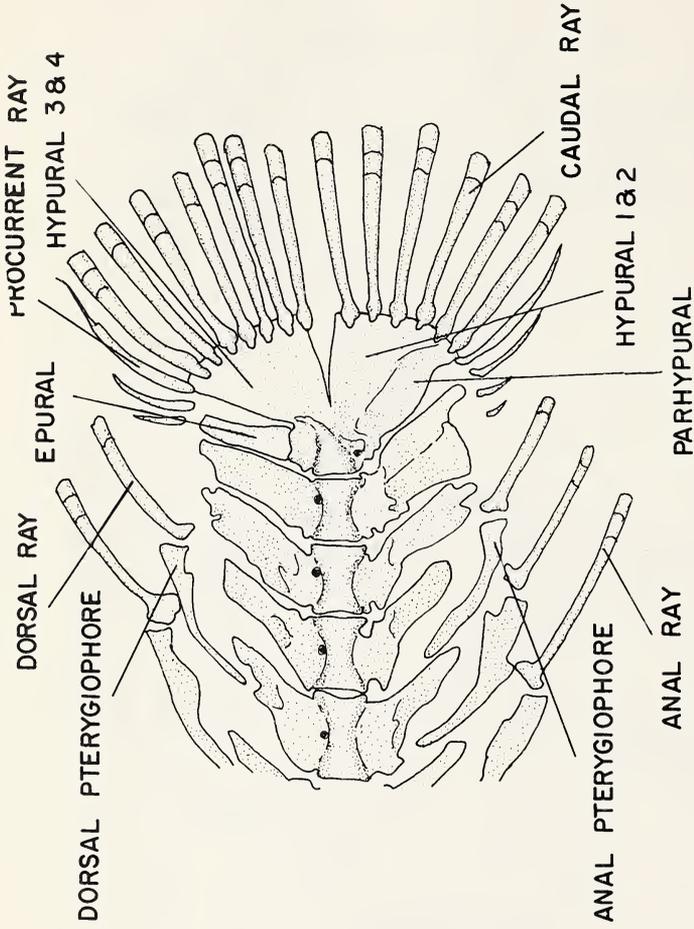
### M. SANDAE

FIGURE 3. Cranial skeleton, *Mccoskerichthys sandae* (SI070-358)



**M. SANDAE**

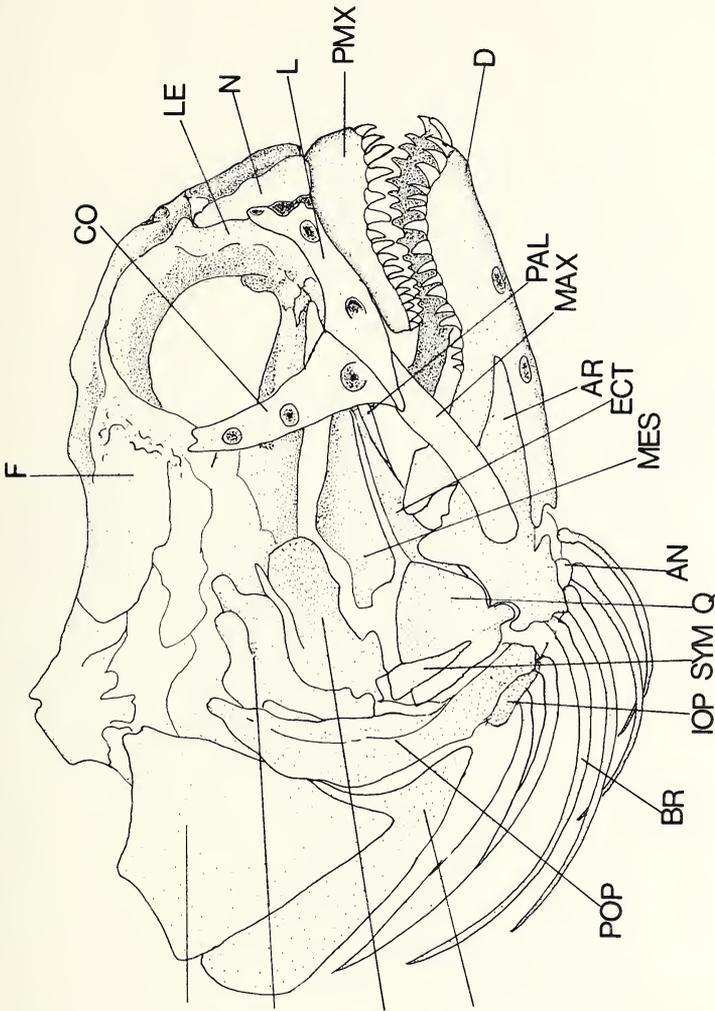
FIGURE 4. Neurocranium, *Mccoskerichthys sandae* (SIO70-358)



M. SANDAE

CAUDAL

Caudal skeleton, *Mccoskerichthys sandae* (SI070-358)



**P. BICIRRIS**

FIGURE 6. Cranial skeleton, *Protoblemaria bicirris* (UCLA 65-71)

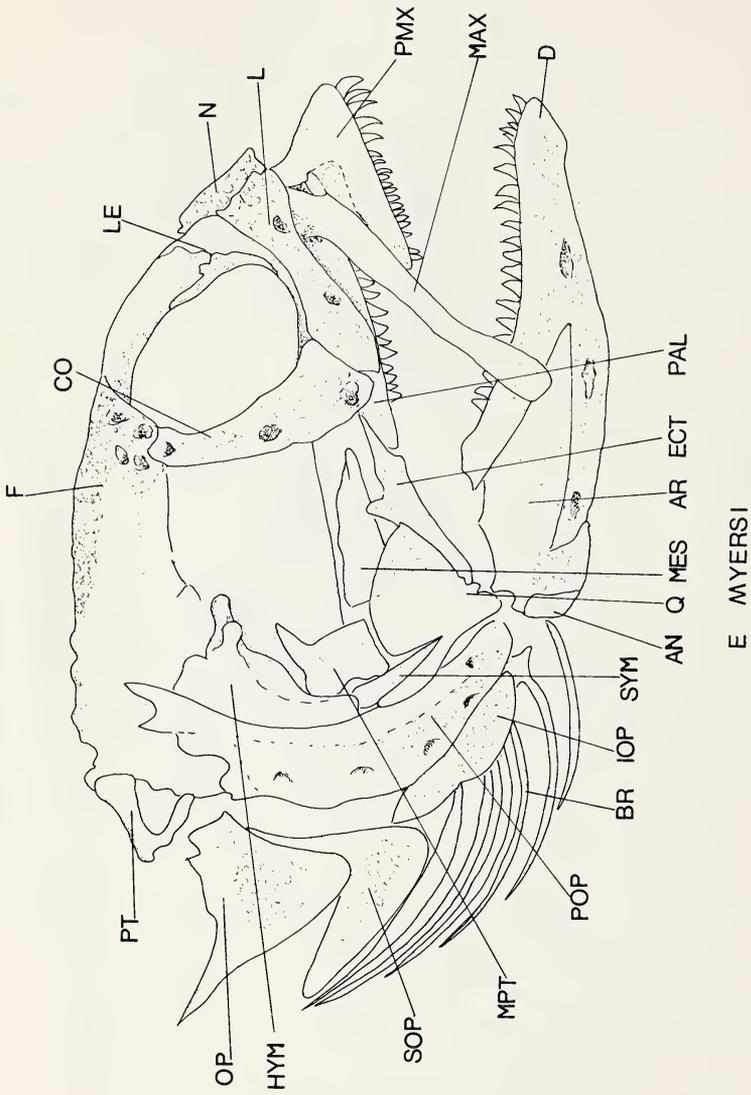
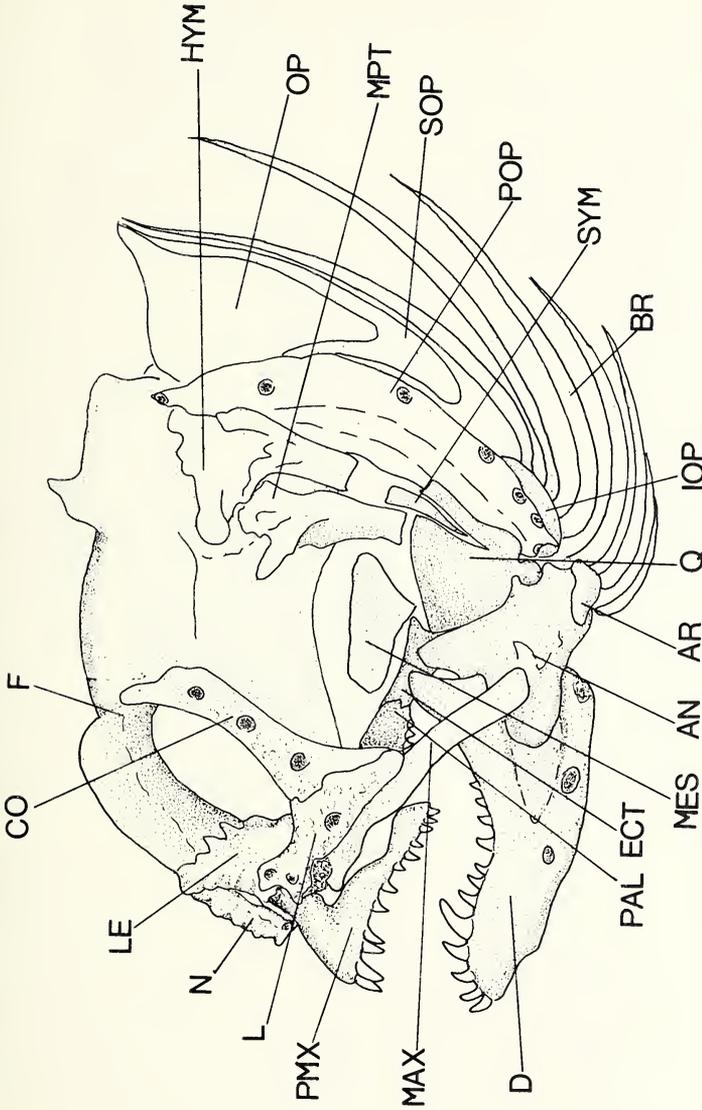
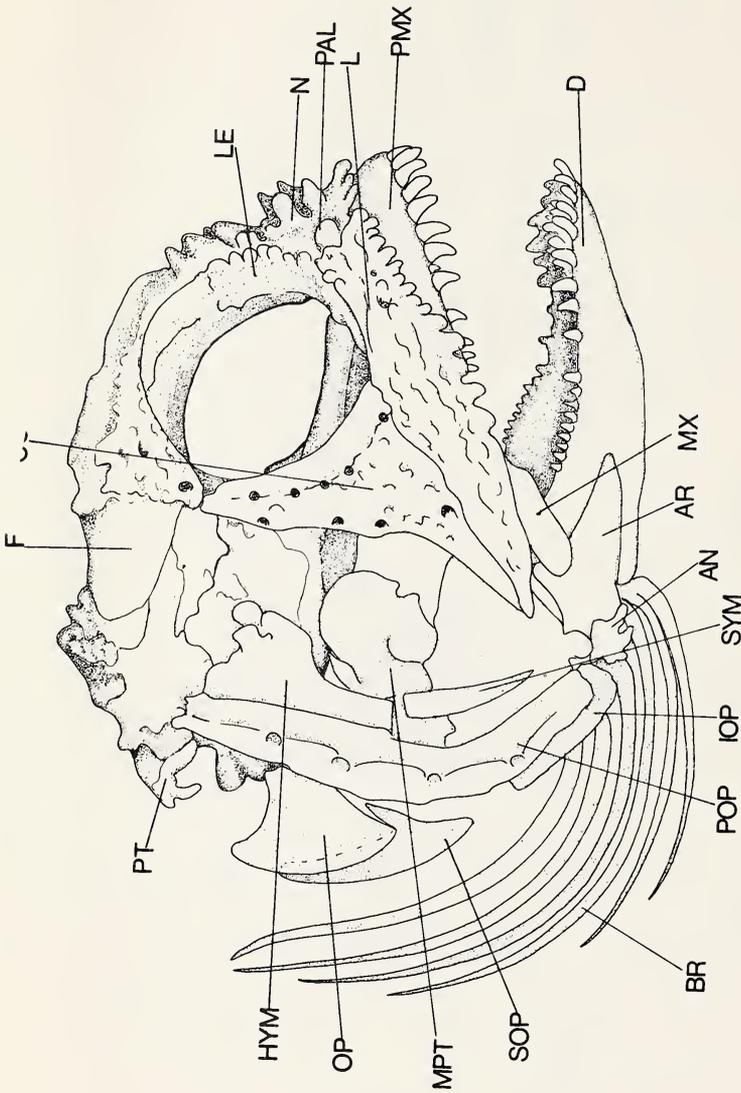


FIGURE 7. Cranial skeleton, *Ekemblemaria myersi* (UCLA 53-86)



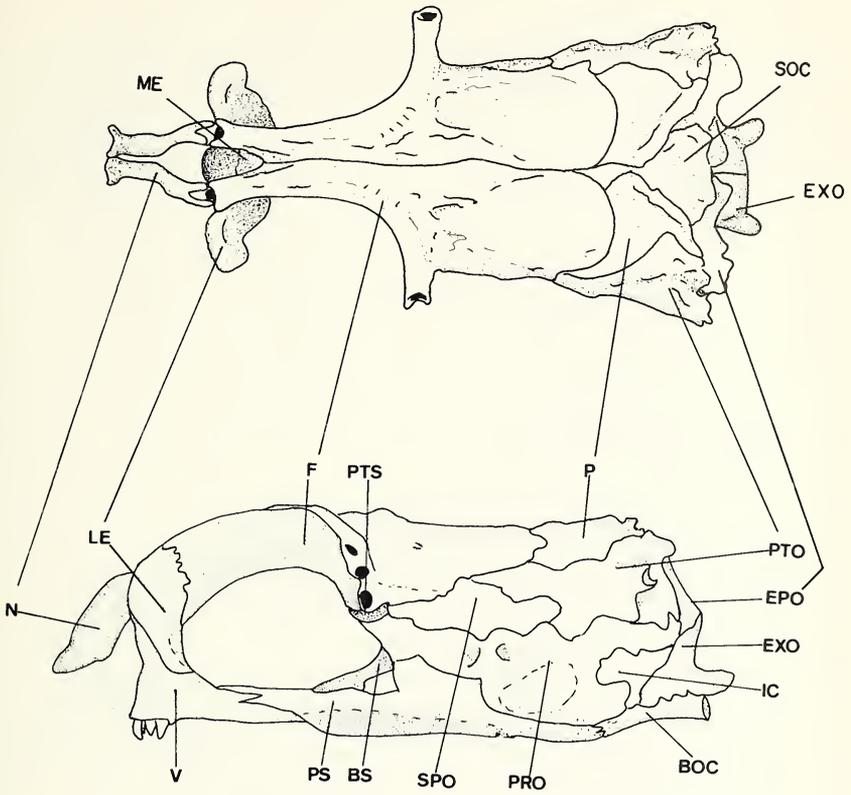
C ANGELICA

FIGURE 8. Cranial skeleton, *Coralliozetus angelica* (right side damaged) (UCLA 65-86)



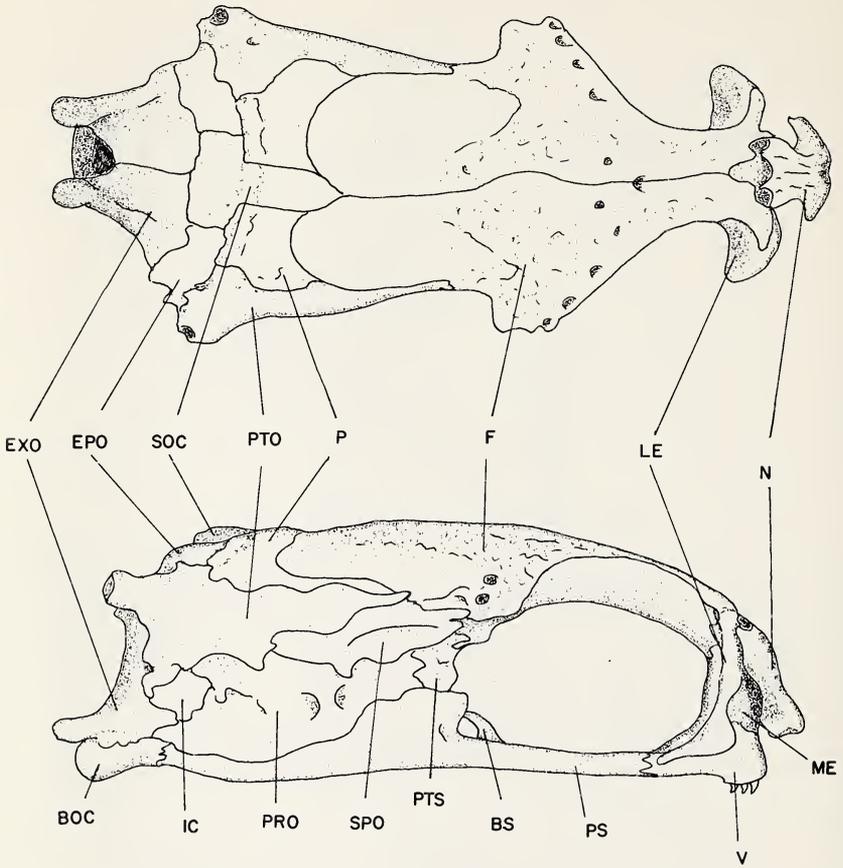
### A. CASTROI

FIGURE 9. Cranial skeleton, *Acanthemblemaria castroi* (UCLA 64-33)



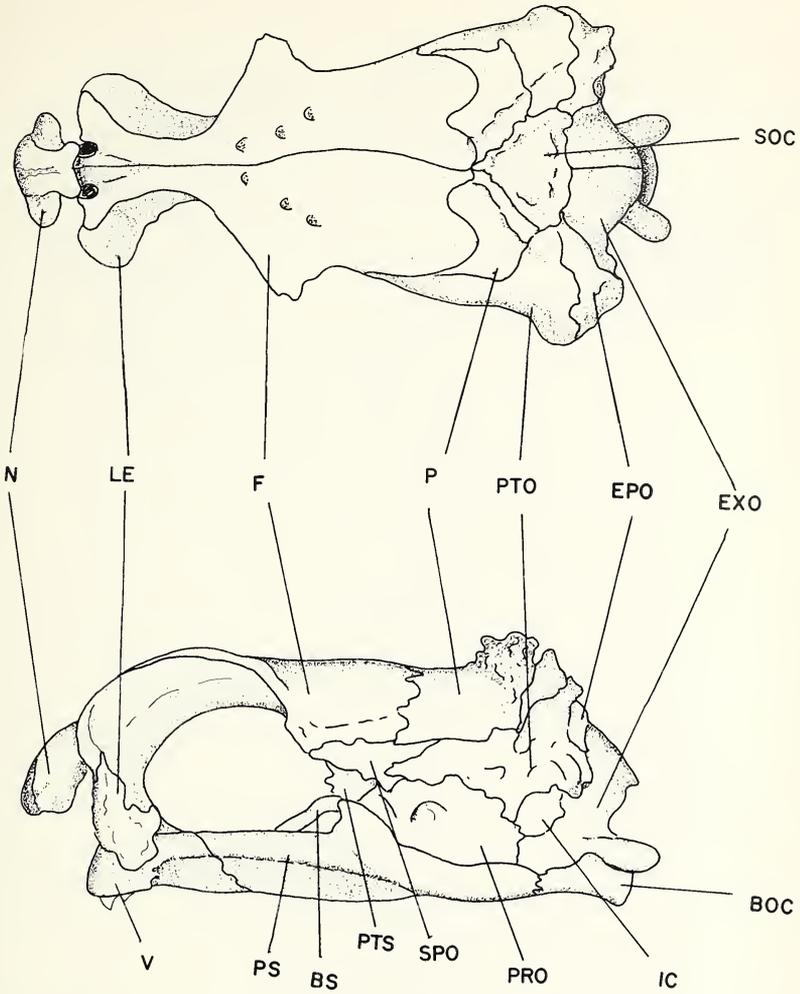
P. BICIRRIS

FIGURE 10. Neurocranium of *Protottemaria bicirris* (UCLA 65-71)



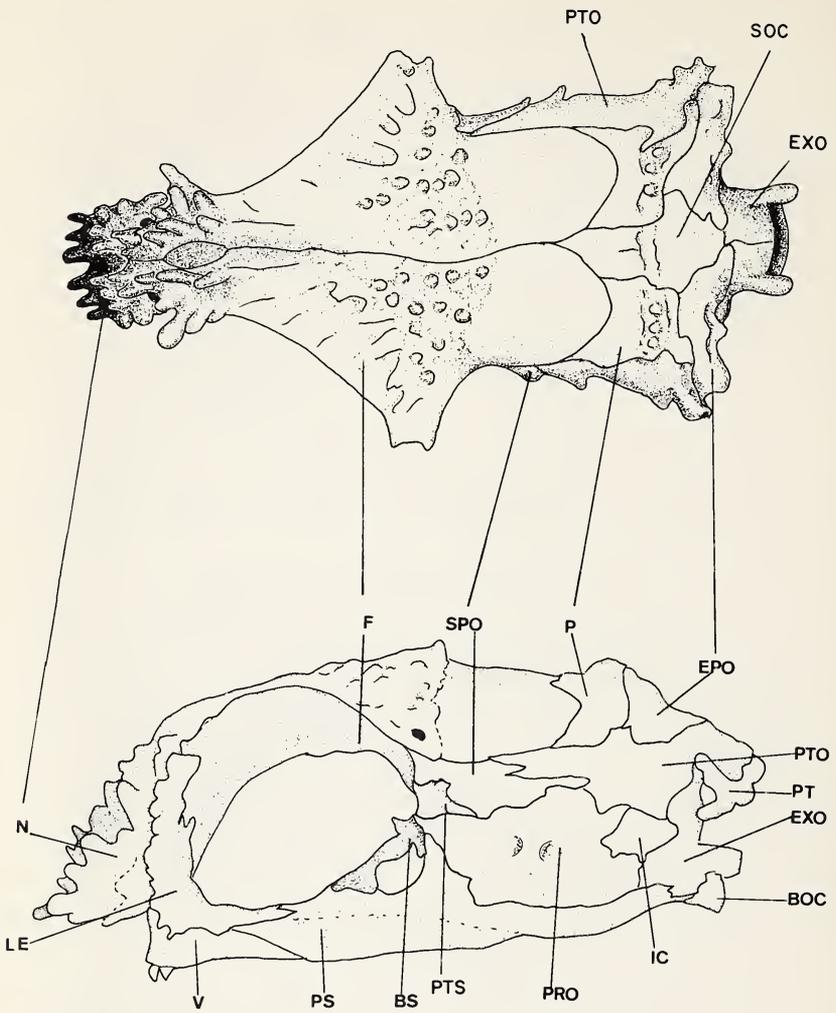
E MYERSI

FIGURE 11. Neurocranium of *Ekemblemaria myersi* (UCLA 53-86)



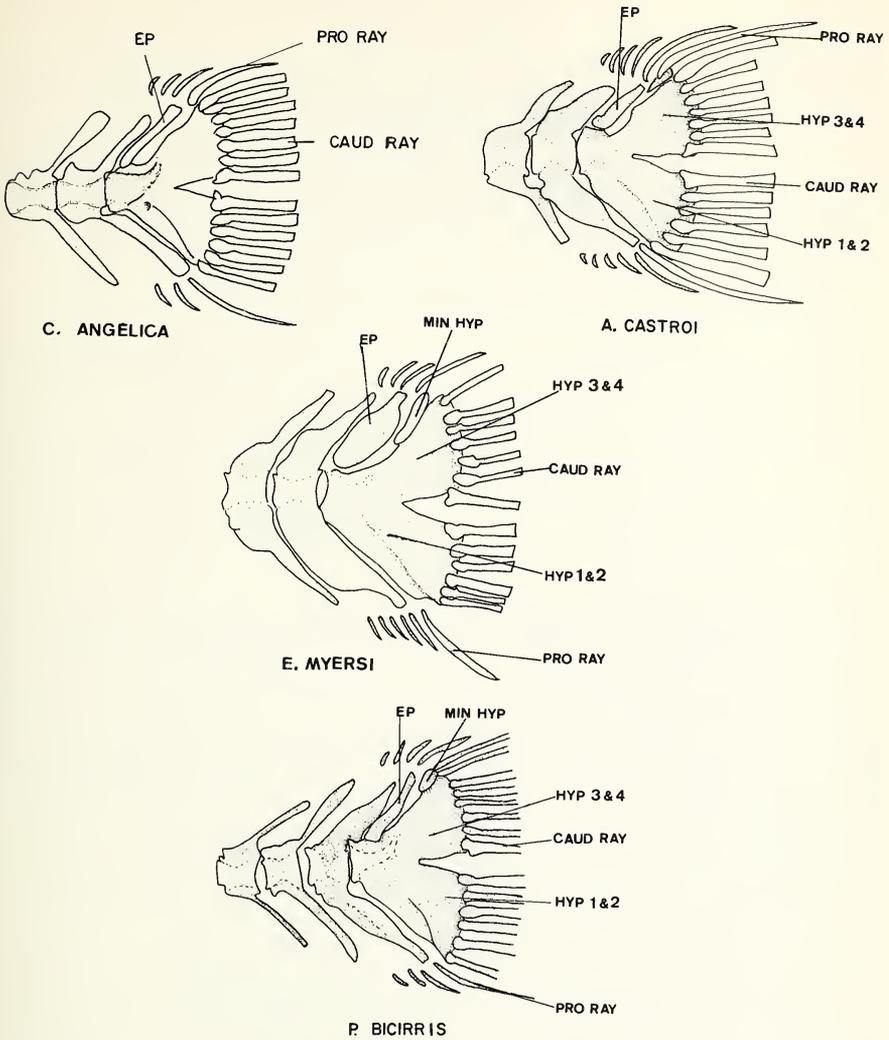
C ANGELICA

FIGURE 12. Neurocranium of *Coralliozetus angelica* (UCLA 65-86)



A. CASTROI

FIGURE 13. Neurocranium of *Acanthemblemaria castroi* (UCLA 64-33)



### CAUDALS

FIGURE 14. Comparative caudal skeletal anatomy, *Protemblemaria* to *Acanthemblemaria* line.

## ACKNOWLEDGMENTS

The Costa Rica collections were made possible by the Janss Foundation; the Panama collections were made from the R/V *ALPHA HELIX*.

The illustration of the holotype was drawn by Brian Burnette. The osteological drawings are by Stephens except for figure 6 by Cassie Cussik. The osteological portion of this study was partially supported by National Science Foundation Grant GB27266 to Stephens.

## A NOTE ABOUT FIGURES AND LEGENDS

The osteological figures do not attempt to illustrate all sensory pores. The following abbreviations are used in the osteological illustrations.

AN, Angular; AR, Articular; BOC, Basioccipital; BR, Branchiostegals; BS, Basisphenoid; CO, Circumorbital; D, Dentary; ECT, Ectopterygoid; EPO, Epiotic; EXO, Exoccipital; F, Frontal; HYM, Hyomandibular; IC, Intercalar; IOP, Interopercular; L, Lachrymal; LE, Lateral ethmoid; MPT, Metapterygoid; MSPT, Mesopterygoid; MX, Maxilla; N, Nasal; OP, Opercular; P, Parietal; PAL, Palatine; PMX, Premaxilla; POP, Preopercular; PRO, Prootic; PS, Parasphenoid; PTO, Pterotic; PTS, Pterosphenoid; Q, Quadrate; SOC, Supraoccipital; SOP, Subopercular; SPO, Sphenotic; SYM, Symplectic; V, Vomer.

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A NEW SPECIES OF CHIROPTEROTRITON (AMPHIBIA: CAUDATA)  
FROM BAJA VERAPAZ, GUATEMALA, WITH COMMENTS ON  
RELATIONSHIPS AMONG CENTRAL AMERICAN  
MEMBERS OF THE GENUS

By JAMES F. LYNCH AND DAVID B. WAKE

NATURAL HISTORY MUSEUM OF LOS ANGELES COUNTY

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A NEW SPECIES OF *CHIROPTEROTRITON* (AMPHIBIA: CAUDATA) FROM  
BAJA VERAPAZ, GUATEMALA, WITH COMMENTS ON RELATIONSHIPS  
AMONG CENTRAL AMERICAN MEMBERS OF THE GENUS<sup>1</sup>

By JAMES F. LYNCH<sup>2</sup> AND DAVID B. WAKE<sup>3</sup>

ABSTRACT: *Chiropterotriton veraepacis*, a diminutive species of plethodontid salamander with very large nostrils, is described. It occurs inside bromeliads in an area of montane cloud forest south of Purulhá, Baja Verapaz, Guatemala, and in nearby areas of Alta Verapaz, Guatemala. In most structural features *C. veraepacis* resembles *C. nasalis* of northeastern Honduras, a shorter tailed, wider headed species with larger nostrils. The new species is similar to species of the *bromeliacia* group from Guatemala and Chiapas in ecology and in many structural features but differs from them in osteology. Although *C. nasalis* and *C. veraepacis* are very distinct from the Costa Rican species *C. picadoi* in most morphological and ecological features, they resemble that species in osteology. Some additional information is presented concerning the poorly known species *C. richardi* (Costa Rica) and *C. barbouri* (Honduras), and possible relationships among all of these species are discussed.

### INTRODUCTION

In a recent paper (Lynch and Wake 1975) we assigned two new Guatemalan species of *Chiropterotriton* (*C. cuchumatanus* and *C. rabbi*) as well as three previously known Chiapan and Guatemalan forms (*C. megarhinus*, *C. xoloccalcae*, and *C. bromeliacia*) to the *bromeliacia* species group. In that paper we noted the importance of Nuclear Central America as an evolutionary center for *Chiropterotriton* and other tropical plethodontid genera (see also, Wake and Lynch 1976), and remarked that other undescribed *Chiropterotriton* existed in the area.

This paper reports the discovery of a new species of *Chiropterotriton* from the Department of Baja Verapaz, in east-central Guatemala. This form was first encountered in the spring of 1973 by Thomas Uzzell, Academy of Natural Sciences, Philadelphia (ANSP), who collected four individuals in an area of montane cloud forest a few kilometers south of the village of Purulhá. The locality is some 130 km east of the closest populations of *bromeliacia*-group *Chiropterotriton* in Huehuetenango, Guatemala, and is over 100 km west of the nearest known localities for *C. nasalis*

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

ROBERT L. BEZY

ARDEN H. BRAME, JR.

RICHARD HIGHTON

JOHN W. WRIGHT

<sup>2</sup>Chesapeake Bay Center for Environmental Studies, Smithsonian Institution, Route 4, Box 622, Edgewater, Maryland 21037.

<sup>3</sup>Research Associate in Herpetology, Natural History Museum of Los Angeles County, 900 Exposition Boulevard, Los Angeles, California 90007, and Museum of Vertebrate Zoology, 2593 Life Sciences Building, University of California, Berkeley, California 94720.

in Honduras. In 1972 the present authors had collected two species of *Bolitoglossa* at the same locality where Uzzell found *Chiropterotriton*, but we did not encounter salamanders of the latter genus on that visit, nor on a later trip (August, 1973). Because Uzzell's specimens clearly represented an undescribed member of the genus, we returned to the Purulhá area a third time in November, 1974, in hopes of securing additional material. On this occasion we collected a series of eleven *Chiropterotriton*. We name this species for its provenance, a beautiful land of true peace:

*Chiropterotriton veraepacis* NEW SPECIES

Figure 1

*Holotype*: MVZ 112499. An adult male from 4.2 km (by road) S Purulhá, Baja Verapaz, Guatemala, collected by James F. Lynch, David B. Wake, and Theodore J. Papenfuss, 14 November 1974. The holotype is one of a series taken at elevations between 1740 and 1780 meters.

*Paratypes*: MVZ 112495-98 (4 specimens), LACM 123803 same data as holotype. MVZ 112490-112494 (5 specimens) collected at the type locality 13 November 1974. ANSP 28194-28197 (4 specimens) collected at the type locality in early 1973 by Thomas M. Uzzell, Jr.

*Diagnosis*: Compared to other Central American *Chiropterotriton*, *C. veraepacis* is a rather small species, with an unusually long tail and narrow head. Eight sexually mature individuals of both sexes measure 26.1-31.2 mm (mean 28.6 mm) SL<sup>4</sup>. The tail is 1.26-1.43 times SL in undamaged adult males, whereas head width is 0.13-0.14 times SL. Maxillary teeth are abundant (range 45-57; mean 49.0 for adults), vomerine teeth are few (range 8-11; mean 9.6 for adults), and the nostrils are notably enlarged (diameter equals 0.4-0.6 mm in adults). *C. veraepacis* is distinguished from *C. nasalis* by longer tail, much narrower head, smaller feet, and somewhat smaller nostril<sup>5</sup>; from *C. picadoi* by somewhat longer tail, narrower head, much longer limbs, much larger feet, more maxillary teeth, and much larger nostrils; from *C. bromeliacia* by somewhat smaller average size, narrower head, longer tail, and many more maxillary teeth; from *C. cuchumatanus* by much longer tail, narrower head, more maxillary teeth, and somewhat fewer vomerine teeth; from *C. rabbi* by smaller average size, longer tail, much narrower head, and smaller nostrils; from *C. xolocalcae* by much longer tail, much narrower head, more vomerine teeth, and much larger nostrils; from *C. megarhinus* by much longer tail, much narrower head, and somewhat smaller nostrils. Other species of *Chiropterotriton* from Central America have a light inter-

<sup>4</sup>SL = standard length, here defined as the distance from the snout to the posterior angle of the vent.

<sup>5</sup> Statements concerning proportional distinctions between species are based on comparisons of adult males at a common projected SL (30 mm). All character differences noted in the diagnoses are significant at the 0.05 level or above.

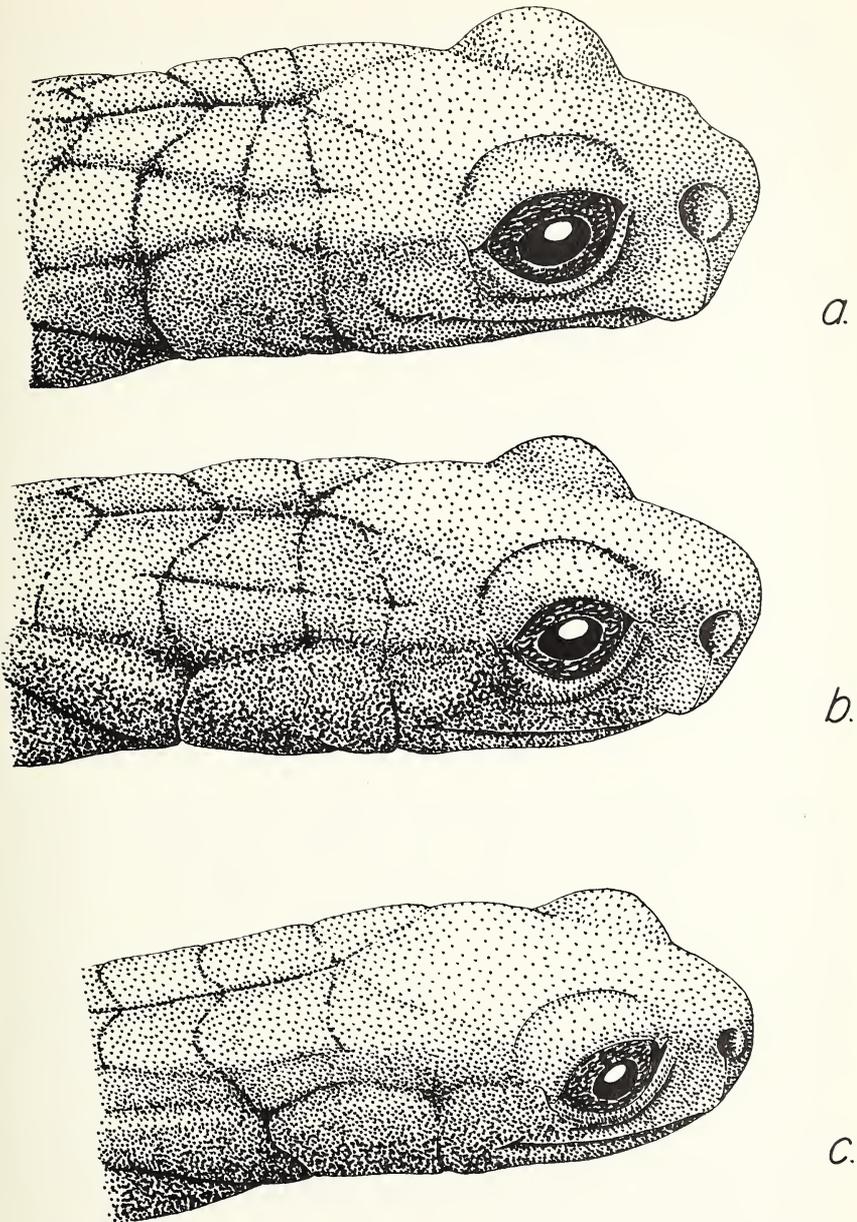


FIGURE 1. Heads of adult males of species of *Chiropterotriton*, drawn to same scale. (a) *Chiropterotriton veraepacis*, (b) *Chiropterotriton bromeliacia*, (c) *Chiropterotriton picadoi*.

orbital pigment band, at least in some specimens, but we have not seen any indication of this feature in *C. veraepacis*. Both *C. veraepacis* and *C. nasalis* have nostrils that are clearly visible by examination of the dorsal surface of the head from directly above the specimen. In *C. picadoi*, *C. richardi* and members of the *bromeliacia* group the nostrils are only slightly, or not at all, visible in dorsal view.

*Description:* To judge from the limited sample, *C. veraepacis* is a relatively small member of the genus, the largest of fifteen specimens measuring 31.2 SL. The species has the longest relative tail length and the narrowest relative head width of any of the seven other northern Central American *Chiropterotriton* for which we have data (the eighth known species from the region, the rarely collected *C. barbouri* of Honduras, is not considered here). The number of maxillary teeth increases dramatically with SL ( $r = 0.82$ ;  $P < 0.01$ ), but no size related increase in vomerine tooth count is evident ( $r = 0.24$ ;  $P > 0.1$ ). The nostrils are moderately large in juveniles and subadults. Nostrils increase in size in adults, contrary to what is seen in *C. xoloccalcae*, *C. rabbi*, and *C. picadoi*. The only adult female in the type series (MVZ 112497) has a shorter tail and more maxillary teeth than have males of equivalent SL. Adult males possess conspicuous oval-shaped mental hedonic glands.

*Measurements of the holotype (in mm):* Head width 3.9; snout to gular fold (head length) 5.7; head depth at posterior angle of jaw 2.7; eyelid length 2.0; eyelid width 1.0; anterior rim of orbit to snout 1.8; horizontal orbit diameter 1.5; interorbital distance 2.3; distance between vomerine teeth and parasphenoid tooth patch 0.5; snout to fore limb 7.9; distance separating internal nares 0.8; distance separating external nares 0.8; snout projection beyond mandible 0.3; snout to posterior angle of vent (SL) 28.2; snout to anterior angle of vent 25.7; axilla to groin 14.3; tail length 39.8; tail width at base 2.4; tail depth at base 2.6; fore limb length 6.7; hind limb length 7.6; width of right hand 1.9; width of right foot 2.3.

*Coloration (in life):* The dorsum of the holotype is dark vinaceous brown. A red-orange patch of pigment is present in the sacral region, but in contrast to the situation seen in most Central American *Chiropterotriton*, there is no interorbital bar of light pigment. A pair of obscure, red-brown patches of color are present in the otic region. There is a hint of a jagged-edged dorsal stripe on the tail. The dense dorsal melanin network is lighter laterally. A few small white iridophores are present at the side of the head and trunk. The limb bases are light pink. The venter is slate gray, with the tail somewhat darker than the belly and chin. Small white iridophores are scattered on the chin, with fewer on the belly, and none on the underside of the tail. The animal is fundamentally very dark, with other pigments (save at the tail base) becoming evident only on close examination.

The paratypes generally resemble the holotype in coloration. All fourteen paratypes are dark brown to black dorsally, all possess a light sacral patch (red, red-brown, orange, or obscure red-orange), and all lack an interorbital bar of light pigment. Ventral coloration shows more variation, ranging from medium gray to nearly black. Contrast between the chin and the belly is greatest in those individuals with darker bellies. The number of ventral white iridophores ranges from none to moderately abundant, especially in the gular region. Most individuals show at least a few white

flecks along the side of the head. In most individuals there is an obscure, irregularly bordered caudal stripe, and in some it is faintly visible on the back as well.

*Habitat:* The type series was collected in an exceptionally humid cloud forest which extends for several kilometers to the west and east of the type locality along the north-facing slopes of the Sierra de Chuacús. According to the vegetational classification of Holdridge (1967), the type locality supports lower montane wet evergreen forest (see also Savage, 1975). Large bromeliads, orchids, and other epiphytes are conspicuously abundant, as are the tree ferns that are typical of cloud forests elsewhere in Guatemala. Low palms are common in the understory of the forest. There are no relevant weather data for nearby sites, but to judge from the aspect of the vegetation and from the generalized precipitation map published by the Instituto Geografico Nacional of Guatemala (1966), annual rainfall probably exceeds 3000 mm. The local topography is extremely rugged, and much of the area is inaccessible to collecting due to the extreme steepness of slope.

Ten of the eleven *Chiropterotriton* collected by the present authors were found inside arboreal bromeliads (*Tillandsia* and *Catopsis* spp) during daylight hours. The eleventh specimen was encountered after dark on the upper surface of a palm leaf approximately 1 m above the ground. Uzzell obtained the four ANSP paratypes and an additional six specimens (ANSP 2885-90, too poorly preserved to measure) from large bromeliads, 2-8 feet off the ground.

Other arboreal amphibians which occur at the type locality of *C. veraepacis* include two species of *Bolitoglossa* (a population tentatively assigned to *B. helmrichi* and a less common, undescribed all-black species), *Hyla bromeliacia*, *Plectrohyla quecchi*, and a large, fringe-limbed hylid similar to *Hyla miliaria*. All of the foregoing species were found in arboreal bromeliads, but some occur under the loose bark of downed logs as well. Terrestrial amphibians and reptiles collected in the vicinity of the type locality include *Eleutherodactylus brocchi*, *E. rugulosus*, *Anolis cobanensis*, *A. crassulus*, *Barisia moreleti*, *Sceloporus taeniocnemis*, and *Thamnophis cyrtopsis*.

The cloud forest inhabited by *C. veraepacis* became easily accessible in the summer of 1972 upon completion of an all-weather road through the mountains of Baja Verapaz and Alta Verapaz. This previously undisturbed tract of forest is rapidly being destroyed by lumbering and agricultural activities, and the prospects of continued survival of *C. veraepacis* and other as yet undescribed endemic amphibians are bleak.

*Range:* Known only from the type locality and a nearby locality in Alta Verapaz, Guatemala. To be sought in montane cloud forest along the humid, north-facing slopes in the Chuacús-Minas mountain ranges of Baja Verapaz and Alta Verapaz. Thomas Uzzell collected two specimens of *Chiropterotriton* in a bromeliad 30 feet above the ground on the top of a ridge above Finca Volcán, Alta Verapaz (ANSP 28198-28199). Stuart (1948) reports an altitude of 925 meters for the finca, and Uzzell's collecting site is somewhat higher. Although these specimens are poorly preserved and cannot be measured, we assign them to *C. veraepacis* on the basis of their general form, large nostrils, light pigment spots at the base of the tail and absence of an interorbital bar of pigment. *C. veraepacis* is the first species of salamander to be reported from Baja Verapaz.

## COMPARATIVE OSTEOLOGY

In our previous paper (Lynch and Wake 1975) we reviewed the osteological characters of the five species that comprise the *C. bromeliacia* group. An additional five species of *Chiropterotriton* occur south and east of the Isthmus of Tehuantepec: *C. veraepacis* of Guatemala, *C. nasalis* and *C. barbouri* of Honduras, and *C. picadoi* and *C. richardi* of Costa Rica (Wake and Lynch 1976). These ten species constitute *Chiropterotriton*-beta.

In addition to the skeletal material for the *bromeliacia* group that was available for our previous study, we have examined a second specimen of *C. cuchumatamus*. A partial skeleton of the rare *C. richardi* provided limited information (Wake 1966), and we have had one hand and one foot of an additional specimen (MVZ 99516). We have examined one cleared and stained *C. veraepacis*, two *C. nasalis*, five *C. picadoi*, and one specimen (ANSP 28200) of a population from the mountains south of Pueblo Viejo, Depto. Yoro, Honduras, that is tentatively assigned to *C. barbouri*.

*C. veraepacis* differs sharply from all members of the *C. bromeliacia* group in having prefrontal bones, in having frontal processes of the premaxillary bone which arise separately and then fuse, separating again near their tips (Fig. 2), in having the

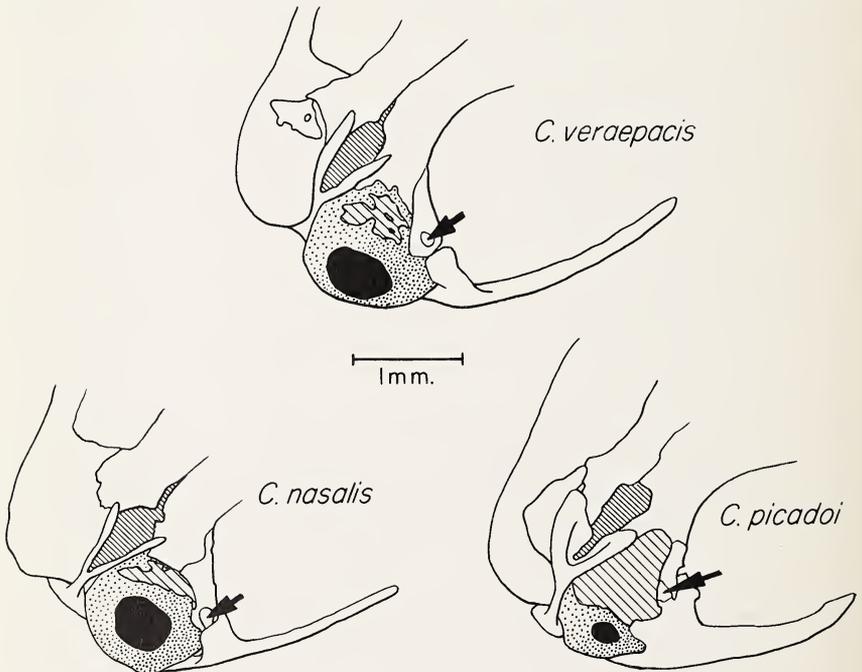


FIGURE 2. Three-quarter, anterolateral view of the nasal capsule region of three species of *Chiropterotriton*, illustrating important features. Heavy lines, nasal bone; fine lines, internasal fontanelle; stipple, cartilaginous nasal capsule; blackened area, opening in nasal capsule for external naris. Arrows point to area through which nasolacrimal duct passes ventrally into the nasal capsule.

fourth and fifth distal tarsals fused, and in having reduced numbers of carpal elements, the result of ulnare-intermedium fusions (Fig. 3). In these characters it resembles both *C. nasalis* and *C. picadoi* (Wake 1966, reported prefrontals to be present or absent in *C. abscondens* = *C. picadoi*). This statement is based on one apparently pathological specimen that has heavy ossification and in which the prefrontals and nasals are fused. In the other four individuals examined the situation illustrated in figure 2 is seen.). *C. veraepacis*, *C. nasalis*, and *C. picadoi* all lack septomaxillary bones and columellar processes of the opercular apparatus, which are present in some of the *bromeliacia* group. The new specimen of *C. cuchumatamus* has a pair of distinct septomaxillary bones, so the elements have now been found in all members of the *bromeliacia* group except *C. xolocalcae*.

In most osteological features *C. nasalis* and *C. veraepacis* are especially similar. They differ from all members of the *bromeliacia* group in a number of derived characters (the erratically structured, reduced nasal bones, the fused frontal processes of the premaxillary, and the carpal and tarsal fusions). The members of the *bromeliacia* group differ from these two species in one derived character, loss of the prefrontal bones. Additional derived features of *C. nasalis* and *C. veraepacis* distinguish them from some to most members of the *bromeliacia* group; these include loss of the septomaxillary bones and the preorbital processes of the vomers. *C. nasalis* has only a rudimentary tibial spur, while the process is absent in the *bromeliacia* group. *C. veraepacis* has a tibial spur.

The nasal capsules of *C. nasalis* and *C. veraepacis* have an orientation that distinguishes them from the members of the *bromeliacia* group and the other species discussed here. The external nares are shifted so as to have a more dorsal orientation than the nares of most species, which are typically directed anterolaterally in a nearly vertical plane.

*C. richardi* and *C. barbouri* are the least well known species of *Chiropterotriton*-beta, but we have some useful information. Both species have prefrontal bones, preorbital processes of the vomers, and tibial spurs, but lack septomaxillaries and columellar processes of the operculum. The ulnare and tibiale are fused in both, as are distal tarsals four and five. Frontal processes of the premaxillary are fused for a short distance above their origin in *C. barbouri* but not in *C. richardi*.

In the *bromeliacia* group the nasals are the main bony link between the frontals and the maxillaries, but in *C. nasalis*, *C. veraepacis* and *C. barbouri* the prefrontals provide that link. The nasals are reduced in the first two species. These features suggest that enlarged nostrils have evolved in different ways in the two species assemblages, and that no constant set of characters accompanies nostril enlargement. Some accommodation for the enlarged nostrils is required in the facial region of the skull, but it may be the result, (a) of prefrontal loss and movement of nasals into the "prefrontal zone", (b) of nasal reduction and increased prefrontal importance, (c) or of both nasal and prefrontal reduction, but with both retaining important connecting functions in the facial part of the skull (as occurs in *C. richardi*).

Both *C. veraepacis* and *C. nasalis* differ from *C. picadoi* and *C. richardi* in lacking preorbital processes on the vomer and in having tear-drop shaped prefrontals that are pierced for passage of the nasolacrimal ducts (Fig. 2). *C. barbouri* has preor-

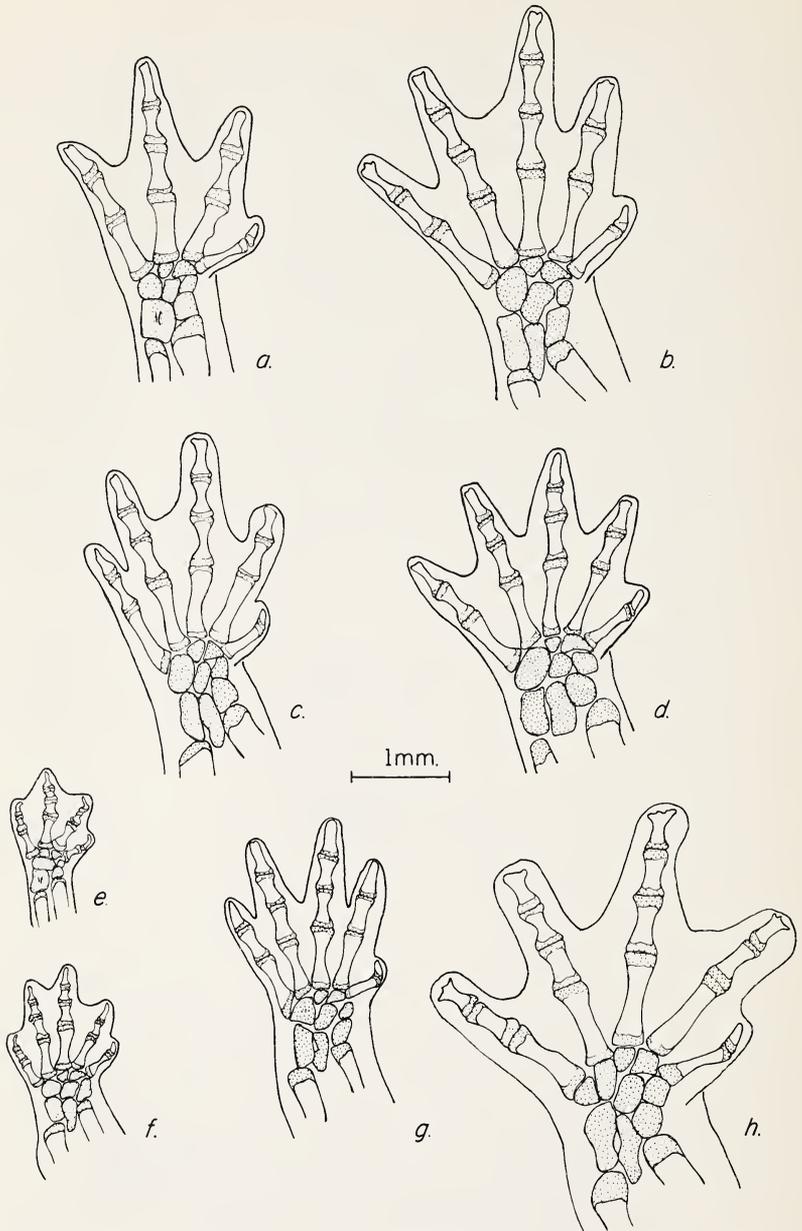


FIGURE 3. Hands and feet of species of *Chiropterotriton*, drawn to same scale from cleared and stained specimens with aid of microprojector. Cartilage stippled. (a) Left hand and (b) foot of *C. veraepacis*; (c) foot of *C. barbouri*; (d) foot of *C. nasalis*; (e) hand, and (f) foot of *C. richardi*; (g) foot of *C. picadoi*; (h) foot of *C. bromeliacia*.

bital processes, but also has prefrontals very similar to those of *C. veraepacis*. The nasal bones of *C. veraepacis* and *C. nasalis* are very reduced in size and irregular in shape; the bones have weak or no articulations. Nasals are large, regular in form, and well articulated in *C. picadoi* and *C. barboursi*. The small nostriled *C. picadoi* has a very solid, strongly articulated skull, while the relatively large nostriled *C. richardi* and the small nostriled *C. barboursi* have the more restricted articulation typical of Guatemalan, Honduran, and Chiapan species of *Chiropterotriton*. In *C. richardi* the nasals are rather small, but less reduced than in *C. veraepacis* and *C. nasalis*.

If the *bromeliacia* group is accepted as a monophyletic assemblage, the osteological data are consistent with a reasonably clear cladistic network for the eight species we are able to consider in detail (Fig. 4). The characters used are as follows (upper case letters indicate primitive states, lower case derived state; see Wake 1966, for detailed analysis of characters):

A. Prefrontal and nasal form the bony connecting link between the frontal or the center of the skull and the maxillary; the nasolacrimal duct passes between the prefrontal and the nasal. a. No prefrontal bone; only the nasal bone is involved in the link, and the nasolacrimal duct passes behind it. a'. Nasal bone reduced in size and does not span frontal and maxillary; only prefrontal involved in link; nasolacrimal duct pierces expanded ventrolateral part of prefrontal. States a and a' represent independent derivations from A in very different directions.

B. Septomaxillary present. b. Septomaxillary absent.

C. Frontal processes of premaxillary arise separately and do not fuse. c. Processes fused at base but separate distally.

D. Distal tarsals 4 and 5 discrete. d. Distal tarsals 4 and 5 fused.

E. Vomer has a preorbital process. e. No process.

F. Intermedium and ulnare discrete in carpus. f. Intermedium and ulnare fused.

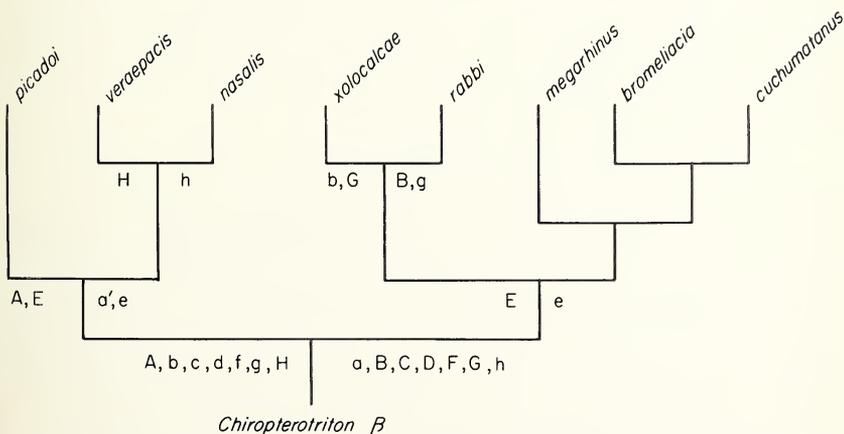


FIGURE 4. Cladogram of eight species of *Chiropterotriton*-beta, constructed by use of osteological characters. The character states indicated apply to all species along the branch unless modified states are indicated at a higher level in the dendrogram. See text for explanation.

- G. Columellar process of operculum present. g. Process absent.  
H. Tibial spur present. h. No tibial spur.

The first branching separates the *bromeliacia* group from all other species. The second branching separates *C. picadoi* from *C. veraepacis* and *C. nasalis* on the basis of loss of the preorbital process of the vomer and piercing of the prefrontals in the latter two species. On osteological grounds *C. nasalis* and *C. veraepacis* are closest to *C. barbouri*, and they are very distinct from the species of the *bromeliacia* group. The osteological formulas for the poorly known species are, for *C. barbouri*: A (but the nasolacrimal duct pierces the prefrontal as in a'), b, c (but the amount of fusion is slight), d, E, f, g, H; for *C. richardi*: A, b, C, d, E, f, g, H. If placed on the cladogram *C. richardi* would be on a branch derived from (but not a sister group of) the main branch leading to *C. picadoi*, *C. nasalis*, and *C. veraepacis*. A branch leading to *C. barbouri* would be a more primitive, non-sister group of the *C. veraepacis-C. nasalis* line. In osteological formula *C. barbouri* is identical to *C. picadoi*, but when one takes into account additional features, especially the shape of bones such as the prefrontal and the route of the nasolacrimal duct, it seems clear that it is more similar to its more osteologically derived neighbors than to *C. picadoi*.

The cladogram contains four convergences. We have rather arbitrarily coded *C. nasalis* as h, even though a rudimentary tibial spur might be present. We have never seen tibial spur rudiments in the *bromeliacia* group, but with larger samples it would not be surprising to find an occasional rudiment. Septomaxillaries have not been observed in *C. xolocalcae*, but experience has shown that these bones are found in at least a small percentage of other members of the group, and the absence here may reflect the small sample size. It is likely that the remaining two convergences (e and g) are real.

In addition to the easily coded characters which have been used above, the general arrangement and shape of the bones of *C. nasalis*, *C. veraepacis* and *C. barbouri* are similar, and in some details of foot structure (the shape of the terminal phalanges, fig. 3) these species, *C. picadoi* and *C. richardi* are similar and differ from all members of the *bromeliacia* group.

#### MORPHOMETRIC ANALYSIS

##### *Methods*

Lynch and Wake (1975) used a number of analytical approaches in comparing the five species of the *Chiropterotriton bromeliacia* group. The number of specimens of *C. veraepacis*, while small, is sufficient for some of the same kinds of quantitative comparisons. Specifically, we have undertaken linear regression analysis of single characters as they vary with SL, and multiple discriminant analysis of all characters simultaneously in an attempt to clarify the phenetic and phyletic relationships among eight of the ten Central American species of *Chiropterotriton* (*C. bromeliacia*, *C. cuchumatanus*, *C. megarhinus*, *C. nasalis*, *C. picadoi*, *C. rabbi*, *C. veraepacis*, *C. xolocalcae*). *C. barbouri*, a poorly known species from western Honduras, and *C. richardi*, a poorly known Costa Rican form, have been omitted due to lack of sufficient comparative material. The reader is referred to our earlier paper for detailed

description of statistical methodology and for discussion of the choice and scaling of individual characters.

*Analysis of individual characters:* Eight characters are considered: standard length (SL), head width (HW), nostril diameter (ND), combined length of hind limb and fore limb (CL), foot width (FW), tail length (TL), number of maxillary teeth (MT), and number of vomerine teeth (VT). As described in detail in Lynch and Wake (1975), we have used linear regression techniques to project means and 95 percent confidence limits for characters 2-8 to a common value of SL = 30 mm. To eliminate the confusing effects of secondary sexual dimorphism and possibly nonlinear rates of character change across very wide ranges of SL, only post-juvenile males (SL greater than 24 mm) are included in the regression analysis.

*Multivariate analysis of characters:* The same eight morphological characters examined in the regression analysis were utilized in the discriminant function analysis. The purpose of this exercise was to define the combination of phenetic traits which best distinguishes the Central American species of *Chiropterotriton* from one another, and to eliminate the effects of intercorrelation among characters in assessing morphological similarity among species. This latter aim is realized because discriminant analysis defines statistically independent composite axes, each of which corresponds to independently varying character complexes (see Blackith and Reyment 1971). The Smithsonian Institution's version of the SPSS program for stepwise discriminant analysis was used for all computations.

*Phenetic clustering of taxa:* The discriminant analysis defines the centroid of each species cluster with respect to each of the seven discriminant axes which exist for an analysis of eight groups and eight characters. Because the distances between points in discriminant space ("D-space") are not biased by intercorrelations among characters, as is the case if phenetic distance is measured in simple Euclidian space, it is often preferable to base phenetic clustering on the scores along the major discriminant axes (for an example of the different results of these two metrics see Robinson and Hoffmann 1975). The latter axes are said to define a "reduced space" because most interspecific differentiation can be expressed using only a few of the maximum possible number of discriminant axes. A two- or three-dimensional representation of the group centroids (or of individual specimens) in discriminant space often suffices as a summary of significant interspecific variation.

With the above in mind, we have used the generalized distance (=Mahalanobis Distance) between the group centroids with respect to the first three discriminant axes as the basis for phenetic clustering. The unweighted pair group method using arithmetic averages (UPGMA), as described by Sokal and Sneath (1963) and Sneath and Sokal (1973) was the clustering algorithm employed. The UPGMA technique is a sequential, agglomerative, hierarchic, non-overlapping method (see Sneath and Sokal, 1973) which begins by defining a cluster (or several clusters) consisting of the least dissimilar Operational Taxonomic Units (OTU's), then adds individual OTU's or other clusters to pre-existing clusters on the basis of average phenetic similarity.

A second technique, the Prim algorithm (see Prim 1957; Farris 1970; Sneath and Sokal 1973), was used to form a minimum-spanning network connecting the eight OTU's, again based on the generalized distance separating them. This algorithm min-

imizes the total length of the internodes connecting the OTU's, and results in closest phenetic neighbors always being linked by an internode. When superimposed on a display of group centroids in reduced space, the Prim network provides a useful check on the adequacy of the visual impression of inter-OTU distances (see Sneath and Sokal, 1973: 255-256).

Results

*Analysis of individual characters:* Figure 5 and Table 1 summarize the results of the regression analysis of single characters in post-juvenile males of the eight species of *Chiropterotriton*. *C. veraepacis* has a longer tail and narrower head than the other species in the comparison. The 95% confidence limits of the projected mean values of TL and HW at SL = 30 mm show no overlap between *C. veraepacis* and any of the remaining taxa. Some overlap is evident with respect to the other five characters considered in the analysis, but *C. veraepacis* differs significantly ( $P < 0.05$ ) from every other species in from three to six characters. The 95% confidence limits for projected character values tend to be relatively broad for *C. veraepacis* and *C. nasalis*, probably reflecting their small sample sizes.

A mosaic pattern of differentiation is found. For example, high maxillary tooth counts may be associated with high vomerine tooth counts (*C. xolocalcae*), moderate

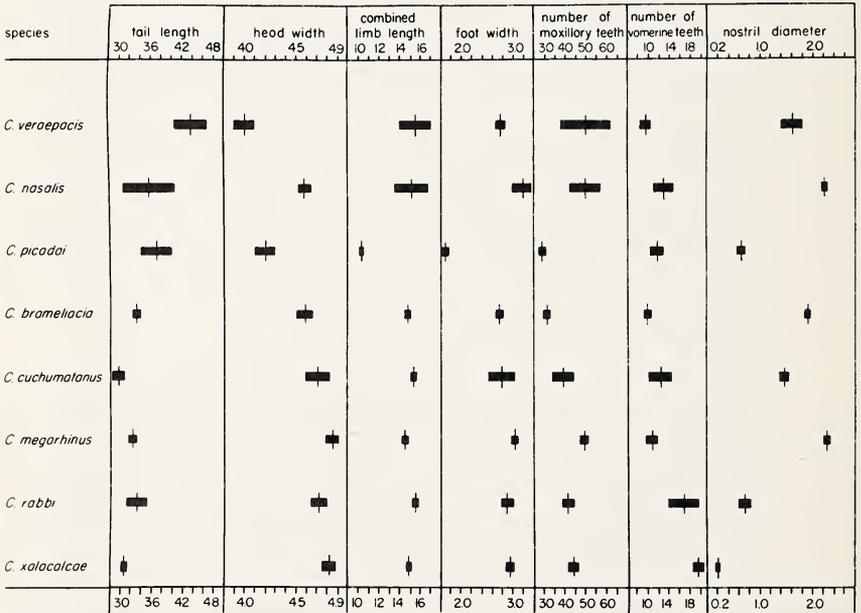


FIGURE 5. Predicted mean (vertical line) and 95% confidence limits (solid bar) for eight characters in post-juvenile males of eight species of *Chiropterotriton*-beta. See text for further explanation. Note that the column "head width" was incorrectly labeled "head length" in a similar figure in Lynch and Wake (1975, fig. 7). All figures in mm.

TABLE 1

Predicted mean character values and 95% confidence limits (in parentheses) for post-juvenile male *Chiropterotriton* at SL = 30 mm. Values obtained by linear regression analysis (see text), except where no significant correlation was found between dependent variable and SL. In such instances, indicated by asterisk (\*), univariate means and confidence limits are given. Symbols for characters: SL = standard length; TL = tail length; HW = head width; CL = combined limb length; FW = foot width; MT = maxillary tooth count; VT = vomerine tooth count; ND = nostril diameter.

SPECIES	N	SL	CHARACTERS						
			TL	HW	CL	FW	MT	VT	ND
<i>C. veraepacis</i>	8	27.8	43.7 (40.6-46.8)	4.0 (3.9-4.1)	15.6 (14.1-17.1)	2.8 (2.7-2.8)	49.9 (37.8-61.9)	9.4* (8.4-10.4)	0.53* (0.47-0.59)
<i>C. nasalis</i>	7	28.0	35.6 (30.6-40.6)	4.6 (4.5-4.6)	15.2 (13.6-16.8)	2.8 (3.0-3.4)	49.7* (42.4-57.0)	13.1* (11.2-15.1)	0.73 (0.72-0.75)
<i>C. picadoi</i>	16	28.3	37.0 (34.0-40.0)	4.2 (4.1-4.3)	10.4 (10.2-10.6)	1.7 (1.6-1.8)	29.3 (27.5-31.1)	11.8 (10.6-13.0)	0.21 (0.18-0.24)

(*C. nasalis*), or low (*C. veraepacis*) vomerine tooth counts. An exception to the pattern of independent variation of characters is the invariable association of large nostril size with low numbers of vomerine teeth (previously noted in the *bromeliacia* group, Lynch and Wake 1975). *C. picadoi* is exceptional in having both few vomerine teeth and very small nostrils. This species possesses a well-developed preorbital vomerine process, as do the other small-nostriled species (*C. rabbi*, *C. xoloccalcae*) in the analysis, but the presence of the process is not always associated with a large complement of vomerine teeth in other plethodontid salamanders (see Wake 1966; Lynch and Wake 1975: 34-35). Thus, our earlier conclusion that the preorbital vomerine process is necessary, but not sufficient, for the presence of a large number of vomerine teeth, is not affected by the pattern seen in *C. picadoi*.

*Discriminant analysis:* Figure 6 and Table 2 summarize the results of the stepwise discriminant analysis of interspecific variation. The absolute magnitudes of the standardized discriminant coefficients (Table 2) are proportional to the relative importance of each character in separating the species along each discriminant axis. The first three discriminant axes, representing the first three discriminant functions, together account for 95.7% of the observed interspecific morphological variation. Although the con-

TABLE 2

Summary of results of stepwise multiple discriminant analysis of variation in post-juvenile male *Chiropterotriton*. Raw (unstandardized) and standardized coefficients are given for the first three discriminant functions, which together account for 95.7% of the observed interspecific variation. The magnitudes of the standardized coefficients are proportional to the relative contribution of each variable on a given discriminant axis. The most important variables on each axis are marked with an asterisk (\*).

CHARACTER	DISCRIMINANT FUNCTION					
	FIRST		SECOND		THIRD	
	Raw	Stand.	Raw	Stand.	Raw	Stand.
SL	0.008	0.022	0.058	0.157*	-0.076	-0.204*
TL	0.003	0.012	0.029	0.128*	0.021	0.092
HW	-0.078	-0.042	-0.083	-0.045	-0.167	-0.090
CL	0.006	0.015	-0.147	-0.362*	-0.040	-0.100
FW	-0.076	-0.046	-0.060	-0.036	0.183	0.111
MT	0.001	0.011	-0.003	-0.028	0.036	0.350*
VT	-0.012	-0.060	-0.007	-0.038	-0.008	-0.041
ND	0.521	0.403*	-0.061	-0.047	-0.050	-0.038
CONSTANT		-0.391		0.280		1.172
PER CENT VARIATION EXPLAINED		54.13		32.98		8.59

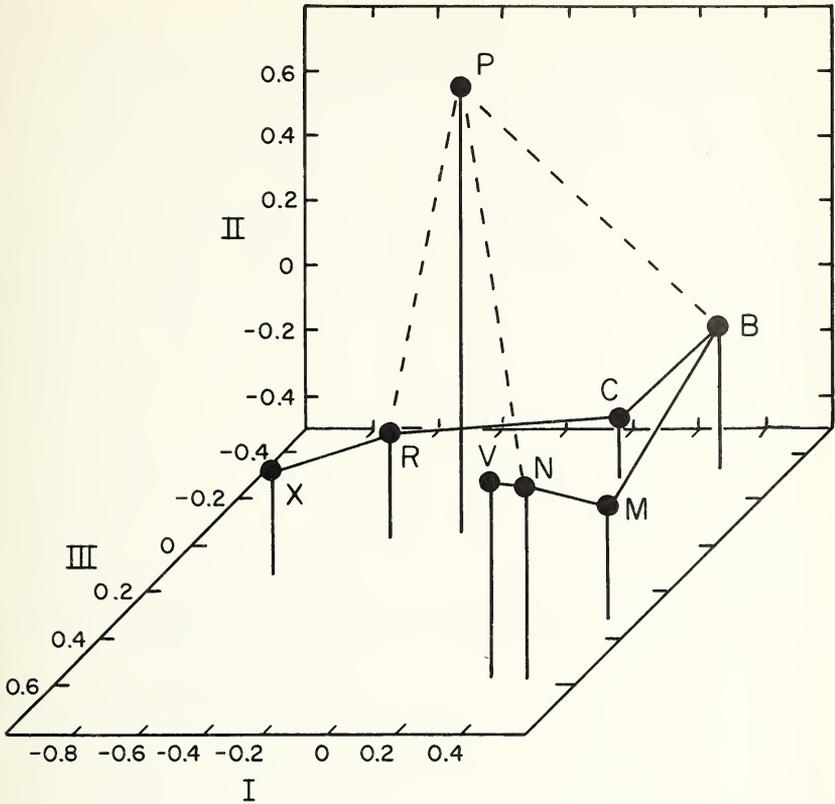


FIGURE 6. Plot of the first three discriminant axes separating post-juvenile males of the species of the *Chiropterotriton bromeliacia* group [*bromeliacia* (B), *cuchumatanus* (C), *megarhinus* (M), *rabbi* (R), *xolocalcae* (X)] plus *C. veraepacis* (V), *C. nasalis* (N), and *C. picadoi* (P). The dots are the positions of the group centroids for each species relative to these three variates. The centroids are connected by a computed Prim network, which links the closest phenetic neighbors. *C. picadoi* is about equally close to three species. See text for further explanation.

tributions of three of the remaining four discriminant axes are statistically significant ( $P < 0.05$ ), their cumulative impact on the discriminatory process is small (4.3%). The first discriminant function accounts for 54.1% of the interspecific variation; nostril diameter (ND) is by far the most important determinant of the score along this axis, as was also found to be the case in our earlier study of the *bromeliacia* group. The second discriminant function (33.0% of interspecific variation) is influenced most strongly by limb length (CL), and its most obvious effect is to sharply distinguish the short-limbed *C. picadoi* from all other species. The third discriminant function (8.6% of interspecific variation) shows high loading for maxillary tooth count (MT) and, to a lesser extent, standard length (SL) and foot width (FW). This axis tends to separate *C. veraepacis* and *C. nasalis* from *C. picadoi* and the *bromeliacia* group species.

TABLE 3

Generalized (Mahalanobis) distance values for centroids of eight OTU's.

 $\bar{D}$  = mean generalized distance.

SPECIES	2	3	4	5	6	7	8	$\bar{D}$
1. <i>C. bromeliacia</i>	1.142	0.865	0.368	0.664	0.905	0.912	1.123	0.854
2. <i>C. xolocalcae</i>		0.402	0.871	1.211	1.126	1.214	1.166	1.019
3. <i>C. rabbi</i>			0.595	1.012	0.996	1.073	1.075	0.860
4. <i>C. cuchumatanus</i>				0.725	0.940	0.953	1.226	0.811
5. <i>C. megarhinus</i>					0.406	0.323	1.307	0.807
6. <i>C. veraepacis</i>						0.144	1.124	0.806
7. <i>C. nasalis</i>							1.253	0.839
8. <i>C. picadoi</i>								1.182

A three dimensional projection of the group centroids of each of the eight species in relation to the first three discriminant axes (Figure 6) summarizes the differentiation achieved by these axes. Viewed in D-space, *C. picadoi* appears to be the most isolated of the eight species, mainly by virtue of its very high positive score along the second discriminant axis. A close phenetic relationship between *C. nasalis* and *C. veraepacis* is evident, and these two species appear more similar to *C. megarhinus* than to any of the other *bromeliacia* group.

Table 3 gives the Mahalanobis distances separating the group centroids of the eight species in the D-space defined by the first three discriminant axes. The impressions gained from inspection of the three dimensional plot of group centroids are strengthened by these distance estimates. The most similar pair of species is *C. nasalis* and *C. veraepacis* ( $\bar{D} = 0.14$  units); no other species pair is separated by less than 0.32 units, the latter being the distance between *C. nasalis* and *C. megarhinus*. At the other extreme, *C. picadoi* shows no strong similarity to any of the other species ( $\bar{D} = 1.18$ ; range 1.07-1.31).

Despite the similarities of most of the species in gross appearance, the discriminant analysis succeeded in assigning 95% of the 130 individual specimens to the "correct" home population on the basis of morphometric criteria alone (Table 4). This result confirms the utility of multivariate approaches in making morphological comparisons among OTU's which show complex patterns of overlap in single characters and which exhibit size-related variation in most morphological traits. Of the seven misidentifications which occurred, three were assignments of *C. bromeliacia* and *C. rabbi* to *C. cuchumatanus*, three were assignments of *C. rabbi* to *C. xolocalcae*, or vice versa, and one is a misclassification of *C. nasalis* as *C. megarhinus*. In spite of the small overall phenetic separation of *C. nasalis* and *C. veraepacis* individuals of both species were not mismatched by the discriminant procedure.

*Phenetic clustering*; The Prim network linking the eight *Chiropterotriton* species is superimposed over the three-dimensional projection of the group centroids in figure 6. The distortion resulting from the geometry of the projection and from the omission

TABLE 4

Classification matrix based on discriminant analysis of post-juvenile male *Chiropterotriton* from eight populations. Entries along the main diagonal are "correct" matches of individuals to their source population based on eight morphological characters. See text for further explanation.

		PREDICTED GROUP MEMBERSHIP							
		1	2	3	4	5	6	7	8
Actual Group	N								
1. <i>C. bromeliacia</i>	33	32	0	0	1	0	0	0	0
2. <i>C. xolocalcae</i>	22	0	21	1	0	0	0	0	0
3. <i>C. rabbi</i>	22	0	2	18	2	0	0	0	0
4. <i>C. cuchumatanus</i>	9	0	0	0	9	0	0	0	0
5. <i>C. megarhinus</i>	13	0	0	0	0	13	0	0	0
6. <i>C. veraepacis</i>	8	0	0	0	0	0	8	0	0
7. <i>C. nasalis</i>	7	0	0	0	1	0	0	6	0
8. <i>C. picadoi</i>	16	0	0	0	0	0	0	0	16

of the fourth and higher discriminant axes evidently is small, for the Prim linkage of OTU's which show the highest phenetic similarity conforms well with the visual impression of similarities gained from the projection. The network is basically a chain which connects seven of the species in the order *xolocalcae-rabbi-cuchumatanus-bromeliacia-megarhinus-nasalis-veraepacis*. The eighth species, *C. picadoi*, lies well off this main sequence, and is about equally as distant from *C. rabbi*, *C. bromeliacia*, and *C. nasalis*.

The UPGMA phenogram, based on the same matrix of generalized inter-OTU distances used to construct the Prim network, is shown in figure 7. Summarizing, we see a tight cluster formed by *C. veraepacis* and *C. nasalis*, which is connected to the "looser" grouping of four *bromeliacia* group species by *C. megarhinus*, the fifth species in that group. *C. picadoi* shows slightly more similarity to the small-nostriled members of the *bromeliacia* group than to the other OTU's, but it is not very similar to any of the species. The linkage pattern among the five species of the *bromeliacia* group produced by the UPGMA analysis is identical to that derived previously (Lynch and Wake 1975: Fig. 10a) from an 11-character phylogenetic clustering algorithm, the WISS method of Farris, Kluge, and Eckhardt (1970).

## DISCUSSION

The species of *Chiropterotriton* considered in this paper have several ecologically important features in common. All are small, arboreal or crevice-dwelling salamanders which inhabit wet montane forest, and all have very limited geographic ranges. Sympatry between congeners is unknown in northern Central American *Chiroptero-*

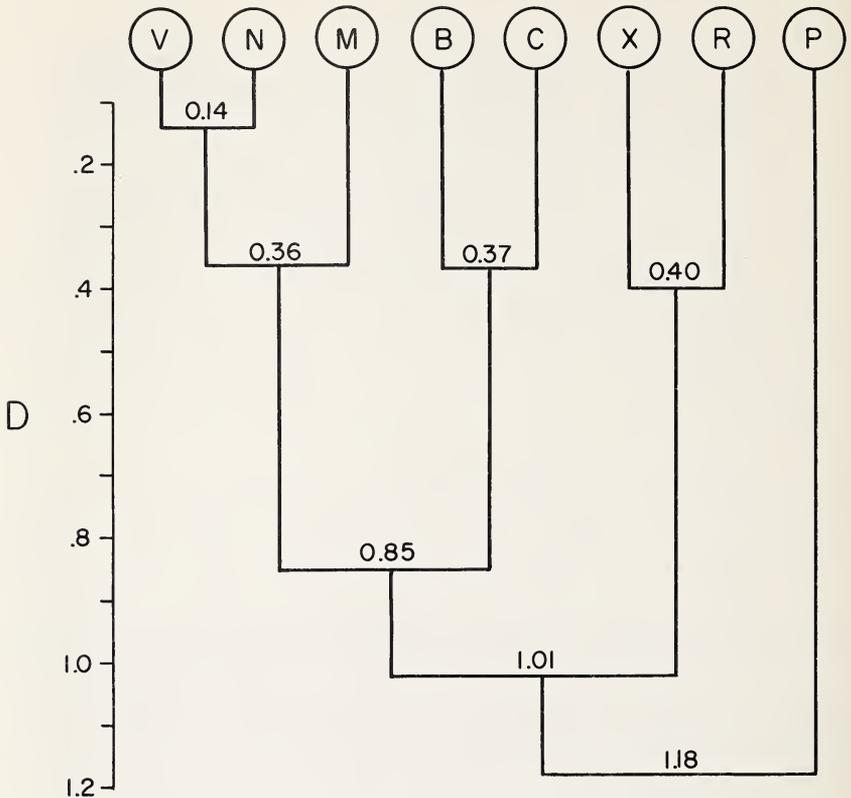


FIGURE 7. UPGMA phenogram of eight species of *Chiropterotriton* based on Mahalanobis Distance between group centroids with respect to the first three discriminant axes. (B) *C. bromeliacia*; (C) *C. cuchumatanus*; (M) *C. megarhinus*; (N) *C. nasalis*; (P) *C. picadoi*; (R) *C. rabbi*; (V) *C. veraepacis*; (X) *C. xolocalcae*. See text for further explanation.

*triton*, although co-occurrence of several pairs of species of *Chiropterotriton*-alpha has been documented north of the Isthmus of Tehuantepec in the Sierra Madre Oriental. In addition, *C. picadoi* and *C. richardi* of the beta assemblage are sympatric in Costa Rica. In the absence of a sympatry test, one can always argue that the isolated populations of *Chiropterotriton* in Central America do not merit full specific rank. However, the unique combination of external morphometric traits which characterizes each of the Central American populations, combined with the osteological differences between most of the forms, makes it highly likely that these populations do in fact represent separate evolutionary units. We are actively investigating genetic divergence between species of tropical salamanders, and results to date lend support to our conclusions based on morphology.

The data from morphometrics and from osteology produce somewhat conflicting

pictures of evolutionary relationships. The UPGMA clustering technique based on the external morphology and dentition places *C. nasalis* and *C. veraepacis* well within the *bromeliacia* group. These seven species share more in common ecologically than they do osteologically. All are small species that occur in basically arboreal sites in cloud forests. They appear to be ecomorphs, with similar, adaptive structural responses to similar selective pressures. Certainly one reasonable hypothesis is that they are close relatives, derived from a common stock that was, itself, adapted to climbing in cloud forest habitats.

On osteological grounds this suggestion does not appear to be valid. An alternate hypothesis postulates an early separation between the ancestors of the *bromeliacia* group and the ancestors of all other *Chiropterotriton*-beta. These two lineages are sister groups, in the sense of Hennig (1966), with both lineages displaying both primitive and derived characters. The *bromeliacia* group has remained in Nuclear Central America, and has speciated but not undergone much additional differentiation. In contrast, the other assemblage is rather diverse, and widespread. *C. veraepacis* and *C. nasalis* are close relatives, distinct from each other in morphometric features but not in osteology. The cladistic species pattern of figure 4 leads us to suggest that morphological similarity of these two species to the *bromeliacia* group results from convergence by different stocks in response to similar selective pressures.

On osteological grounds both *C. richardi* and *C. barbouri* seem allied with *C. picadoi*, *C. nasalis*, and *C. veraepacis* rather than with the *bromeliacia* group. *C. barbouri* is a relative of *C. nasalis* and *C. veraepacis* and is somewhat intermediate between these two species and *C. picadoi* in osteological structure. Possibly *C. richardi* is the earliest known derivative of a *Chiropterotriton*-beta stock. It is the only species in Central America with any degree of resemblance to members of the genus *Oedipina*, lives sympatrically with species of that genus, and, like *Oedipina*, has been found living in holes in moss-covered earth banks. This elongate, diminutive animal with very short limbs and a long tail, closely resembles juvenile *Oedipina* in habitus. Possibly it is a semi-fossorial form.

A general character state formula for the genus *Oedipina* is: a, b, c, d, E, f, g, h (one population of one species of *Oedipina* appears to have septomaxillaries but b rather than B is used because of the clear preponderance of that state). This formula is compatible with the hypothesis that an animal rather like *C. richardi* might have given rise to *Oedipina*. Further suggestion of relationship comes from details of the structure of the feet of *C. richardi* and *Oedipina*. In addition to having the carpal and tarsal fusions typical of the *nasalis* group (character states d, f), *C. richardi* also has a fusion of the centrale and distal carpal 4, (Fig. 3). *Oedipina* also typically has all of these fusions, and fusion of distal carpal 4 and the centrale has also been reported in *Parvimolge townsendi* and various species of *Thorius* (Wake 1966). Fusion of the tibiale and centrale occurs in the tarsus of *C. richardi*, but has not been encountered elsewhere.

The relationship of *C. picadoi* to other species of *Chiropterotriton*-beta is obscure. On the basis of sharing many derived states with *C. barbouri*, *C. nasalis*, and *C. veraepacis* (b, c, d, f, g) we are tempted to postulate close relationship. Yet, *C.*

*picadoi* is very different from these three species in external morphological features and dentition. It has very short limbs and small feet, and in many features resembles the even more elongate and short-limbed *C. richardi*.

We earlier (Wake and Lynch 1976) assigned *C. nasalis*, *C. barbouri*, *C. richardi*, and *C. picadoi* to a *nasalis* group, thus placing all *Chiropterotriton*-beta in but two groups. We retain that arrangement here, but note that the *nasalis* group is morphologically far more diverse than the *bromeliacia* group.

Zoogeographic patterns conform well with our hypothesis concerning evolutionary relationships. The *bromeliacia* group is a cluster of species with high phenetic similarity sharing many derived osteological characters. They are so far known from a number of localities in western Guatemala and Chiapas. The *nasalis* group is far more diverse than the *bromeliacia* group in morphometric and osteological traits. When additional information becomes available it may be possible to subdivide the *nasalis* group into three parts: 1) *C. nasalis*, *C. barbouri*, and *C. veraepacis*, a mainly northeastern group of arboreal species from Guatemala and Honduras that seems well defined osteologically; 2) *C. picadoi* of Costa Rica, allied to the former three species by derived osteological traits but not by ecology or external morphology; 3) *C. richardi* of Costa Rica, a highly distinctive, diminutive, elongate species with a combination of generalized (skull) and specialized (feet) osteological traits that distinguish it from all other species of *Chiropterotriton*.

The recent (February, 1976) Guatemalan earthquake has led to renewed interest in the structure and history of Nuclear Central America, one of the most complex and seismically active regions of the world. As a result of detailed investigations of land movements during the earthquake, the principal faults have been sharply defined, and the history of the region has been placed in new perspective. The Cocos plate is moving from the southwest and being subducted where it meets the Caribbean and North American plates in what Plafker (1976) calls the Middle American Megathrust. The North American plate is moving mainly westward, and the Caribbean plate is being forced eastward by the combined plate movements. The Motagua fault, clearly outlined by the recent earthquake, lies at the border of the Caribbean and North American plates. The extreme western end of the Caribbean plate is being "squeezed" between the Cocos and North American plates, and Plafker speaks of this region as being "decoupled" from the plate. This is the area of maximum volcanic activity in southern Guatemala. The amount of movement along the Motagua fault has been great, with a probable minimum movement of 200 km since Miocene being estimated by Plafker. Estimates of total movement along the fault range from a few hundred to over 1000 km. The movements are great enough and recent enough to have had profound impact on salamander distribution and evolution in the area. *Chiropterotriton*, for example, is restricted to montane and lower montane cloud forests in Central America. Low mountain ridges of nearly continuous cloud forest are required for dispersal of these salamanders. In the present instance, we have shown that *C. veraepacis* and *C. nasalis* are similar in structure and we think that they are close relatives. *C. veraepacis* is found in a region that lies a little over 100 km west of the nearest population of *C. nasalis*. However, *C. veraepacis* occurs to the north of the Motagua fault, right along a branch of the Polochic fault, on the edge of the North American

plate, while *C. nasalis* occurs to the south and east of the fault zone, on the Caribbean plate. Thus there is no continuous montane link between the two areas now, and it is extremely unlikely that one has extended across the fault in the past. It is more likely that the two species populations have dispersed to their present sites by routes extending from the west in both instances. Presumably these populations have been separated for long periods of time.

*Chiropterotriton*-beta is sufficiently different from *Chiropterotriton*-alpha that the erection of a new genus for the former group might be justified. We choose not to do so at this time, for *Chiropterotriton*-beta is so diverse in structure that it would be difficult to diagnose meaningfully. Further, the osteological evidence presented here suggests that even a finer division of *Chiropterotriton* may be required than a simple two-way split. The key species in any future taxonomic revision of this group is *C. richardi*, a highly specialized species that might be derived from an early stock that gave rise not only to the remainder of *Chiropterotriton*-beta but also *Oedipina*.

The present study supports the view that a great amount of evolutionary differentiation has occurred in the lineages of plethodontid salamanders in the New World tropics.

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#### RESUMEN

En este trabajo se describe una diminuta nueva especie de salamandra plethodóntida de grandes narinas, *Chiropterotriton veraepacis*, que habita en bromeliaceas en la zona de bosque nublado montano al sur de Puruhlá, Baja Verapaz, Guatemala y en las zonas cercanas de Alta Verapaz, Guatemala. *C. veraepacis* muestra semejanzas en muchos caracteres fenéticos con *C. nasalis* del nordeste de Honduras, que es una especie de cola mas corta, cabeza mas ancha y narinas de mayor tamaño. La nueva especie se asemeja en ecología y algunos caracteres estructurales a las especies del grupo *bromeliacea* de Guatemala y Chiapas, pero difiere de ellas en caracteres osteológicos.

A pesar de que *C. nasalis* y *C. veraepacis* son muy distintos en la mayoría de caracteres morfológicos y ecológicos de la especie costarricense *C. picadoi*, estas especies son parecidas en osteología. También se presenta información adicional referente a las poco conocidas especies, *C. richardi* (Costa Rica) y *C. barbouri* (Honduras). Asimismo se tratan las posibles relaciones entre las especies de este género.

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FISHES OF THE SANTA CLARA RIVER SYSTEM,  
SOUTHERN CALIFORNIA

By MICHAEL A. BELL



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# FISHES OF THE SANTA CLARA RIVER SYSTEM, SOUTHERN CALIFORNIA<sup>1</sup>

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

**ABSTRACT:** The distribution of fishes within the Santa Clara River and most of its tributaries in which fishes were found is described from field observations and 46 fish collections. Fifteen species of fishes were collected, of which five probably are native to the system. All native species are peripheral freshwater fishes so there is no evidence of faunal exchange with adjacent river systems. *Gasterosteus aculeatus* and *Gila orcutti* occurred at almost all collecting stations while five species occurred at only one. This river system contains a high diversity of freshwater fishes for southern California streams. The Santa Clara River system is vulnerable to habitat destruction by urbanization, and potential threats to fishes of the system are discussed.

## INTRODUCTION

Although many papers have discussed individual fish species from the Santa Clara River system (Girard 1854; Hubbs 1967; Hubbs, Hubbs and Johnson 1943; Miller 1960, 1968, 1972, 1973; Ross 1973; Smith 1966), its fish fauna has not been described previously. By virtue of its proximity to Los Angeles, this drainage currently is subject to rapid urbanization with the attendant dangers of habitat destruction and pollution. The only known native population of the endangered unarmored threespine stickleback, *Gasterosteus aculeatus williamsoni* (Girard), still survives in this drainage. This drainage also harbors some introduced fishes endemic to southern California and some species of game fishes. Thus, it is desirable to describe the fish fauna before disturbance of the ecosystem causes the elimination of some species. This description will serve in the future as a base line to assess the impact of urbanization on the fish fauna.

## MATERIALS AND METHODS

Forty-six fish collections were made at varying intervals from the mouth of the Santa Clara River system to as far upstream as water existed except in Piru and Santa Paula creeks primarily between September 4 and November 9, 1975 (Fig. 1). Collections were made in the Santa Clara River, Todd Barranca, Sespe Creek, Piru Creek

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

ROBERT J. LAVENBERG  
J. D. MCPHAIL  
ROBERT R. MILLER  
CAMM C. SWIFT

<sup>2</sup>Research Associate in Ichthyology, Natural History Museum of Los Angeles County, and Department of Biology, University of California, Los Angeles, California 90024.

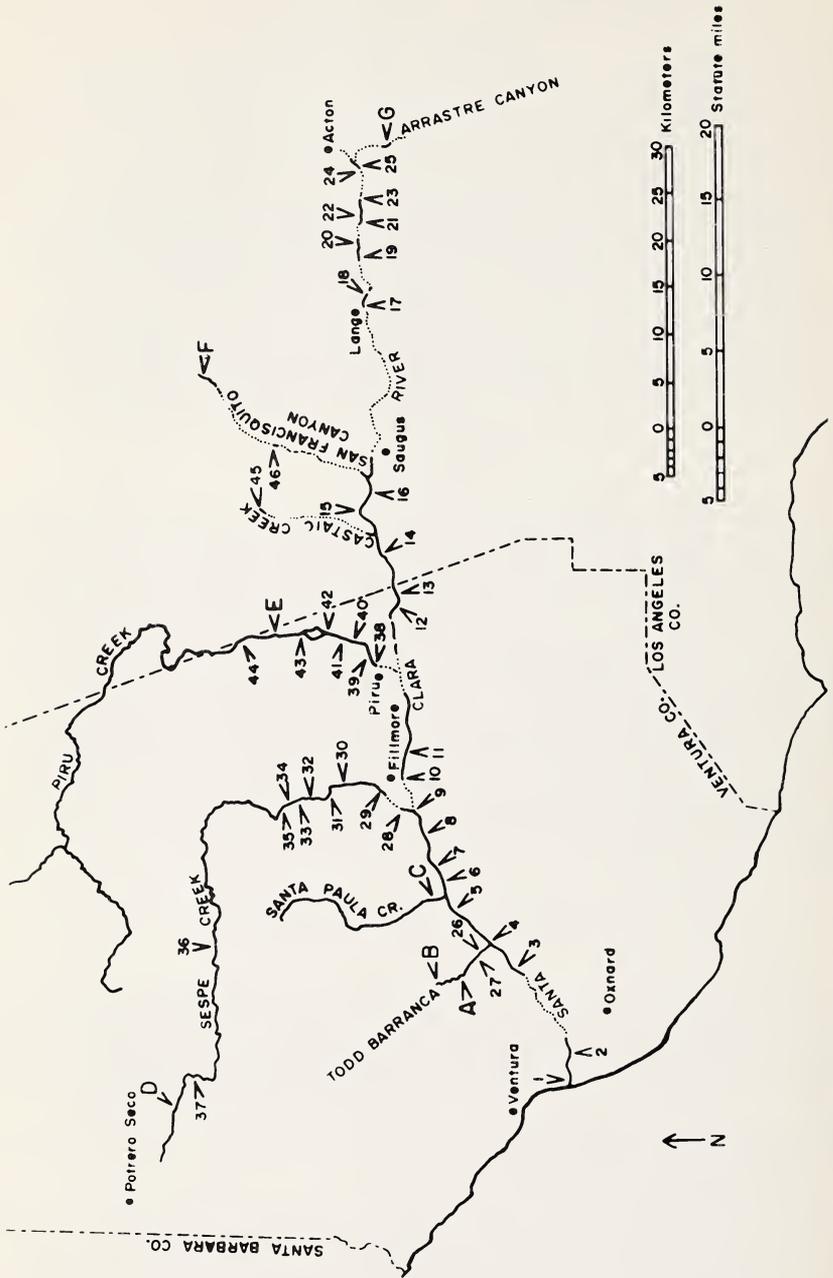


FIGURE 1. Map of the Santa Clara River system showing the location of collections (numbers) and observations (letters).

and San Francisquito Canyon. Arrastre Canyon and Santa Paula Creek were examined briefly, but no collections were made. The original purpose of the sampling program was to determine the distribution of threespine stickleback (*Gasterosteus aculeatus*) phenotypes. This species favors areas of low velocity flow so most collections were made in backwaters, side streams, pools and mainstream margins. Samples are thus biased against those species preferring rapidly flowing water. For this reason, estimates of abundance, which may be misleading were not made, and the absence of a species from a sample should be interpreted with caution.

Collecting stations were selected for accessibility and the presence of suitable habitat for *Gasterosteus*. The position of stations was determined in the field using local landmarks, and they were recorded on U.S.G.S. 7.5 minute series (topographic) maps. The distance of collection stations from the mouth in the Santa Clara River and from the confluence with the Santa Clara River in tributaries was determined by stepping off that distance on the topographic maps using dividers set at 0.1 km. Stream gradient was determined by stepping off the distance between one or two contour lines up and downstream of the station with dividers set for 500 or 200 feet. Because of irregularities in stream course, the distance from the mouth or confluence tends to be a slight underestimate and the gradient a slight overestimate using this method.

Surface temperature and velocity were measured where the majority of fishes was collected at each station. Thermometers were calibrated to within 0.5 C of the freezing and boiling point of distilled water. Water temperature tended to vary with the air temperature. Water velocity was determined by measuring the time required for a vial partially filled with water (so only a corner protruded above the surface) to drift 5 m. Water depth, stream width, amount of vegetation, bottom composition and water color were typical of the habitat, but collecting frequently extended across a heterogeneous segment of stream.

Fishes were collected with a 10 foot (3.048 m), 1/8 inch (3.175 mm) mesh knitted nylon seine. The collecting effort usually varied inversely with the abundance of *Gasterosteus*. Specimens were fixed in 10% formalin and transferred to 50% isopropyl alcohol 4 to 10 days after collection. Eddy (1957), Kimsey and Fisk (1960), Robins and Miller (1957) and Smith (1966) were useful for identification. The current scientific and common names were verified in Baily (1970). All collections were deposited in the fish collection of the Natural History Museum of Los Angeles County (LACM). These are station 1, LACM 34071, station 2 to 44, LACM 34198 to 34240 respectively, station 45, LACM 35228, and station 46, LACM 34241. LACM 35227 also came from station 31 and LACM 35648 was collected near station 30. Additional specimens from the California Academy of Sciences Fish Collection (CAS) were examined to verify early collection records (CAS 20283, CAS 20284 and CAS Acc. No. X:30).

I attempted to determine whether species presently occurring in or previously reported from the Santa Clara River system were native or introduced. This is a relatively simple task for species known to be introduced from distant sources, but those native to southern California present a problem. One must depend on historical records, distribution patterns, the original presence of appropriate habitats and the existence of dispersal routes for entry into the system. Only negative historical data can

be brought forth to support the hypothesis that a species is introduced. The failure of a species to be observed or collected (negative data) until recent times may be a result of recent introduction or from erroneous observation, identification or incomplete collection in the past. Even if there is a record of introduction, the species may already have been present before the introduction. The confidence placed in the conclusion based on historical data that a species is introduced depends on the quality of the original observation. Reasoning based on distribution patterns, the presence of appropriate habitats and dispersal routes is inferential. Fishes do not always occur in habitats that they can disperse into and that appear to be appropriate for them. Thus, as much evidence as possible must be brought to bear on the question of whether a fish species is native, and the answer obtained may never be satisfactory.

## RESULTS

### DESCRIPTION OF STREAMS

The Santa Clara River system is composed of the Santa Clara River and a large number of tributaries primarily draining from the north (Fig. 1). The drainage is bounded on the southwest by the Santa Susana Mountains and on the southeast by the San Gabriel Mountains. No substantial tributaries of the Santa Clara River drain these mountain ranges. The Santa Susana Mountains are drained to the south by Calleguas Creek and its tributaries. The southern slope of the San Gabriel Mountains is drained by tributaries of the Los Angeles and San Gabriel Rivers.

In the west, the headwaters of Sespe and Piru creeks are interdigitated with those of the Cuyama River, a tributary of the Santa Marie River and tributaries of the small Ventura River system.

Drainage north of the Santa Clara River system is by creeks which eventually disappear into the southern San Joaquin Valley. The eastern corner of the Santa Clara River system is bounded by these creeks as well as those of the Los Angeles River system and some draining into the Mojave desert.

The Santa Clara River, Santa Paula, Sespe, Piru and Castaic creeks, San Francisquito and Arrastre canyons and Todd Barranca were studied. Other tributaries east of Saugus were not studied because J. N. Baskin (personal communication) reported no fishes there. Some tributaries in the western portion of the drainage could not be studied or received cursory examination because of limitations of time, funds or access.

The Santa Clara River was examined from its headwaters to its mouth. Flow is intermittent over substantial lengths of the stream (dotted lines, Fig. 1) and the geographic extent and duration of desiccation varies yearly. The section between Lang and Saugus is dry except during heavy downpours, a condition that apparently has existed since at least the middle of the last century (Miller 1960). The Santa Clara River and its tributaries are subject to flooding some winters. The river flows through a broad, primarily sandy-bottomed valley. In most places, the flood plain is lined by earth and rock or wire and debris barriers. The Southern Pacific Railroad runs the length of the Santa Clara River, built across the flood plain on elevated grades in places. Upstream of Saugus the flood plain is occupied by gravel pits, small recrea-

tional parks or is undeveloped. The Saugus area presently is undergoing rapid urbanization. The flood plain, beginning just upstream of Piru Creek, is occupied by citrus orchards, which bound most of the river on both sides except for small gaps at the cities of Fillmore, Santa Paula, Satacoy and Oxnard. The Oxnard-Satacoy region also is an area of rapid urban growth.

The first tributary studied was Todd Barranca, a small stream that drains Wheeler Canyon and flows across the flood plain of the Santa Clara River, entering it at Santa Paula. Fishes were present in the lower portion.

Only the lower kilometer of Santa Paula Creek, which is enclosed in a rock and earth levee was examined (stat. C). No fishes were seen.

Sespe Creek is a large tributary of the Santa Clara River. Numerous small waterfalls a few centimeters to more than 3 m high occur from 12 to 17 km (and probably farther) upstream of the confluence with the Santa Clara River (stats. 32-35). Much of the stream flows through deep, narrow canyons over rocky substratum. Practically the whole Sespe Creek drainage is contained in Los Padres National Forest (including the Sespe Condor Sanctuary, where no samples could be collected) and is protected as recreational land or wildlife sanctuary.

Piru Creek is the largest tributary to the Santa Clara River. Flow volume fluctuates according to the amount of water released from Lake Piru through Santa Felicia Dam, and the creek receives imported water from Pyramid Reservoir. The canyon through which Piru creek flows in that portion studied is broad and sandy-bottomed. Piru Creek is primarily within the Los Padres National Forest.

Castaic Creek is located in a dry, broad, sandy-bottomed valley. Castaic Lake is a reservoir that receives imported water from Pyramid Reservoir. The only flowing water seen in this creek during the summer was water being released from a small impoundment below Castaic Lake at station 45.

San Francisquito Canyon contains three areas of continuous flow: where it joins the Santa Clara River, and at two points upstream. One point upstream is where water released from Drinkwater Reservoir tumbles out of Drinkwater Canyon and flows for about 200 m along the bottom of San Francisquito Canyon before sinking into the sand. On February 1, 1976 this stream segment had increased to 1400 m long. Such extensions are characteristic of the Santa Clara River system in the winter. The second point upstream where the stream flows is for a few kilometers below San Francisquito Powerhouse No. 1. The canyon bottom varies in width and generally is dry and sandy.

Arrastre Canyon is one of several canyons that converge to form the headwaters of the Santa Clara River. A small flow descends the steep sandy bottom of this shallow canyon, sinking into the sand and forming small pools. Like San Francisquito Canyon, this is a remote and little disturbed canyon.

#### FISH DISTRIBUTIONS

Fifteen fish species were collected from 46 collecting stations. The characteristics of these stations are indicated in Table 1. Fishes collected are listed below (numbers in parentheses indicate the number of stations at which the species was collected):

*Gasterosteus aculeatus* Linnaeus Threespine stickleback (42)

*Gila orcutti* (Eigenmann and Eigenmann) Arroyo Chub (37)

TABLE I

Physical characteristics of collecting stations. The values under Distance Upstream column opposite tributaries indicate the distance of the confluence of the tributary with the Santa Clara River from the mouth. Numbers in the Bottom column indicate: 1, detritus and/or mud; 2, sand; 3, gravel; 4, cobble; and 5, rock.

STREAM and STATION	DISTANCE (Km)	WATER TEMP. (C)	WATER DEPTH (cm)	STREAM WIDTH (m)	WATER VELOCITY (cm/sec)	PLANT COVER	BOTTOM	WATER COLOR	GRADIENT (%)
St. Clara									
1	1.1	24	12	6	35.7	+	1,2	clear	0.24
2	3.9	25	5	3-4	25.0	+	1,2	"	0.21
3	14.2	22	50	96	none	+	2	"	0.36
4	18.0	21	30	14	negligible	+	1,2	"	0.40
5	23.3	23	25	12	55.5	+	2	"	0.42
6	25.6	25	20	5	negligible	+	1,2,4	"	0.57
7	27.7	24	15	13	50.5	+	2,3	"	0.30
8	32.0	19	12	3.5	20.0	+	1,2	"	0.27
9	35.3	21	15	5-6	20.0	-	2	"	0.42
10	39.3	21	70	3	35.7	+	2,3	"	0.56
11	42.3	17	40	11	21.7	+	1,2	"	0.59
12	58.8	26	20	3	35.7	+	2	green	0.56
13	60.4	28	40	8	rapid	+	2,3	brown	0.67
14	64.7	18	35	20	variable	+	2	"	0.59
15	71.8	23	15	2.5	negligible	+	2	clear	0.76
16	74.5	20	15	3.5	20.0	+	2	brown	0.69
17	97.6	19	70	30	none	+	2	clear	0.89
18	98.1	18	15	25	negligible	+	2,3,4	"	0.89
19	103.7	27	30	4.5	55.5	-	2,3	"	1.08
20	105.3	21	30	4	83.3	+	2,3	"	1.25
21	107.4	20	45	16	negligible	+	2	"	1.26

22	108.2	20	70	13	negligible	+	2,4	"	1.90
23	110.5	20	30	4-5	negligible	+	2	"	1.25
24	114.2	21	50	18	negligible	+	1,2,4	"	1.54
25	114.6	19	15	3-4	45.5	+	2	"	2.08
Todd									
	17.3								
26	1.1	20	13	4	29.4	+	2	"	.95
27	2.6	19	40	2	16.1	+	2	"	1.21
Sespe									
	35.3								
28	1.6	21	10	5	12.5	+	2,3,4	"	0.67
29	4.3	20	60	1	negligible	+	2,3,4	"	0.59
30	8.0	19	50	3	negligible	+	2,4	"	0.80
31	11.7	?	100	?	negligible	-	2,4,5	"	2.05
32	13.1	?	100	4.5	none	+	2,4,5	"	9.41
33	14.2	23	100	7	negligible	+	4,5	"	2.58
34	15.2	24	150	?	negligible	+	2,3,4,5	green	3.64
35	16.5	23	130	7.2	negligible	+	2,4	clear	4.00
36	49.0	12	40	4	15.2	+	1,4	"	0.46
37	70.9	10	65	3	negligible	-	1,4	"	1.56
Piru									
	51.8								
38	2.0	27	50	2	negligible	+	1	brown	0.89
39	3.5	27	50	9	33.3	+	1,2,4	green	0.73
40	5.9	24	40	3	35.7	+	1	brown	0.89
41	7.5	25	30	9	55.6	+	1,2,4	"	0.77
42	9.1	23	30	9.5	23.3	+	1,4	green	0.89
43	12.0	27	20	?	none	-	1	brown	0.80
44	18.7	19	50	6	variable	-	1,2,4	clear	0.71
Castaic Cr									
	69.8								
45	8.1	25	30	10	variable	+	2	"	0.80
S. Frqto									
	75.4								
46	13.9	24	25	5	29.4	-	2,4	"	1.08

- Gambusia affinis* (Baird and Girard) Mosquitofish (24)  
*Catostomus (Pantosteus) santaanae* (Snyder) Santa Ana sucker (20)  
*Pimephales promelas* Rafinesque Fathead minnow (15)  
*Salmo gairdneri* Richardson Rainbow trout (5)  
*Lepomis cyanellus* Rafinesque Green sunfish (6)  
*Micropterus salmoides* (Lacépède) Largemouth bass (4)  
*Ictalurus punctatus* (Rafinesque) Channel Catfish (1)  
*Cottus asper* Richardson Prickly sculpin (3)  
*Notemigonus crysoleucas* (Mitchill) Golden shiner (1)  
*Dorosoma petenense* (Günther) Threadfin shad (1)  
*Eucyclogobius newberryi* (Girard) Tidewater goby (1)  
*Lepocottus armatus* Girard Pacific staghorn sculpin (1)  
*Lampertra tridentata* (Gairdner) Pacific lamprey (2)

Fish collection records are summarized in Table 2 and the locations of collection stations are shown in figure 1.

*Gasterosteus acculeatus* occurred in every stream where fishes were found except in Arrastre Canyon and Castaic Creek. It was abundant at all stations where it occurred except in the Santa Clara River between Saugus and Piru and in the headwaters of some tributaries. This species was collected by J. N. Baskin (personal communication) at my station F, farther upstream in San Francisquito Canyon than I was able to find it.

*Gila orcutti* penetrates farther into headwaters than *Gasterosteus*. In addition to being widespread in the Santa Clara River and all tributaries in which fishes were found, it was observed in Arrastre Canyon (stat. G) and farther up San Francisquito Canyon (stat. F), Sespe Creek (stat. D) and Piru Creek (stats. 43, 44, E) than *Gasterosteus*.

*Gambusia affinis*, *Catostomus santaanae* and *Pimephales promelas* are all widespread in the Santa Clara River but are restricted in some tributaries. *Gambusia affinis* apparently is absent above station 22 in the upper Santa Clara River and was not found above station 30 in Sespe Creek or station 39 in Piru Creek. Generally the absence of *Gambusia* is associated with an increase in stream gradient (Table 1). *Catostomus santaanae* was absent from small tributaries like Todd Barranca, San Francisquito Canyon and Arrastre Canyon and also from the headwaters of Sespe Creek (above stat. 32). However, J. N. Baskin (personal communication) found it and *Gila orcutti* in isolated pools in Mill Canyon, which joins the Santa Clara River near station 23. *Pimephales promelas* has a more restricted distribution. In the Santa Clara River, it occurred below station 14 and has only entered the lower gradient portions of Sespe Creek, below station 30. However, fathead minnows were seen above Lake Piru and were collected in the lake, in two stations downstream in Piru Creek and below Castaic Lake.

The only other widespread species is *Lepomis cyanellus*, which was taken at six disjunct stations in the Santa Clara River, Todd Barranca, Castaic Creek and seen in Sespe Creek. It probably occurs elsewhere, but may be rare and difficult to collect.

Other species found in the system are either locally abundant or associated with unusual conditions. *Salmo gairdneri* lives in the discharge of Fillmore Fish Hatchery







(trout) and in favorable riffle and pool habitats of Sespe Creek. It was observed but not collected above Lake Piru (stat. E). *Lampetra tridentata* is restricted to Sespe Creek. One dead adult specimen was collected at station 31, one badly decomposed adult was observed at station 32 and D. L. Soltz (personal communication) collected several adults from near station 29 in June 1975. I also obtained two ammocetes (LACM 35648) at station 30. *Notemigonus crysoleucas*, *Dorosoma petenense*, *Cottus asper* and *Micropterus salmoides* were found mainly in the vicinity of Lake Piru. *Micropterus* also was collected below Castaic Lake and in the Santa Clara River, 5 km downstream of the juncture with Castaic Creek (stat. 14). It also was observed in private ponds along the upper reaches of the Santa Clara River (near stat. 19) but not in the river. *Cottus asper* was found at stations 42, 44 and below Castaic Lake at station 45 and was observed at station E, near Lake Piru. *Dorosoma petenense* and *Notemigonus crysoleucas* were collected only in Lake Piru.

*Eucyclogobius newberryi* and *Leptocottus armatus* are species that frequently occupy the mouths of rivers but fail to penetrate far inland. They were taken only at station 1. Other marine fishes that enter stream mouths might have been collected if it had been possible to collect closer to the mouth of the river.

## CONCLUSIONS AND DISCUSSION

### LIMITATIONS OF DATA

To collect fishes by seining is at best an incomplete sampling method, although it is the most practical one considering the large number of samples and the limited resources available to make collections. The distributions here presented are based on a series of collections made mostly during a short time span, obtained from a varying number of seine hauls, generally from slow moving to still water because sampling of sticklebacks was the primary objective. Seining is not ideal to obtain a complete representation of the distribution of diverse fishes. Some species may have been overlooked because special collecting techniques are required for capture. For instance, *Lampetra tridentata* was found in Sespe Creek only by making a special trip to look for adults during the spawning season. Rarer species, such as *Lepomis cyanellus*, might have been collected at more stations if collecting had been more intense. Abundance or distribution of some species varies seasonally and these species would have occurred at more stations had they been sampled year round. Thus, the results of these collections are minimal measures of species diversity and distribution in the Santa Clara River.

### NATIVE FISHES

Of the 15 fishes collected, *Gasterosteus aculeatus*, *Eucyclogobius newberryi*, *Leptocottus armatus*, *Salmo gairdneri* and *Lampetra tridentata* are native. *Gasterosteus aculeatus* was found in the headwaters of the Santa Clara River near Acton during surveys for a Pacific railroad route in the middle 1800's (Miller 1960). This form was described as *Gasterosteus williamsoni* by Girard (1854) from "Williamson's Pass," now known as Soledad Canyon (Miller 1960). Sticklebacks were present in the area

now occupied by the Santa Clara River system as early as the Pliocene (David 1945; Bell 1973). Miller (1968) stated that *Gasterosteus aculeatus* was the only fish originally present in the Santa Clara River system. It appears to be native to most of the system and in 1947 was collected in San Francisquito Canyon (CAS 20284) where it may or may not be native. Two subspecies of *G. aculeatus* have been recognized from this drainage (Miller and Hubbs 1969): *G. A. williamsoni*, mostly upstream of Saugus, and *G. a. microcephalus* from the headwaters of Sespe Creek. Intergrades between these two subspecies occupy much of the remainder of the drainage (Bell 1976).

Hubbs (1946) reported large and consistent runs of *Salmo gairdneri* into the Santa Clara River. Sespe Creek between stations 31 and 35 is high gradient and consists of riffles and pools. Although water temperature is near the upper limits for *Salmo* during the summer, they still are abundant. Thus, *Salmo* almost certainly is native to Sespe Creek. Piru Creek and the Santa Clara River are much less suitable for *S. gairdneri*. Rainbow trout are restricted to a few deep spots in the generally shallow Piru Creek. California Department of Fish and Game records indicate that *S. gairdneri* has been planted in Piru Creek since at least 1931, and these may be the original source of trout observed at station E. Those observed at station 11 in the Santa Clara River certainly had escaped from the Fillmore Hatchery just upstream of the station. Although they were very abundant in the artificially cooled water flowing out of the hatchery, they were absent 3 km downstream at station 10.

*Eucyclogobius newberryi* and *Leptocottus armatus* are euryhaline species that have entered the Santa Clara River from the sea. There is no reason to believe that they are introduced.

A fifth native species is *Lampetra tridentata* (placed in this genus by Hubbs 1971), the Pacific lamprey. Hubbs (1967) reported on three specimens from Sespe Creek about 3 miles north of Fillmore (near stats. 30 and 31).

The native fishes of the Santa Clara River system have one thing in common, they all are either anadromous or peripheral freshwater fishes. Peripheral freshwater fishes are those restricted to freshwater immediately adjacent to the sea and the distributions of which are the result of dispersal through the sea (Darlington 1957), whereas anadromous fishes spend a portion of their life cycle in marine water but enter fresh water to spawn. Thus, all native fishes could have entered the Santa Clara River system from the sea and there is no evidence that there has been any exchange between the ichthyofauna of the Santa Clara River system and those of adjacent river systems.

#### CALIFORNIA FISHES INTRODUCED TO THE SANTA CLARA RIVER SYSTEM

Miller (1968) listed three fish species from California which have been introduced to the Santa Clara River system. *Rhinichthys osculus* (Girard), the speckled dace, is native to Santa Ana River system (Culver and Hubbs 1917), San Luis Obispo Creek (based on Jordan 1894) and other coastal streams north of the latter. Miller (1968) commented on the disjunct distribution of this species but concluded that it was introduced to the Santa Clara River system. I did not collect this species there. Another

native to the Santa Ana River system, *Catostomus (Pantosteus) santaanae* (Snyder 1908), apparently is introduced to the Santa Clara River system. Miller (1968:175) concluded that the Santa Ana sucker is introduced based on the testimony of "An old resident of that drainage. . . ." that a fish (i.e., *Gasterosteus aculeatus*) ". . . about 2 or 3 inches long, that swam in a jerky fashion and curled its tail when at rest." was the only species originally present. *Catostomus santaanae* had been introduced to the Santa Clara River by 1934, when it also was found in Piru Creek (R. R. Miller personal communication). It was abundant in the Santa Clara River between Piru and Fillmore, and in the lower reaches of Sespe Creek by 1940 (Hubbs et al. 1943). Hubbs et al. (1943) reported another unidentified *Catostomus* of the subgenus *Catostomus* and numerous hybrids between it and *Catostomus santaanae* collected between 1939 and 1942. Smith (1966) stated that *C. santaanae* from the Santa Clara River drainage has features indicating introgression by a sucker of the subgenus *Catostomus* (i.e., papillae on the anterior face of the upper lip). The source of the second species of *Catostomus* was unknown to Hubbs et al. (1943), but it is referred to the Owens sucker, *Catostomus fumeiventris* Miller (1973) in his synonymy of that species. It apparently was introduced by a release of Owens River water from the Los Angeles Aqueduct. Owens suckers are endemic to the Owens River basin but have been introduced to June Lake in Mono basin and the Santa Clara River drainage (Miller, 1973). I detected neither *C. fumeiventris* nor its hybrids and backcrosses with *Catostomus santaanae* in my samples, but other recent surveys have reported them to be present (A. W. Wells and J. S. Diana personal communication).

*Gila orcutti* is the third California species that has been introduced to the Santa Clara River system. Miller (1968) also concluded that this species was introduced because of the report that *Gasterosteus aculeatus* was the only native fish. *Gila orcutti* is native to many streams from San Luis Rey River (Riverside County) north to Malibu Creek (Los Angeles County) (Miller 1968). This species was first collected in the Santa Clara River in 1934 (Miller 1968) when it also was found in Piru Creek (R. R. Miller personal communication). Arroyo chubs were collected in San Francisquito Canyon in 1947 (CAS 20253), and they are now the most widespread fish in the system.

*Cottus asper* ranges south to Ventura County (Eddy 1957), and it has been collected in the Ventura River (R. R. Miller personal communication) which enters the Pacific Ocean just north of the Santa Clara River. Prickly sculpins were found only in the vicinity of Lake Piru (stats. 42, 44, E) and Castaic Lake (stat. 45) but nowhere else. R. R. Miller sampled Piru Creek several times since 1934 without collecting *C. asper* (R. R. Miller personal communication). Both Lake Piru and Castaic Lake receive water from Pyramid Reservoir which receives its water from the Sacramento and San Joaquin River drainages. *C. asper* occurs in the Sacramento River (Evermann and Clark 1931) and this is probably the original source of all *Cottus* in the Santa Clara River system.

#### OTHER FISHES INTRODUCED TO THE SANTA CLARA RIVER SYSTEM

Other fishes found in the Santa Clara River system are not native to California. *Pimephales promelas* first was collected in California in 1950 and since has been

introduced to many waters (Shapovalov, Dill and Cordone 1959). *Gambusia affinis* was introduced to California in 1922 and has become widespread for mosquito control (Miller 1961). *Lepomis cyanellus* probably was introduced with bluegill (*Lepomis macrochirus* Rafinesque) which it resembles when it is small (Evermann and Clark 1931). *Ictalurus punctatus* was first introduced to California in 1895 (Evermann and Clark 1931) and has been introduced widely. *Ictalurus melas* (Rafinesque), the black bullhead, was reported from near station 17 by J. N. Baskin (personal communication), but I did not collect it anywhere in the system.

Two fishes associated with Lake Piru probably were introduced there as forage species for *Micropterus salmoides*, which was introduced for sport fishing. One, *Dorosoma petenense*, was introduced to California in 1953 because it is suited to the warm fluctuating waters of reservoirs (Kimsey 1954). The other, *Notemigonus crysoleucas*, was reported in small creeks near San Diego by Evermann and Clark (1931) and since has been introduced to many reservoirs.

#### DISTRIBUTION PATTERNS

Threespine sticklebacks and Arroyo chubs are the most widespread fishes in the Santa Clara River system. Native *Gasterosteus aculeatus* are found throughout the drainage wherever there is slowly moving water, except in the smallest headwaters. However, introduced *Gila orcutti* is more widespread, occurring farther upstream than the native stickleback. *Gila orcutti* has dispersed well probably because it is native to small coastal streams similar to the Santa Clara River system and can withstand a stronger current than can *Gasterosteus* (J. N. Baskin personal communication). But another coastal stream fish, *Catostomus (Pantosteus) santaanae*, apparently is not sustained by the smaller flows (i.e., Arrastre Canyon, San Francisquito Canyon and Todd Barranca) and has not penetrated above the low falls in Sespe Creek (stat. 32).

Three other introduced fishes, though widespread, have not penetrated higher gradient tributaries. *Gambusia affinis* is present in the stream margins and pools of low gradient areas but apparently has not become established in some of the steeper tributaries. Mosquitofish have entered the upper Santa Clara River but have not spread to its higher reaches. *Pimephales promelas* is restricted to low gradient portions of the system except Piru Creek and below Castaic Lake. In Piru Creek, it was found in Lake Piru and upstream (stat. E) and downstream (stats. 38, 39) of the lake. Fathead minnows also occur at most stations in the Santa Clara River downstream of station 14 and only have penetrated a short distance up Sespe Creek (stat. 31). The distribution of *P. promelas* indicates that it may have been introduced in imported water, but unlike *Cottus asper*, successfully has dispersed. R. R. Miller (personal communication) over several years of collecting never obtained fathead minnows from Piru Creek, supporting the view that it was introduced recently.

Native species such as *Salmo gairdneri*, *Lampetra tridentata*, *Eucyclogobius newberryi* and *Leptocottus armatus* only are found in geographically restricted habitats. *Salmo gairdneri* was found in cooler (stat. 11) and higher gradient (stats. 32 to 37) water (Table 1). *Lampetra tridentata* is restricted to the unique riffle and pool habitat of Sespe Creek. *Eucyclogobius newberryi* and *Leptocottus armatus* were found only at station 1, near the sea.

*Notemigonus crysoleucas*, *Dorosoma petenense* and *Micropterus salmoides* ap-

parently were introduced to Lake Piru and with the exception of the latter, are found only there. *Dorosoma petenense* is a fragile fish (Kimsey 1954), which probably could not survive in the small streams of the Santa Clara River system. *Notemigonus crysoleucas* also frequents quiet waters (Hubbs and Lagler 1952). *Micropterus salmoides* favors sluggish waters also (Hubbs and Lagler 1952). Specimens at station 14 in the Santa Clara River, which is typical stream habitat, may have been washed down from Castaic Lake.

The distribution of *Cottus asper* can be easily explained. It was found just above and below Lake Piru and below Castaic Lake and apparently was introduced in imported water (see above). It may be such a recent arrival in the drainage that it has not dispersed. High water temperature and other adverse habitat characteristics may retard or limit its ultimate distribution.

#### VULNERABILITY OF THE ICHTHYOFAUNA

The Santa Clara River system includes diverse aquatic habitats ranging from high gradient streams to sluggish, meandering streams with ponds and swampy areas. These diverse habitats support at least 15 species of fishes which are threatened by human activities. One problem is the increase of the human population centering around Saugus. Human population growth probably will increase habitat destruction, stream pollution, introduction of aquatic species, ground water exploitation and public pressure to channelize streams in the drainage. Another problem is the storage of imported water within the drainage.

*Salmo gairdneri* is probably immune to human disturbance because it is practically restricted to Los Padres National Forest. However, other fishes are more vulnerable because they are either found primarily in the Santa Clara River and lower portions of tributaries that are, for the most part, outside of the national forest or pass through this part of the drainage during spawning runs (i.e., *Lampetra tridentata*). This part of the drainage, from about the town of Piru to the sea, is occupied by citrus groves that seem to be compatible with the survival of fish populations. However, in some places, water draining from the citrus orchards has left a residue of silt. It is possible that fertilizers and pesticides also are being washed out of the orchards, though there is no evidence.

While the citrus orchards along much of the Santa Clara River afford some protection for the fish fauna, urbanization rapidly is spreading near Saugus (between stats. 16 and 17) and in the Oxnard-Satacoy area (near stats. 1 and 2). Urban growth in the vicinity of Saugus already has produced some pressure to channelize parts of the Santa Clara River drainage. On December 11, 1972, a hearing was held in Newhall, California where the U.S. Army Corps of Engineers proposed channelization of about 46 km (26.5 miles) of the Santa Clara River system. This proposal included channelization of about 18 km of river between Saugus and Lang, a generally dry stretch of river. This proposed project would not result in the direct destruction of fish habitats, but resultant increased runoff would have unpredictable consequences for habitats downstream. If the proposed concrete-lined channel were constructed, continuous water flow between the upper and lower portions of the Santa Clara River might result. Continuous flow might allow movement of fishes across this area, allowing increased

introgression of the endangered subspecies, *Gasterosteus aculeatus williamsoni* (Miller 1972; California Fish and Game Code Sec. 2050 to 2055), by *G. a. microcephalus* (unpublished data). *G. a. williamsoni* is a distinct subspecies divergent from other *Gasterosteus* (Ross 1973; Bell 1976) and its introgression would constitute destruction of an unusual subspecies that is protected by federal and state laws. Channelization also might allow other fishes to invade the upper Santa Clara River.

Extension of channelization into the range of *Gasterosteus aculeatus williamsoni* probably would result in its extinction in the Santa Clara River (J. N. Baskin personal communication). An example of the effect of channelization can be seen in the lower part of Santa Paula Creek. Santa Paula Creek at station C is comparable in gradient (1.54%) to Todd Barranca at stations 26 and 27. Yet three or four species of fishes (including *Gasterosteus aculeatus*) live in the habitat of the latter two stations whereas in the channelized portion of Santa Paula Creek there are no fishes.

Another threat to the fishes of the Santa Clara River is the introduction of organisms that adversely affect fishes. The probability of such introductions is increased by greater human population density through release of bait and aquarium pets. *Xenopus laevis*, the African clawed frog, discovered by J. N. Baskin (personal communication) within the Santa Clara River drainage, probably was introduced by the release of pets and is considered to be a threat to fishes (St. Amant, Hoover and Stewart 1973). Aquatic organisms also may be introduced to the drainage with imported water. Introgression of *Catostomus santaanae* by *Catostomus fumeiventris* apparently resulted from the release of imported Owens River water. The storage of imported water recently has increased within the Santa Clara River basin. Pyramid Reservoir began to fill on January 6, 1972 and water immediately was released from it into Piru Creek. Any fishes that have survived passage through pumping and power plants en route to Pyramid Reservoir may colonize the Santa Clara River. I suggested above that *Cottus asper* and *Pimephales promelas* may have been introduced by this means. Colonization by other species may result in the introgression of *Gasterosteus aculeatus*, *Gila orcutti* and *Catostomus santaanae*, which are known to hybridize with con-familial species in nature (Hagen 1967; Greenfield and Greenfield 1972; Hubbs et al. 1943). New introductions also may compete with fishes already present in the drainage.

An estimate of the impact of urban growth and channelization may be obtained by examining the ichthyofauna of the Los Angeles Basin. Culver and Hubbs (1917) reported the presence of *Lampetra tridentata*, *Gasterosteus aculeatus williamsoni*, *Salmo gairdneri*, *Gila orcutti*, *Rhinichthys osculus* and *Catostomus santaanae* in the basin. Since 1917, most low gradient portions of the drainage have been urbanized, most of the streams have been channelized and several fishes have been introduced. Between 1929 and 1942 *Gasterosteus aculeatus williamsoni*, which previously was abundant throughout the system (Culver and Hubbs 1971), became extinct in the basin (Miller 1961). Miller (1961) attributed this extinction to the introduction of *Gambusia affinis*. However, mosquitofish coexist with *G. a. williamsoni* in the Santa Clara River, so its disappearance from the Los Angeles Basin probably was not caused solely by the introduction of *Gambusia*. Miller (1961) also cited the deterioration of surface flow as a contributory factor in the disappearance of *G. a. williamsoni*, and

this may have been critical. Recent efforts to collect *Lampetra tridentata* in the Los Angeles Basin also have failed, and this species probably is extinct there (C. C. Swift personal communication). The other four species listed by Culver and Hubbs (1917) have persisted with much reduced ranges, although the presence of *Catostomus santaanae* is questionable. Thus, the condition of the fish fauna of the Los Angeles Basin does not inspire optimism for the future of the fishes of the Santa Clara River system.

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Personal communications from J. N. Baskin are based on his 1974 report, "Survey of the Unarmored Threespine Stickleback (*Gasterosteus aculeatus williamsoni*) in the Upper Santa Clara River Drainage." (Unpublished final report for Bureau of Sport Fisheries and Wildlife Contract No. 14-16-001-5387SE. iv + 67 p.) The personal communication from A. W. Wells and J. S. Diana is based on their 1975 report, "Survey of the Freshwater Fishes and Their Habitats in the Coastal Drainages of Southern California." (Unpublished final report for California Department of Fish and Game Contract No. AB-26. vi + 364 p.) I thank them for permitting me to cite their unpublished data.

C. L. Hubbs and R. R. Miller were invaluable sources of unpublished information, and I have depended extensively on their published and unpublished records.

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A NEW DEEP-SEA FISH FROM THE EASTERN NORTH PACIFIC  
*PSYCHROLUTES PHRICTUS* (PISCES: COTTIDAE [PSYCHROLUTINAE])



By DAVID L. STEIN AND CARL E. BOND

NATURAL HISTORY MUSEUM OF LOS ANGELES COUNTY

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A NEW DEEP-SEA FISH FROM THE EASTERN NORTH PACIFIC  
*PSYCHROLUTES PHRICTUS* (PISCES: COTTIDAE [PSYCHROLUTINAE])<sup>1</sup>

By DAVID L. STEIN<sup>2</sup> AND CARL E. BOND<sup>3</sup>

**ABSTRACT:** *Psychrolutes phricus*, new species, is described and compared with its only congener *P. paradoxus*, from which it differs primarily in greater head length (45.3 - 60.6% SL), larger adult size (over 500 mm), color pattern, and greater number of pectoral fin rays (22-26). The systematic status of the subfamily Psychrolutinae is discussed.

*Psychrolutes phricus* is a very large benthic cottid, known between Monterey, California, and northern Oregon at depths between 1006 m and 2800 m. Individuals between 34 and 558 mm SL have been collected, all in otter trawls, beam trawls, or benthic fish traps. We examined 19 preserved and three skeletonized specimens.

We concluded from analyses of stomach contents that *P. phricus* is probably an opportunistic feeder. Stomach contents included 24 different items; the most common of these were sea pens (three species), snails (two species), and crabs (*Chionoecetes* sp.). Among other items found were ophiuroids, fishes, hermit crabs, octopod beaks, and rocks. One specimen (309 mm SL) captured at 1097 m contained otoliths of a large number of pelagic fishes. Capture of individuals of pelagic species by *P. phricus* probably depends upon those individuals swimming near the bottom; *P. phricus* does not appear to be capable of pelagic predation.

Since 1960, specimens of an undescribed, very large *Psychrolutes* have been collected off the Pacific coast between Monterey, California, and northern Oregon. The School of Oceanography of Oregon State University has collected individuals between 34 and 469 mm SL on the continental slope off Oregon, at depths between 1026 and 2800 m. Acquisition of small and intermediate-sized specimens has made a complete description of the species possible.

The family Psychrolutidae originally was characterized by lack of a spinous dorsal fin, presence of a suborbital stay, pseudobranchiae, thoracic ventrals, three and a half gill arches, and naked skin (Günther 1861:516). Jordan and Gilbert (1882:686) indicated that *P. paradoxus*, the type species by monotypy, has a spinous dorsal fin although it is buried in loose skin and flesh. Those authors and Gill (1889) believed that differences between Psychrolutidae and Cottidae did not warrant a separate family, and, therefore, included *Psychrolutes* in the latter family. Since then, some authors (Jordan and Starks 1896; McCulloch 1926; Taranets 1941) maintained a separate family designation for *Psychrolutes*; and others (Jordan and Evermann 1896; Jordan

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

J. D. MCPHAIL  
JOSEPH S. NELSON  
CAMM C. SWIFT

<sup>2</sup>School of Oceanography, Oregon State University, Corvallis, Oregon 97331.

<sup>3</sup>Department of Fisheries and Wildlife, Oregon State University, Corvallis, Oregon 97331.

and Starks 1904; Hart 1973) included the genus in the Cottidae. We follow Gill (1889), and consider the Psychrolutinae as a subfamily of the Cottidae.

## METHODS

Counts and measurements follow Hubbs and Lagler (1964) except for counts requiring dissection (pectoral fin, pelvic fin, gill rakers). These were made on the right sides of the specimens. Pectoral and pelvic fin lengths are total (with dissection) to base. Vertebral numbers were obtained from radiographs. Counts as given are the mode, and in parentheses, the range. Morphometric ratios are given as the means, with the range in parentheses; counts and ratios of the holotype are in brackets. Not all measurements were made on all specimens because some individuals were badly deformed during or subsequent to capture. The number of individuals examined (n) follows each range. One specimen (OSUO 2040) was cleared and stained for comparison with *P. paradoxus* specimens that were treated similarly (OS 5300, 5301).

Stomach contents were examined without removal of stomachs from the specimens. Many specimens had otoliths removed before our examination; the otoliths are in the care of John E. Fitch, California Department of Fish and Game. Fitch also removed and examined stomach contents of 16 fish. OSUO specimens were collected by 3 m beam trawl (BMT) and 12 m otter trawl (OTB). Methods of collection for other specimens are written out in materials examined.

## MATERIALS

Specimens examined are on deposit at the National Museum of Natural History (USNM), Auke Bay Biological Laboratory (ABBL), California Academy of Sciences (CAS), Natural History Museum of Los Angeles County (LACM), Department of Fisheries and Wildlife, Oregon State University (OS), School of Oceanography, Oregon State University (OSUO), and University of British Columbia (BC).

## ACKNOWLEDGMENTS

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Joanne Laroche (OSUO) cleared and stained specimens for us and supplied information on cottid development.

John Fitch, California Dept. of Fish and Game, supplied information on stomach

contents. The manuscript was reviewed by W. G. Pearcy (OSUO), B. J. Verts (OS), and J. S. Nelson. Bond was supported by Oregon Agricultural Experiment Station.

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*Psychrolutes phrictus* NEW SPECIES

FIGURES 1 and 2.

Holotype: USNM 216253 (ex OSUO 1839), 1 (383 mm SL, ♀), OTB 92, 44°44.3'N, 125°41.3'W, 2800 m, 24 October 1965.

Paratypes: CAS 32580, 1 (478 mm SL, ♀), sablefish trap, 36°44.5'N, 122°04.5'W, 600 fm (1097 m), 22 April 1975; LACM 35230-1, 3 (495, 522, 558 mm SL, ♀ ♀ ♀), otter trawl, 40°37.3'N, 124°43.0'W, 600 fm, (1097 m), 29 November 1974; LACM 35232-1, 1 (519 mm SL, ♀), otter trawl, 40°37.3'N, 124°43.0'W, 600 fm (1097 m), 14 November 1974; LACM 34338-1, 1 (380 mm SL, ♀), otter trawl?, 40°45.3'N, 124°47.4'W, 700 fm (1280 m), 13 February 1974; LACM 35234-1, 1 (501 mm SL, ♀), otter trawl, 40°45.7'N, 124°44.0'W, 600 fm (1097 m), 3 April 1975; LACM 34185-1, 2 (475, 522 mm SL, ? ♀), otter trawl, 40°45.8'N, 124°43.3'W, 550 fm (1006 m), 26 August 1974; LACM 35561-1, 1 (298 mm SL, ♂), otter trawl? approx. 40°46.0'N, 124°44.0'W, 600 fm (1097 m), 8 August 1972; LACM 30807-4, 1 (508 mm SL, ♀), otter trawl, 41°21.6'N, 124°56.9'W, 725 fm (1326 m), 25 September 1969; OSUO 2057, 1 (440 mm SL, ♀), BMT 419, 42°51.9'N, 124°59.5'W, 1026 m, 17 September 1974; OSUO 2221, 1 (148 mm SL, ♀), OTB 500, 43°22.0'N, 125°09.9'W, 1600 m, 4 April 1973; OSUO 2029, 1 (469 mm SL, ♀), OTB 634, 43°32.0'N, 125°13.0'W, 1580 m, 7 July 1974; OSUO 1524, 1 (399 mm SL, ♀), OTB 64, 44°32.5'N, 125°24.0'W, 2800 m, 9 April 1965; OSUO 2020-2021, 2 (34, 49 mm SL, immatures), OTB 208, 44°36.0'N, 125°10.8'W, 1390 m, 30 October 1967; OSUO 2040, 1 (37 mm SL, immature), OTB 205, 45°51.4'N, 125°15.2'W, 1600 m, 25 October 1967 (cleared and stained).

Additional non-type material: LACM 35771-1, 1 (555 mm SL, ♀), otter trawl, 40°44.3'N, 124°42.3'W, 510-565 fm (933-1051 m), 30 November 1972 (skeleton); LACM 35770-1, 2 (538, 468 mm SL, ♀ ♀), otter trawl, 40°40.5'N, 124°44.8'W, 580-600 fm (1061-1097 m), 27 February 1973 (skeletons).

*Other Collections.*—Four specimens held at the University of British Columbia were not examined by us. These were collected off Oregon in 1963.

*Comparative Material.*—*Psychrolutes paradoxus* Günther 1861: OS 5301, 1 (35 mm SL, ?) Lopez Is., San Juan Islands, Washington, 10 July 1963 (cleared and stained); BC 53-260, 6 (27-29 mm SL, ?), Friday Harbor, San Juan Islands, Washington, July 1950; ABBL 72-74, 1 (42 mm SL, ♀), 5 (about 25 mm SL, ?), southeast shore of Favorite Channel, vicinity of beach between Pt. Louisa and Pt. Lena, near Juneau, Alaska, 10 November 1972; ABBL 64-755, 7 (45-48 mm SL, ?), Sta. 755, northeast of Afognak Is., Gulf of Alaska, 58°26'N, 151°51'W, 13 August 1963; OS 5300, 1 (37 mm SL, ?), Kodiak Is., Gulf of Alaska, 15 June 1970 (cleared and stained).

*Psychrolutes zebra* Bean 1891: Holotype, USNM 45364, sex undetermined, "Albatross" sta. 2848, 55°10'N, 160°18'W, 110 fm (201 m), 31 July 1888.

*Diagnosis.*—A *Psychrolutes* differing from its only congener in the following: Head large, its length 45.3-60.6% SL; gill rakers on first arch 9-13; pectoral fin rays 22-26. Head with small cirri, especially above eyes and on snout and lower jaw;

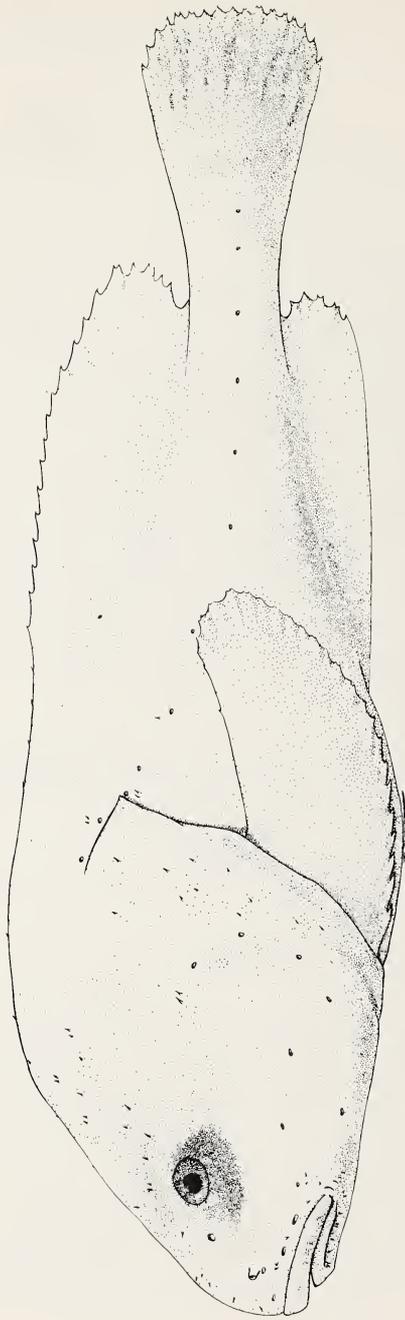


FIGURE 1. *Psychrolutes phrictus*. Holotype; 383 mm SL; USNM 216253.

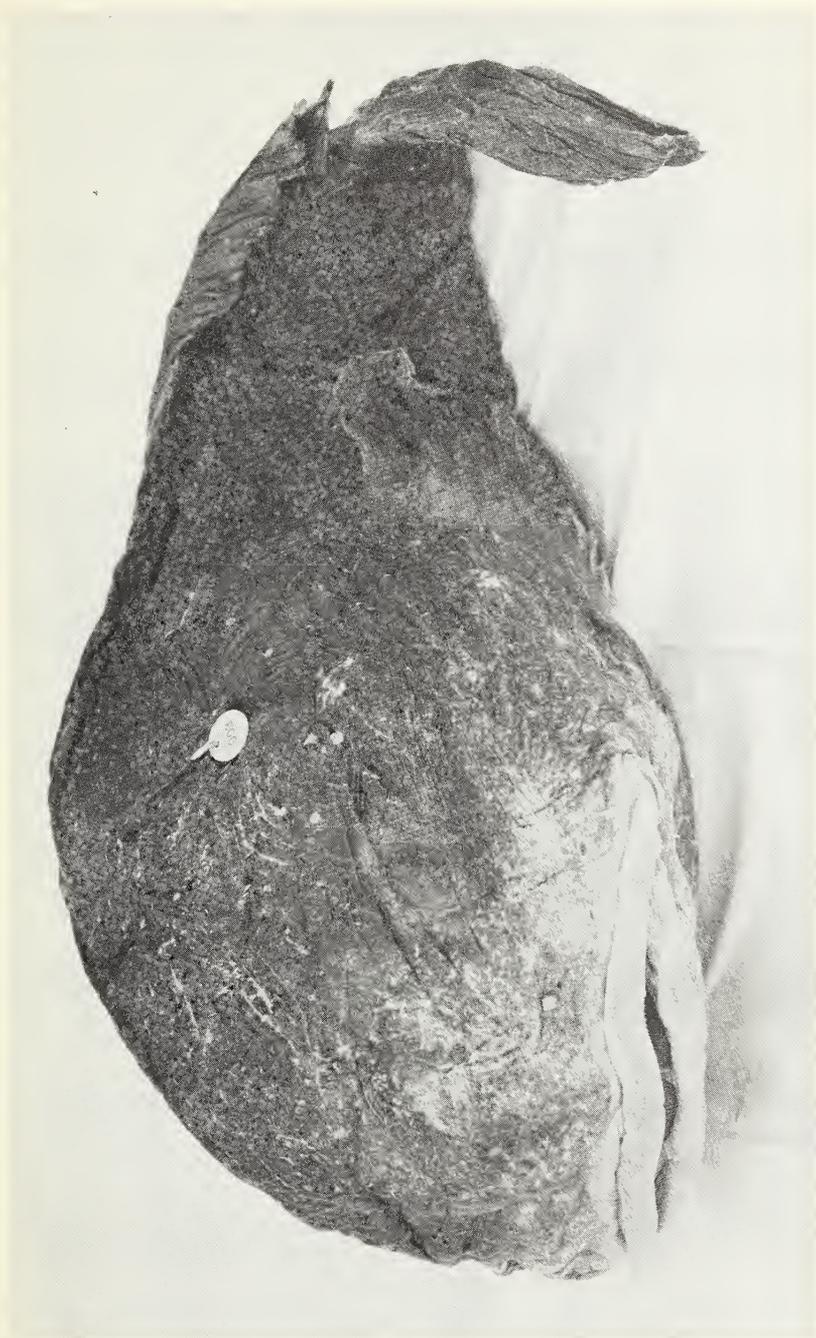


FIGURE 2. Photograph of *Psychrolutes phricus*. Holotype; 383 mm SL; USNM 216253.

scattered cirri on body. Prickles as well as cirri present on heads and bodies of individuals less than 50 mm SL. Color grayish or blackish, sometimes mottled with white, ventral surface often white, but no distinct banding or sharply defined pattern.

*Description.*—Dorsal fin rays VIII, 20 [VIII, 20] (VII-IX, 19-20) (n=19), anal fin rays 13 [13] (12-14) (n=19), pectoral fin rays 24 [23] (22-26) (n=19), pelvic fin rays I, 3 (n=19), principal caudal rays about 13 [type not dissected]. Gill rakers on first arch 11 [12] (9-13) (n=19). Lateral line pores 12 [12] (12-14) (n=16). Vertebrae [33] (33-35) (n=4).

Head length 48.9 [50.7] (43.5-60.6% SL) (n=14); eye 1. 12.8 [9.1] (8.6-24.3% head 1.) (n=14), fleshy interorbital width 35.6 [33.2] (24.4-46.4% head 1.) (n=9), pectoral 1. 55.3 [55.4] (44.9-62.3% head 1.) (n=14), pelvic 1. 26.8 [24.1] (23.3-34.7% head 1.) (n=14), snout-anus 109.8 [105.7] (93.8-132.2% head 1.) (n=15).

Allometry is evident over the size range of individuals examined. Small specimens have longer heads, larger exposed portions of the eye, and an apparently narrower interorbital space than large specimens.

Head unusually large, broad, and flattened. In smaller individuals (less than 50 mm SL), depth at occiput about equal to head width; in larger specimens, depth at occiput about 66% of head width. Nostrils two, the anterior with a very distinct tube, about on a horizontal plane with suborbital stay; the posterior on a horizontal line through pupil of eye, distance anterior to eye about equal to eye diameter. Interorbital space broad, slightly convex. Orbits large, orbital rims very poorly ossified, especially in large individuals, dissection required for their accurate measurement. Eyes relatively large, but exposed portion reduced in specimens greater than 150 mm SL. Mouth broadly curved, slightly oblique, lips fleshy; in individuals greater than 150 mm SL, lower jaw distinctly included. Premaxillaries not reaching fleshy rictus; a wide, distinct gap at medial juncture, a narrower gap present at mandibular symphysis. Premaxillary teeth sharp, stout, small and recurved, posteriorly arranged in irregular oblique rows, especially in small specimens, forming band about four teeth wide in individuals less than 50 mm SL, up to eight teeth wide in large (400 mm SL) specimens. Tooth band becoming uniserial posteriorly in small individuals, in larger ones not narrowing much, not uniserial posteriorly.

Cephalic sensory canals well developed, anterior sensory pores large, distinct, posteriormost pores smaller, difficult to distinguish. Five pores in a series above maxillary, eight in the preoperculomandibular series, one nasal pore close and lateral to anterior nostril. Anterior mandibular pores well separated.

Small cirri present on head as slender, short, sharply pointed filaments, usually single, although some on mandible are paired. Mandibular cirri form a line behind lips although no distinct pattern present; other cirri scattered over ventral surface of mandible. Cirri on upper part of head located between maxillary pores, on snout, interorbital region, and posterior to upper orbits. A line of widely separated cirri present along upper orbital margin. Other cirri scattered widely over entire head and body.

Opercular ossification poor, musculature weak, covered with gelatinous layer. Opercular opening long, extending from far above pectoral fin base to just below it.

Body behind opercular flaps tapering rapidly to caudal fin. Pectoral fins broad, well developed, their bases oblique, rays (except uppermost) evenly graduated in

length to shortest ray at anterior (ventral) point of pectoral base. In specimens above 150 mm SL, approximately the 10 lowest rays with distinct fleshy pads on outer tips; in largest specimens, pads very thick, tough, pale colored.

Pelvic fins with one spine and three soft rays. Length of pelvic fin spine about 50% of total fin length, the first (outer) ray almost equal to inner two rays which are about equal in length. Basal half of fin hidden beneath body skin, apparently not very erectile. Distal half of fin free, covered with thick skin, only tips of rays distinguishable without dissection. Pelvic bases narrowly separated. Pelvic fins relatively longer in small specimens.

Dorsal fin with spinous and soft-rayed portions. Anterior spinous portion deeply buried in loose skin and gelatinous tissue, its origin anterior to upper end of opercular opening, spines well developed, stout, although flexible. Spinous portion externally marked by short free filaments above most spines. A shallow notch present between spinous and soft-rayed fin sections. Soft dorsal fin rays becoming gradually longer posteriorly, fin becoming high and distinctly lobate at its end. Anal fin well developed, of soft rays only, its origin below anterior dorsal fin rays.

Anus distant from origin of anal fin, anterior to a vertical through pectoral tips. Body covered with thick, tough skin, naked, except in specimens less than 50 mm SL, which have simple, sharp, slender prickles distributed over body except head and parts of fins, especially dense around anus. Larger individuals with a thick gelatinous layer between skin and musculature, often with distinct, yellowish fat deposits in concavities of muscles and bones. In specimens greater than 300 mm SL, skin extensively marked with pale lines, circles, and other evidences of injury. Largest specimens (above 400 mm SL) with very distinct areas irregularly covered with pale rings, often overlapping in great numbers. We believe the rings are sucker marks of cephalopods, a known food item. Patterns of rings fit the disposition of suckers on octopod arms.

Lateral line consisting of 12-14 open pores, usually well spaced, but occasionally with two pores close together. Posteriormost two pores located on caudal base or on caudal fin itself. Anteriormost lateral line pore reduced, above gill opening.

Color of skin grayish or blackish dorsally, often pale ventrally, with indistinct mottling especially on head. Mouth pale, opercular cavity pale, peritoneum pale, stomach pale.

*Food Habits.*—Although the data obtained through examination of stomach contents do not warrant statistical analysis, some speculations are possible about the feeding habits of *P. phrictus*. This species apparently has a varied diet; a total of 24 different food items was found in the 25 stomachs examined. The most frequent food items were sea pens (*Stylatula* sp., *Balticina* ? sp., *Funiculina* sp.) in 12 fish; crabs (*Chionoecetes* sp.) in 15 fish; and snails (*Buccinium* sp., unidentified sp.) in 13 specimens. Other food items were *Sebastolobus alascanus*, *Sebastes* sp., octopod beaks (in 4 individuals), ophiuroids, a plastic bag, rocks, hermit crabs (*Pagurus* sp., *Parapagurus* sp.), and possible anemone, sea cucumber, and crinoid remains. One fish, LACM 35561, 309 mm SL, contained a large number of otoliths of *Nansenia* sp. and *Lestidium* sp. in its stomach, plus otoliths of *Sebastes* sp. and *Tetragonurus* sp. Except for *Sebastes*, all are known to be pelagic. Although this individual was the smallest

with stomach contents, we have no other reason to believe it was pelagic. Several of the OSUO specimens were smaller, and were captured with bottom trawls. Because the anatomy of *P. phrictus* is typical of a demersal cottid, we believe that the pelagic species ingested must have become available by swimming near the bottom. The possibility that individuals of *P. phrictus* as small as 300 mm are pelagic is unlikely because all specimens, including those smaller than 300 mm, were taken by bottom trawl.

The presence of octopod beaks in the stomach contents is clear evidence that *P. phrictus* sometimes eats octopods. This may account for the scars on the skin of the head in large specimens. Some of the beaks are large: specimen OSUO 2029, 469 mm SL, contained a beak from an octopod estimated (by the method of Clarke 1962) to weigh about 1 kg.

*Distribution.*—*Psychrolutes phrictus* occurs along the middle and lower continental slope from Monterey (1097 m) to Eureka (1006-1326 m), and off Oregon (1026-2800 m). Its meridional distribution may be wider, especially towards the north where there seems to be no hydrographic or geologic features that might act as barriers.

Males and females may be distributed differently. Of the 25 specimens of known sex, two are males and only one of the 19 fish we examined was a male (LACM 35561-1, 298 mm SL). The other male specimen (Calif. Fish and Game, Eureka Lab. No. 68, 475 mm SL) was not seen by us. Perhaps males are segregated in rocky areas where trawling is difficult.

*Etymology.*—From *φρικτος* (*phrikτος*), Greek, “causing one to shudder,” from the grotesque appearance of the species.

*Relationships.*—*Psychrolutes phrictus* is provisionally thought to be most closely related to *P. paradoxus* Günther 1861. It is distinctly different in the following respects: the head is relatively longer, especially in small specimens; those of 37 to 58 mm have head lengths of 49.6 to 60.6% with the overall range 45.3-60.6% of SL vs. *P. paradoxus* 40.2-44.4%; it has a larger pectoral fin of 25 (22-26) rays vs. *P. paradoxus* 21 (20-22) rays. It has cirri whereas *P. paradoxus* has large numbers of stout, blunt, papillae over its entire body, including outer surfaces of the fins; small specimens have many sharp exposed prickles whereas large *P. paradoxus* have a few in two ventrolateral rows beneath the skin. Its two inner pelvic fin rays are about equal, with the outer ray slightly shorter; *P. paradoxus* has pelvic fin rays evenly graduated in length, the outer shortest. Body color is generally evenly grayish, blackish, or mottled, whereas that of *P. paradoxus* is brown or black, in sharply defined bars or blotches on a light background, in a consistent pattern. Maximum size is at least 558 mm, whereas that of *P. paradoxus* is 58 mm (Hart 1973:534). Depth distribution differs: *P. phrictus* occurs between 1006-2800 m, but *P. paradoxus* is found between 55-220 m (Hart 1973:534).

*Discussion.*—This is the only other species beside *P. paradoxus* now referred to *Psychrolutes*; two other species were described but later removed from the genus or synonymized. *Psychrolutes latus* Hutton was redescribed by Günther (1876) as the type of a new genus, *Neophrynichthys*; *Psychrolutes zebra* Bean (1891) was synonymized with *P. paradoxus* by Jordan and Evermann (1896:2027), with whom we agree.

The relationships of *Psychrolutes* and closely related genera (e.g. *Neophrynichthys* Günther and *Cottunculoides* Barnard) are not well known; the characters separating them are unclear. If future investigations result in merging of these genera, *Psychrolutes* will be the senior synonym. We have placed the new species into *Psychrolutes* because it agrees with the generic description of the following characters: Lack of spines on the head, lack of opercular spines, pelvic fins I, 3, lack of scales on the body, seven branchiostegal rays, vomerine and palatine teeth absent, and dorsal fin spines completely buried in flesh or gelatinous tissue. Comparison of *P. paradoxus* and *P. phrictus* using the above characters leaves little doubt that they are closely related.

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A NEW GENUS AND SPECIES OF CERATIOID ANGLERFISH FROM THE  
NORTH PACIFIC OCEAN WITH A REVIEW OF THE ALLIED GENERA  
*CTENOCHIRICHTHYS*, *CHIROPHYRNE* AND *LEPTACANTHICHTHYS*



By THEODORE W. PIETSCH

NATURAL HISTORY MUSEUM OF LOS ANGELES COUNTY

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A NEW GENUS AND SPECIES OF CERATIOID ANGLERFISH FROM THE  
NORTH PACIFIC OCEAN WITH A REVIEW OF THE ALLIED GENERA  
*CTENOCHIRICHTHYS*, *CHIROPHRYNE* AND *LEPTACANTHICHTHYS*<sup>1</sup>

By THEODORE W. PIETSCH<sup>2</sup>

ABSTRACT: A new genus and species of deep-sea anglerfish is described on the basis of two specimens collected from the north Pacific Ocean. The new form is most strikingly characterized by having an unusually elongate pectoral-fin lobe that bears the fin rays along its dorsal margin, a unique and derived condition shared with three other oneirodid genera: *Ctenochirichthys*, *Chirophryne*, and *Leptacanthichthys*. The new form is described and compared osteologically with its nearest allies. It differs in having an extremely short snout, strongly convex frontal bones, and an oblique jaw suspension, appearing to be intermediate in many ways between more generalized oneirodids and the other three "long-pectoralized" forms. It is probably most closely related phylogenetically to *Ctenochirichthys*. *Chirophryne* is perhaps intermediate between the new genus and *Ctenochirichthys* on one hand, and *Leptacanthichthys* on the other. A key to the "long-pectoralized" genera is provided.

INTRODUCTION

Among the previously described genera of the deep-sea anglerfish family Oneirodidae are three forms unique among the Ceratioidei in having an unusually elongate pectoral-fin lobe that bears the fin rays along its dorsal margin. These genera are *Leptacanthichthys*, *Chirophryne*, and *Ctenochirichthys*. *Leptacanthichthys* was originally described by Regan and Trewavas (1932) as one of five subgenera of the genus *Dolopichthys* Garman (1899) to include a single species, *D. gracilispinis* Regan (1925), based on two metamorphosed female specimens. Since that time the name *Leptacanthichthys* has been given generic status (Bertelsen 1951:94). Pietsch (1974) described the osteology of the genus and discussed its phylogenetic relationships with other oneirodid genera. More recently, Pietsch (1976) reported a case of sexual parasitism in *Leptacanthichthys*, the first known occurrence of this peculiar mode of reproduction in the family Oneirodidae and the first record of a male for the genus.

*Chirophryne* and *Ctenochirichthys* were introduced by Regan and Trewavas (1932) as monotypic genera: *Chirophryne xenolophus*, described from a single metamorphosed female, and *Ctenochirichthys longimanus*, based on two metamorphosed

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

E. BERTELSEN

ROBERT J. LAVENBERG

RICHARD H. ROSENBLATT

CAMM C. SWIFT

<sup>2</sup>Research Associate in Ichthyology, Natural History Museum, Los Angeles, California 90007, and Department of Biology, California State University, Long Beach, California 90840

females. Since the original publication a second female of *C. xenolophus* was reported by Pietsch (1974:31, fig. 58). Two additional larval males and an adolescent male of *C. longimanus* were reported by Bertelsen (1951:95) and Beebe and Crane (1947:166), respectively.

Recently, a fourth 'long-pectored' oneirodid, representing an undescribed genus and species, was discovered among the ceratioids in the collections of the Institute of Oceanography of the Academy of Sciences of the USSR, Moscow, and the Scripps Institution of Oceanography in La Jolla. This new form is described and compared with its nearest allies below.

## METHODS AND MATERIALS

Standard lengths (SL) are used throughout. Measurements were taken on the left side whenever possible and rounded to the nearest 0.5 mm. To insure accurate fin-ray counts skin was removed from the pectoral fins and incisions were made in the skin to reveal the rays of the dorsal and anal fins. Sockets, indicating missing teeth in the jaws and on the vomer, were included in total tooth counts. Jaw tooth counts are the sum of left and right sides. Head length is the distance from the tip of the upper jaw to the posteriormost margin of the preoperculum; head depth is the distance from the tip of the sphenotic spine to the base of the quadrate spine; lower jaw length is the distance from the symphyseal spine to the posteriormost margin of the articular; illicium length is the distance from the articulation of the pterygiophore of the illicium and the illicial bone to the dorsal surface of the esca bulb, excluding esca appendages. Terminology used in describing the various parts of the angling apparatus follows Bradbury (1967). Definitions of terms used for the different stages of development follow Bertelsen (1951:10-11). Study material is deposited in the following institutions: BMNH—British Museum (Natural History), London; IOS—Institute of Oceanographic Sciences, Surrey, England (formerly the National Institute of Oceanography); LACM—Natural History Museum of Los Angeles County; MCZ—Museum of Comparative Zoology, Harvard University; ROM—Royal Ontario Museum, Toronto; SIO—Scripps Institution of Oceanography, La Jolla; CAS-SU—Stanford University (collections now housed at the California Academy of Sciences, San Francisco [CAS]); ZMUC—Zoological Museum, University of Copenhagen.

## OSTEOLOGY

The osteology of *Leptacanthichthys* previously has been described in detail and compared with that of other oneirodid genera (Pietsch 1974). Material sufficient for a thorough osteological study of *Ctenochirichthys* and *Chirophryne* is unavailable; a few comparative aspects however, are discussed based on superficial dissection. An osteological preparation of one of the two known specimens of *Puck* (SIO H52-363), made using the trypsin digestion technique of Taylor (1967), forms the basis for the following description.

Cranium.—The T-shaped supraethmoid of *Puck* has a long ventromedial process that forms, together with the lateral ethmoids and relatively thin, dorsally concave ethmoid cartilage, large, roughly circular, nasal foramina (Fig. 1). This is similar to the condition found in *Oneiroides* and *Danaphryne* (Pietsch 1974:16, fig. 22). Like *Danaphryne*, but again in contrast to *Leptacanthichthys*, the illicial trough of *Puck* is deep and narrow resulting from a lateral compression of the anterior portion of the skull, rather than a medial, dorsoventral depression of the ethmoid region. The width of the ethmoid cartilage and underlying vomer of *Puck* is greater than the distance between the anterolateral tips of the lateral ethmoids (Fig. 1).

The frontal bones of *Puck* (Fig. 2) are similar to those of *Oneiroides* and *Danaphryne*, having a strongly convex dorsal margin and occupying a relatively posterior position on the skull. The frontals of *Leptacanthichthys* are considerably longer, have a nearly linear dorsal margin, and occupy a more anterior position, overhanging and extending past the anterior limits of the ethmoid cartilage and vomer (Pietsch 1974:18-19, figs. 2, 28-31, 34). *Ctenochirichthys* and *Chirophryne* have moderately convex frontals (Figs. 11, 14).

The sphenotics of *Puck*, *Chirophryne*, and *Leptacanthichthys* are large, forming

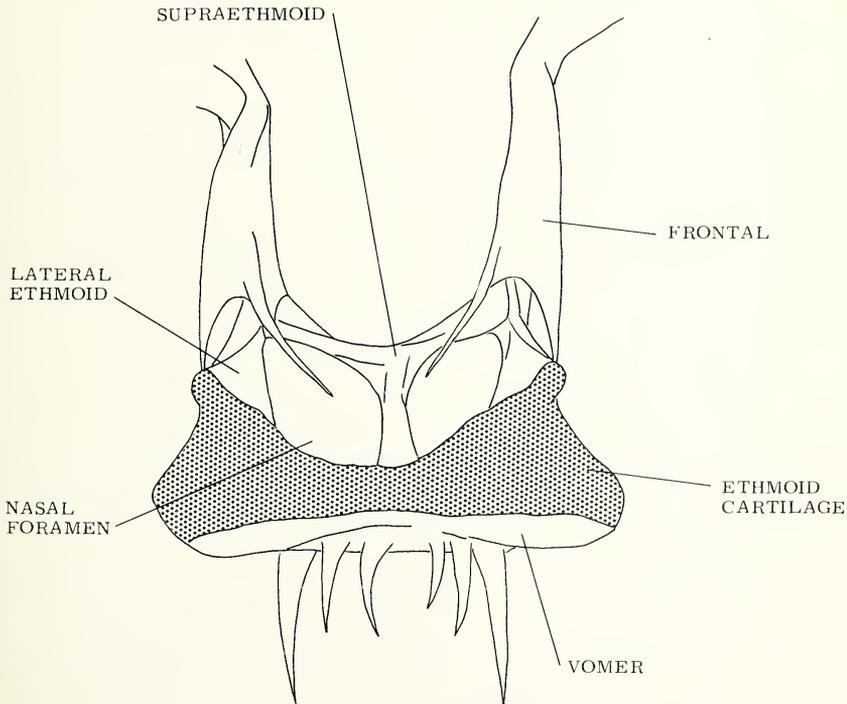


FIGURE 1. Anterior view of anterior half of cranium of *Puck pinnata*, SIO H52-363, 66.0 mm.

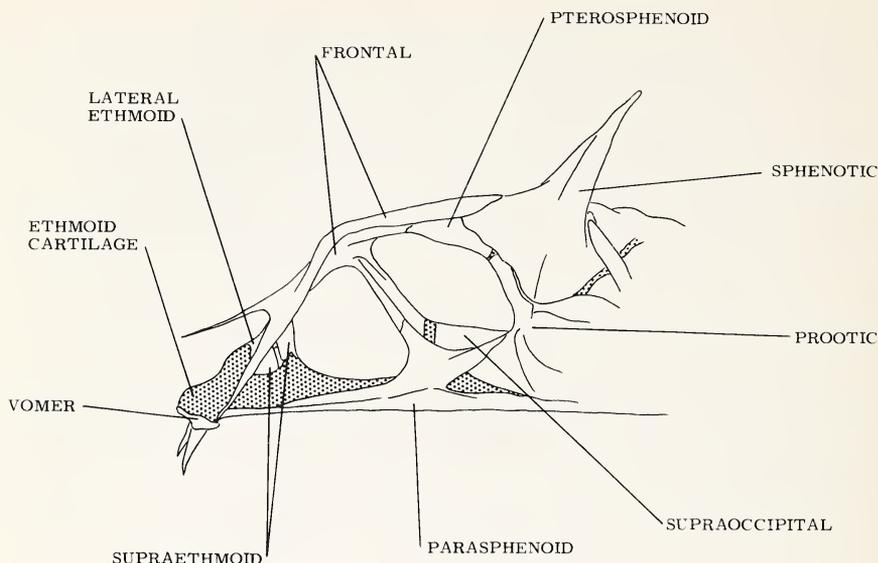


FIGURE 2. Lateral view of cranium of *Puck pinnata*, SIO H52-363, 66.0 mm.

an elongate spine (Figs. 2, 9, 14, 16; Pietsch 1974:19, fig. 34). The sphenotic spines of *Ctenochirichthys* are short, in some specimens not piercing the skin (Fig. 11).

Mandibular, palatine, and hyoid arches.- *Puck* differs from other "long-pectoral-aid" oneirodids in the angle of the jaw suspension. The suspensorium of *Puck* is strongly oblique in a posterior direction, resulting in a more posterior position for the lower jaw. In contrast, the angle of the jaw suspension in *Ctenochirichthys*, *Chirophryne*, and *Leptacanthichthys* is nearly vertical; the lower jaw extends forward slightly beyond the premaxillaries.

*Puck* and *Ctenochirichthys* are similar in that the distal ends of the upper jaw bones are held in a forward position on the dentary by a relatively short anterior maxillomandibular ligament, resulting in a short gape that terminates anterior to the eye (Fig. 3A, B, 9, 11). Although, the anterior maxillomandibular ligament of *Ctenochirichthys* is slightly longer than that of *Puck*, it originates much further forward on the dentary. For this reason, the length of the gape of *Ctenochirichthys* is slightly shorter than that of *Puck*. The anterior maxillomandibular ligament of *Chirophryne* and *Leptacanthichthys* is considerably longer than that of *Puck* and *Ctenochirichthys*, the upper jaw bones are more horizontal in position, and the gape of the mouth extends past the level of the eye (Figs. 3C, D, 14, 16).

In apparent correlation with this difference in jaw mechanism, the suspensoria (as well as the opercular apparatus and pectoral girdles) of *Puck* and *Ctenochirichthys* flare out laterally so that viewed head-on, the crania of these genera are considerably more narrow than the distance between the posterior ends of the lower jaw (Fig. 13A, B). Thus, the mouths of these two genera are short, yet wide, relative to other onei-

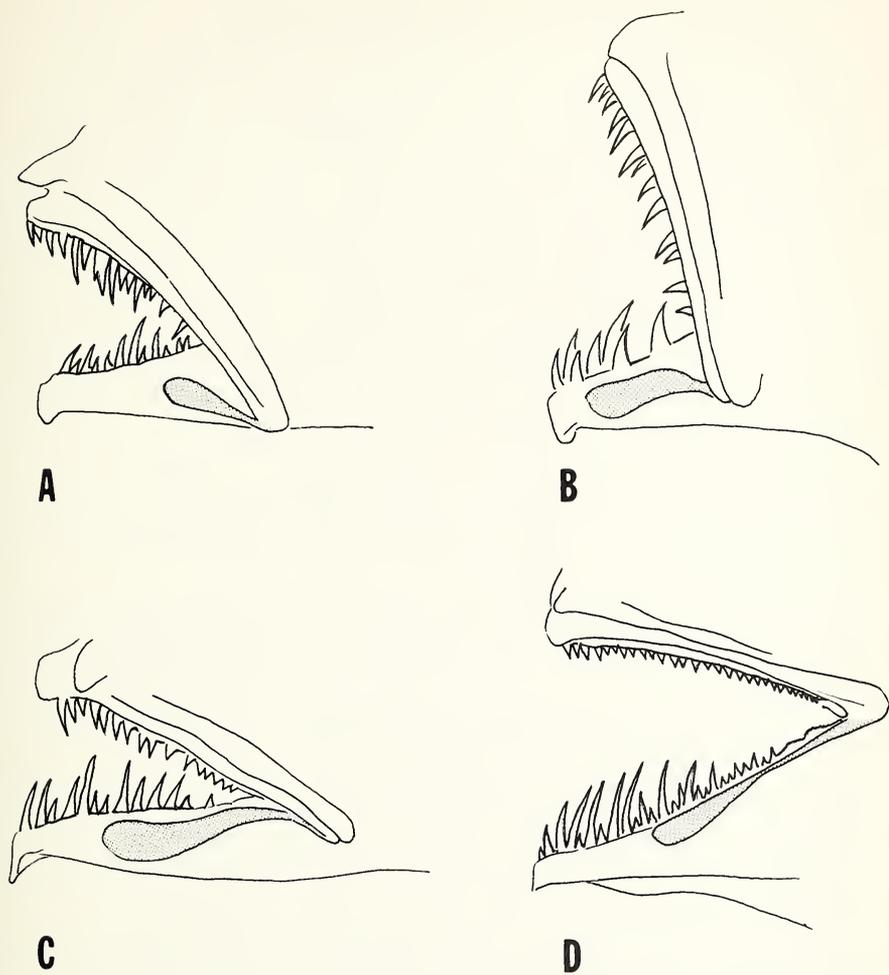


FIGURE 3. Lateral views of jaws with anterior maxillomandibular ligaments indicated by stippling: A. *Puck pinnata*, holotype, LACM 34276-1, 46.0 mm; B. *Ctenochirichthys longimanus*, lectotype, ZMUC P9297, 12.5 mm; C. *Chirophryne xenolophus*, SIO 70-306, 22.0 mm; D. *Leptacanthichthys gracilispinis*, LACM 33625-2, 56.0 mm.

roids. In contrast, the crania of *Chirophryne* and *Leptacanthichthys* are equal in width, or slightly wider than the distance between the posterior ends of the lower jaw (Fig. 13C, D); their mouths are consequently longer, yet more narrow.

Among oneirodids, differences in the size and shape of the bones of the lower jaw are correlated with differences in the length and depth of the cranium (Pietsch 1974:20). *Puck* has a relatively short, deep cranium, and consequently, like *Oneirodes* and *Danaphryne*, has short, deep dentaries and articular bones (Fig. 4; Pietsch 1974:

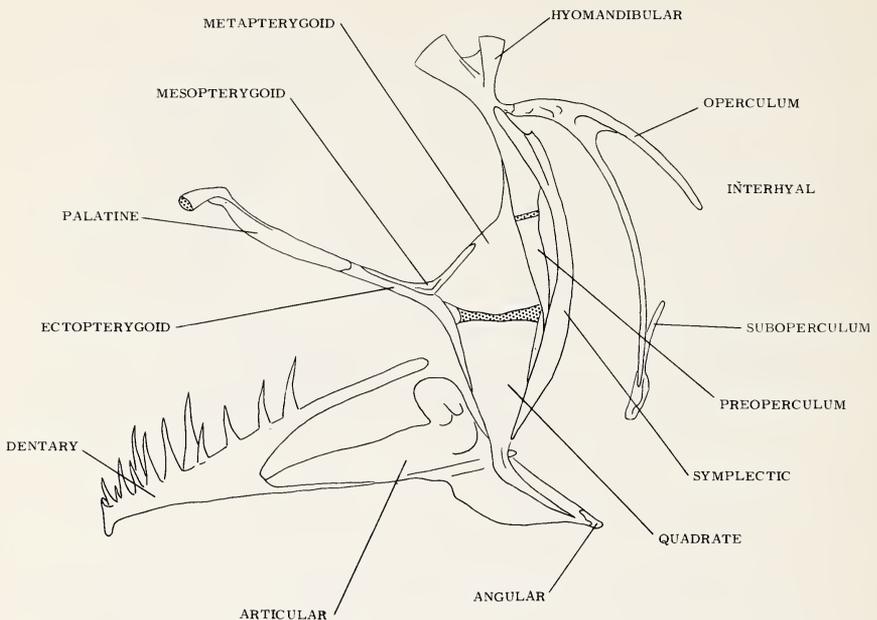


FIGURE 4. Lateral view of left side of lower jaw, suspensorium and opercular apparatus of *Puck pinnata*, SIO H52-363, 66.0 mm.

9, 20-21, figs. 8, 40). *Leptacanthichthys*, on the other hand, is a long-jawed genus with a more elongate, narrow cranium (Pietsch 1974: 20-21, fig. 42).

Variation in the length and width of the palatine arch is also associated with the length and depth of the cranium. *Puck*, *Oneiroides*, and *Danaphryne* have short, broad mesopterygoid, ectopterygoid and palatine bones as compared to *Leptacanthichthys* in which these bones are considerably more elongate and narrow (Fig. 4; Pietsch 1974: 9-10, 21, figs. 8, 40, 42).

At the articulation of the lower jaw and suspensorium, the articular and quadrate bones form spines (the mandibular and quadrate spines, respectively), which vary in relative length among oneirodids. The mandibular spine is considerably shorter than the quadrate spine in *Puck* and *Chirophryne* (Figs. 5A, 14), but, in contrast to all other oneirodids, the mandibular spine is considerably longer than the quadrate spine in *Leptacanthichthys* (Fig. 5B). Both spines are rudimentary in *Ctenochirichthys* (Fig. 11, Table 2).

In all oneirodids the jaw teeth are slender, recurved and depressible, large and small ones intermixed in both jaws. The considerably longer gape of *Leptacanthichthys* provides space for a greater number of upper and lower jaw teeth than are found in *Puck* and *Ctenochirichthys*. *Chirophryne*, known from only two small, adolescent females (11.0 and 22.0 mm), doubtless has a greater number of jaw teeth in larger specimens (Table 2).

Opercular apparatus.—The shape of the subopercular bone varies considerably

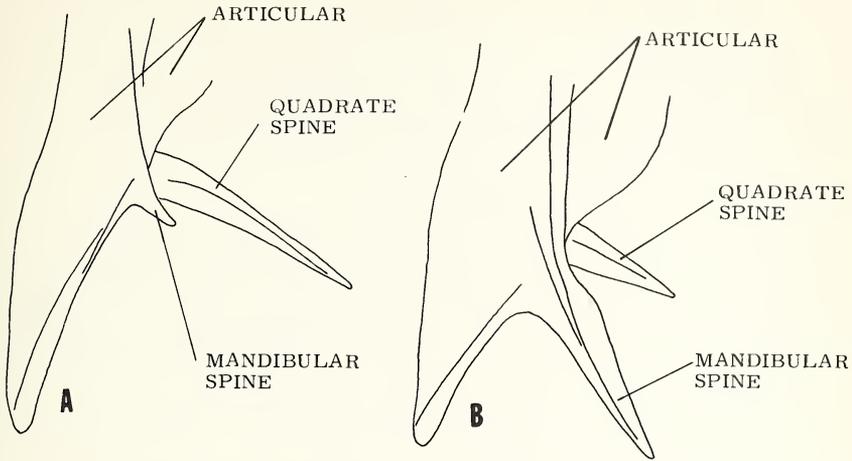


FIGURE 5. Ventrolateral views of posterior part of lower jaw, left side, showing arrangement of quadrate and mandibular spines: A. *Puck pinnata*, holotype, LACM 34276-1, 46.0 mm; B. *Leptacanthichthys gracilispinis*, LACM 33625-2, 56.0 mm.

between genera and is a diagnostic feature of many oneirodids. The subopercula of *Puck* and *Ctenochirichthys* are elongate and slender throughout their length, the upper end tapering to a point (Fig. 6A-C; Bertelsen 1951:94, fig. 51). Those of *Leptacanthichthys* and the two known specimens of *Chirophryne* (11.0 and 22.0 mm) are short and broad, the upper end rounded to bluntly pointed (Fig. 6D-G; Bertelsen 1951:94, figs. 49, 50; subopercula of other oneirodids are figured by Pietsch 1974).

Branchial arches.—The branchial arches of *Puck* are similar to those of *Danaphryne* and *Leptacanthichthys* (Pietsch 1974:25). Pharyngobranchials II and III are well developed and bear eight and ten long, slender teeth, respectively (Fig. 7; Pietsch 1974:25, fig. 51A, C).

Dorsal and anal fins.—*Puck*, *Chirophryne* and most specimens of *Leptacanthichthys* have five dorsal rays; *Ctenochirichthys* has six or seven. *Puck*, *Chirophryne* and most individuals of *Ctenochirichthys* have four anal rays; *Leptacanthichthys* has five or six (Table 1; fin-ray counts for other oneirodids are given by Pietsch 1974:27-28, table 23).

Pectoral lobe.—The pectoral lobe (pectoral fin, excluding fin rays) of *Puck*, *Ctenochirichthys*, *Leptacanthichthys* and, to a lesser degree, *Chirophryne* (but known only from small specimens), is unusually long and narrow (Fig. 8; Regan and Trewavas 1932:35-36, fig. 42C, D; Pietsch 1974:29, fig. 55). Unlike that of other oneirodids, the first radial (uppermost) is considerably shorter than the second; the cartilaginous distal end of the third radial is expanded in an antero-posterior direction to meet the distal end of the considerably shorter second radial. The fin rays, thus articulate along the upper margin of the pectoral lobe (Figs. 9, 11, 14, 16).

A curious division of the distal end of the lowermost radial and its cartilage is present in the pectoral lobe of both known specimens of *Puck* (Fig. 8A), possibly

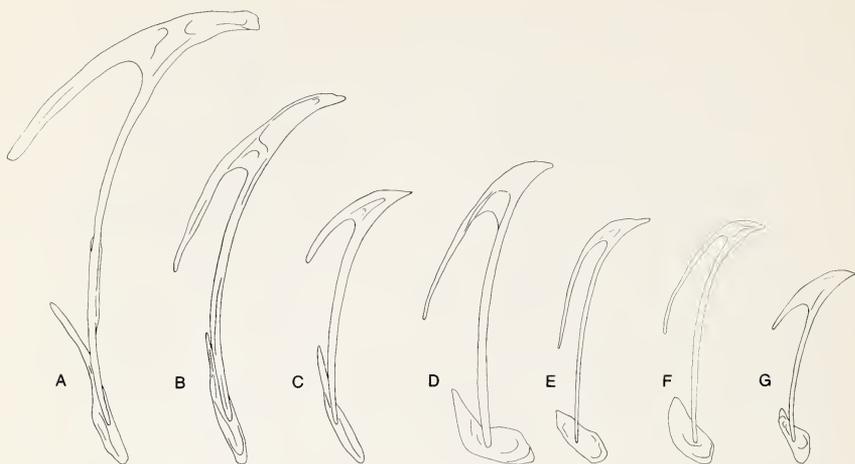


FIGURE 6. Lateral view of opercular bones, right side: A. *Puck pinnata*, SIO H52-363, 66.0 mm; B. *Puck pinnata*, holotype LACM 34276-1, 46.0 mm; C. *Ctenochirichthys longimanus*, paralectotype, BMNH 1932.5.3.20, 36.5 mm; D. *Leptacanthichthys gracilispinis*, ROM 27284, 54.0 mm; E. *Leptacanthichthys gracilispinis*, ROM 27293, 43.0 mm; F. *Leptacanthichthys gracilispinis*, ROM 27274, 41.0 mm; G. *Chirophryne xenolophus*, SIO 70-306, 22.0 mm.

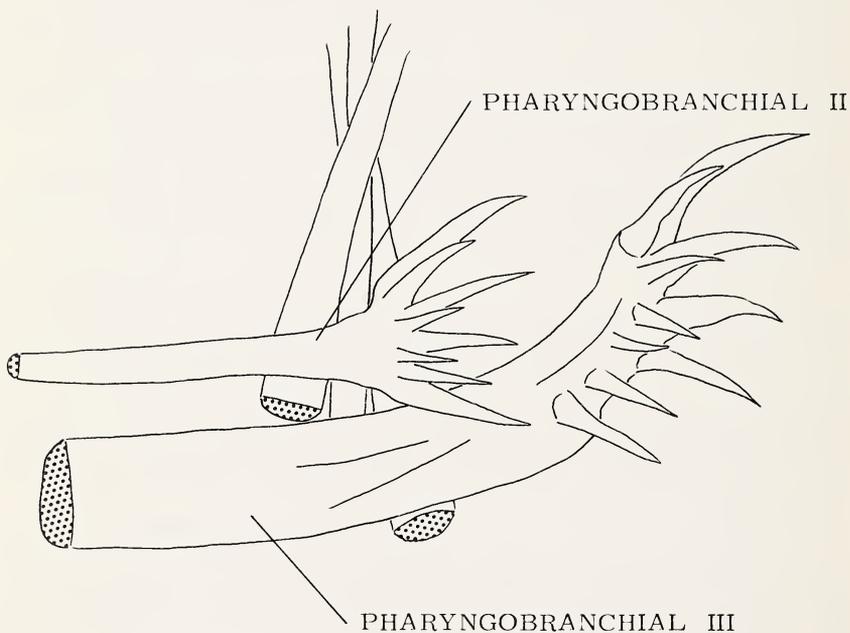


FIGURE 7. Pharyngobranchials of *Puck pinnata*, SIO H52-363, 66.0 mm.

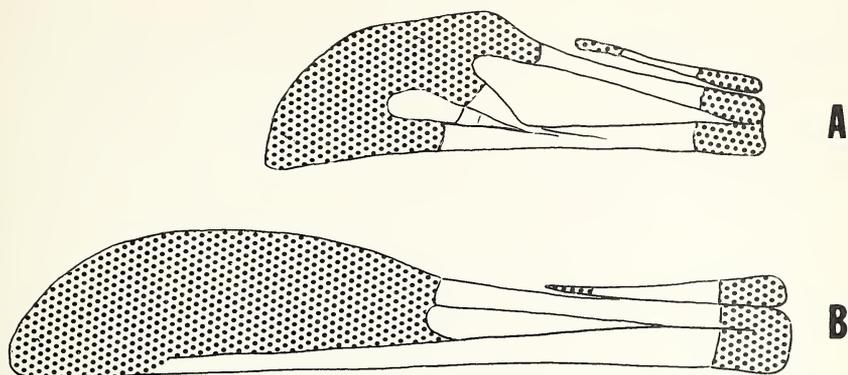


FIGURE 8. Lateral view of pectoral radials, left side: A. *Puck pinnata*, SIO H52-363, 66.0 mm; B. *Ctenochirichthys longimanus*, paralectotype, BMNH 1932.5.3.20, 36.5 mm.

indicating a fusion of two radials (see Pietsch 1972:41-42, fig. 23). All oneirodids are thought to have three pectoral radials, the possible presence of four radials in *Puck* further complicates the already cumbersome diagnosis of the family (Pietsch 1974:30).

*Puck*, *Chirophryne*, and *Leptacanthichthys* have pectoral-fin ray counts ranging from 18 to 21; *Ctenochirichthys* has considerably more pectoral-fin rays ranging from 28-30 (Table 1).

Skin Spines.—Skin spines could not be detected microscopically in the single osteological preparation of *Puck*.

## SYSTEMATICS

### KEY TO THE "LONG-PECTORALED" GENERA OF THE ONEIRODIDAE

- 1A. Sphenotic and articular spines short, in some cases not piercing skin (Fig. 11); length of pectoral lobe greater than 15 per cent of SL; pectoral fin rays 27-30 . . . . . *Ctenochirichthys* Regan and Trewavas 1932.
- 1B. Sphenotic and articular spines long, piercing skin (Figs. 9, 14, 16); length of pectoral fin lobe less than 15 per cent of SL; pectoral fin rays 17-21 . . . . . 2.

TABLE 1

Fin-ray frequencies for "long-pectoraled" genera of Oneirodidae

	Dorsal			Anal			Pectoral (both sides)								
	4	5	6	7	4	5	6	18	19	20	21	—	28	29	30
<i>Puck pinnatus</i>	2				2			4							
<i>Ctenochirichthys longimanus</i>		1	3		3	1							1	2	5
<i>Chirophryne xenolophus</i>	2				2			2	2						
<i>Leptacanthichthys gracilispinis</i>	1	7	2		9	1		1	2	4	7				

- 2A. Length of quadrate spine less than length of mandibular spine (Fig. 5B); dorsal profile of frontal bones nearly linear (Fig. 16); esca with a single appendage arising from dorsal surface (Fig. 17); anal fin rays 5-6 .....  
 ..... *Leptacanthichthys* Regan and Trewavas 1932.
- 2B. Length of quadrate spine greater than length of mandibular spine (Fig. 5A); dorsal profile of frontal bones convex (Figs. 9, 14); esca with more than a single appendage, either five separate appendages arising from dorsal surface or three dorsal appendages and a lateral filament (Figs. 10, 15); anal fin rays 4 ..... 3.
- 3A. Length of anterior maxillo mandibular ligament greater than one-half length of premaxillary, gape of mouth extending beyond eye (Fig. 3C); suboperculum short and broad, upper end rounded (Fig. 6G); esca without a lateral filament (Fig. 15) ..... *Chirophryne* Regan and Trewavas 1932.
- 3B. Length of anterior maxillo mandibular ligament less than one-half length of premaxillary, gape of mouth terminating before eye (Fig. 3A); suboperculum long and narrow, upper end tapering to a point (Fig. 6A, B); esca with a lateral filament (Fig. 10) ..... *Puck* new genus.

#### *Puck* NEW GENUS

Type species. - *Puck pinnata* new species

*Diagnosis for females.*—A member of the Oneirodidae as diagnosed by Pietsch (1974:30) distinguished by the following combination of characters: snout extremely short, dorsal profile of frontal bones strongly convex, gape of mouth terminating anterior to eye; length of anterior maxillomandibular ligament less than one-half length of premaxillary (Fig. 3A); hyomandibular with a double head; anterior end of pterygiophore of illicium exposed, its posterior end concealed under skin; illicium length 10.7 - 18.5 per cent of SL; lower jaw with a small symphyseal spine; sphenotic spines well developed; articular spines present, quadrate spine nearly six times length of mandibular spine (Fig. 5A); angular spine absent; vomerine teeth present; pharyngobranchial I absent; pharyngobranchials II and III present and toothed (Fig. 7); epi-branchial teeth absent; hypobranchial II present; pectoral-fin lobe long and narrow, longer than the longest rays of pectoral fin (Figs. 8A, 9); suboperculum elongate, slender throughout length, upper end tapering to a point, lower end without anterior spine or projection (Fig. 6A, B); anal fin with 4 rays; skin naked (embedded dermal spines cannot be detected microscopically in bleached and stained skin), covering caudal fin to some distance from fin base.

*Puck* resembles the oneirodid genera *Ctenochirichthys*, *Chirophryne*, and *Leptacanthichthys* in having an unusually long and narrow pectoral-fin lobe in which the first radial is considerably shorter than the second, and the second ankylosed to the distal expansion of the third (Fig. 8A, B). *Puck* is clearly distinguished from these forms, however, by its extremely short snout, strongly convex frontal bones, and oblique jaw suspension. It is further distinguished from *Chirophryne* and *Leptacan-*

*thichthys* by having a short anterior maxillomandibular ligament, a short, yet wide mouth (Figs. 3, 13), and an elongate subopercular bone (Fig. 6); and from *Ctenochirichthys* by its well-developed sphenotic and articular spines (Figs. 9, 11, 13).

*Males and larvae*.—Unknown.

*Etymology*.—The name *Puck*, to be treated as a noun of feminine gender, is taken from Germanic folklore, a minor order of mischievous devils, sprites, goblins or demons; a devilish trickster.

***Puck pinnata* NEW SPECIES**

Figures 1-3A, 4, 5A, 6A,B, 7, 8A, 9, 10, 13A, 18

Tables 1, 2

*Holotype*.—LACM 34276-1, 46.0 mm, female; *VITYAZ* Cruise 19, Station 3199, Sample 123b, western north Pacific, 38° 16' N, 152° 34' E; 6 m diameter conical ring net fished open with 5350 m of wire out; bottom depth 5420-5350 m; 0230-0545 hr; 16 October 1954.

*Paratype*.—SIO H52-363, 66.0 mm, female; *HORIZON*, between Stations SB 101 and 102; Berner, Juhl and Schaefer, collectors; eastern tropical Pacific, 6° 58' N, 88° 35' W; 3 m IKMT, fished open between surface and 1464 m; 1 July 1952.

*Description of the holotype*.—Escal bulb with a stout, rounded, anterodorsally directed and internally pigmented anterior papilla; a similar, posterodorsally directed medial papilla without internal pigment; distal ends of anterior and medial papillae darkly pigmented; an unpigmented, compressed posterior appendage bearing anterodorsally a lump of tissue of uncertain morphology; and a tapering, unpigmented lateral filament on each side, slightly less than length of escal bulb (Fig. 10).

Operculum bifurcate, the two forks forming an acute angle of 25°; length of lower fork 23.9 per cent of SL, upper fork 72.7 per cent of length of lower fork; length of suboperculum 40.9 per cent of length of lower fork (Fig. 6A, B).

Teeth as described for family; longest tooth in upper jaw 2.0 mm, in lower jaw 3.0 mm; pelvics absent; caudal fin 9 (2 unbranched - 4 branched - 3 unbranched); branchiostegal rays 6 (2 + 4).

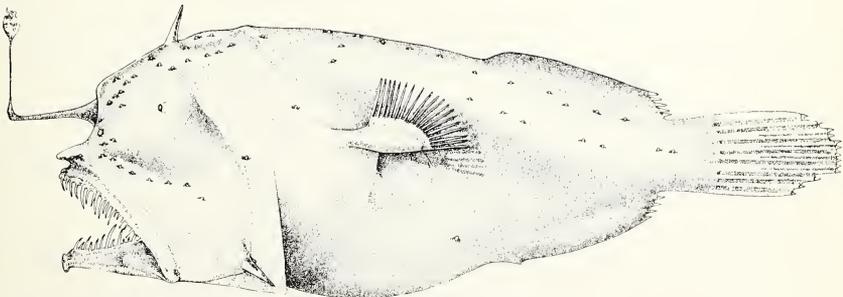


FIGURE 9. Holotype of *Puck pinnata*, LACM 34276-1, 46.0 mm.

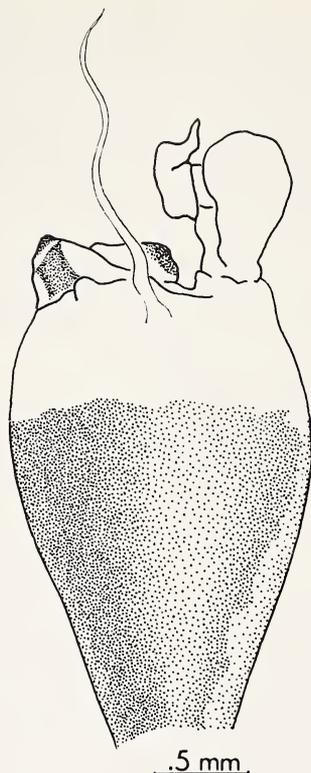


FIGURE 10. Esca of *Puck pinnata*, holotype, LACM 34276-1, 46.0 mm.

Fin ray counts are given in Table 1, tooth counts and body measurements in Table 2.

*Etymology.*—The specific name is derived from the Latin *pinnata*, meaning plumed or winged, in reference to the narrow, elongate pectoral fins.

*Distribution.*—*Puck pinnata* is known from two metamorphosed females: the holotype collected from the western north Pacific at 38° 16' N, 152° 34' E, and a second specimen from the eastern tropical Pacific at 6° 58' N, 88° 35' W (Fig. 18).

#### *Ctenochirichthys* Regan and Trewavas

*Ctenochirichthys* Regan and Trewavas 1932:82, pl. III, fig. 3 (type species *Ctenochirichthys longimanus* Regan and Trewavas 1932, by original designation).

*Diagnosis for Females* (based on two metamorphosed females, 12.5 and 36.5 mm).—The genus *Ctenochirichthys* differs from all other oneirodid genera in having greatly reduced sphenotic and articular spines that, in some cases do not pierce the skin, an extremely elongate pectoral-fin lobe greater than 15 per cent of SL, and a

TABLE 2  
Tooth counts and body measurements in percent of SL for "long-pectoral" genera of Oneirodidae

	<i>Puck pimata</i>			<i>Chirophryne xenolophus</i>				<i>Leptacanthichthys gracilispinis</i>						<i>Ctenochirichthys longimanus</i>						
	Holotype			SIO		Holotype		LACM		ROM		Paralectotype		Lectotype		Lectotype		Paralectotype		
	LACM	SIO	H52-363	SIO	ZMUC	LACM	ZMUC	LACM	ROM	ROM	ROM	BMNH	ZMUC	ZMUC	ROM	LACM	ZMUC	ZMUC	BMNH	P9297
Standard length in mm	46.0	66.0		11.0	22.0	22.0	27.0	27.0	41.0	43.0	43.0	43.0	52.0	54.0	56.0	56.0	12.5	36.5		
Length																				
Head	31.5	31.1		-	36.4	33.2	33.3	31.7	29.1	30.2	30.2	30.8	30.8	30.6	29.5	-	-	-	32.1	
Lower jaw	38.0	35.6		-	40.9	34.1	33.3	34.1	26.7	32.7	32.7	32.7	32.7	33.3	31.2	-	-	-	35.6	
Premaxillary	26.1	27.3		-	27.3	24.1	22.0	22.0	22.1	22.6	22.6	24.6	24.6	-	24.1	-	-	-	27.4	
Illicium	18.5	10.6		22.7	18.2	22.7	24.1	23.2	22.1	23.3	23.3	19.2	19.2	24.1	20.5	31.2	31.2	24.8	24.8	
Pectoral lobe	12.0	9.1		12.7	13.6	10.0	9.3	8.5	8.1	8.6	8.6	9.0	9.0	9.3	7.7	18.4	18.4	18.4	18.4	
Sphenotic spine	6.5	7.6		-	10.4	4.1	4.1	4.9	4.6	4.4	4.4	3.6	3.6	3.7	4.5	-	-	-	1.6	
Quadrate spine	7.6	6.8		-	11.8	4.5	3.3	3.2	3.0	-	-	-	-	2.8	3.4	rudimentary	rudimentary	rudimentary	rudimentary	
Mandibular spine	1.3	1.4		-	2.0	6.8	5.9	4.9	4.6	4.9	4.9	4.8	4.8	4.6	5.7	rudimentary	rudimentary	rudimentary	rudimentary	
Head depth	35.9	44.7		-	36.4	34.1	33.3	32.9	34.9	30.9	30.9	30.8	30.8	31.5	34.8	-	-	-	33.4	
Teeth																				
Vomer	3-3	3-3		4-4	4-4	3-3	5-4	4-4	5-5	6-6	6-6	5-5	5-5	5-5	6-6	2-2	2-2	1-2	1-2	
Upper jaw	35	47		22	30	52	61	85	70	102	102	81	81	120	154	17	17	37	37	
Lower jaw	24	25		25	34	44	71	74	90	105	105	89	89	100	106	16	16	31	31	

high number of pectoral fin rays, 27 to 30. In addition, *Ctenochirichthys* is unique in having the following combination of characters: snout short, dorsal profile of frontal bones convex; gape of mouth terminating anterior to or beneath eye; length of anterior maxillomandibular ligament less than one-half length of premaxillary (Fig. 3B); hyomandibular with a double head; anterior end of pterygiophore of illicium exposed, its posterior end concealed under skin; illicium length 24.8 - 31.2 per cent of SL; lower jaw with a small symphyseal spine; angular spine absent; vomerine teeth present; pharyngo-branchials II and III present and toothed; epibranchial teeth absent; suboperculum elongate, slender throughout length, upper end tapering to a point, lower end without anterior spine or projection (Fig. 6C); anal fin with 4 or 5 rays; skin presumably naked (bleached and stained skin not available for examination), covering caudal fin to some distance from fin base.

*Diagnosis for males and larvae.* — See Bertelsen (1951:95).

*Ctenochirichthys longimanus* Regan and Trewavas  
 Figures 3B, 6C, 8B, 11-13B, 18  
 Tables 1, 2

*Dolopichthys heteracanthus* Regan 1926:28 (in part).

*Ctenochirichthys longimanus* Regan and Trewavas 1932:82, pl.III, fig. 3 (original description; two specimens; lectotype, designated by Bertelsen 1951, ZMUC P9297). Bertelsen 1951:75, 94-96, figs. 51-52, table 16 (redescription of type material; males and larvae described; opercular bones, larval male, adolescent male, and lectotype figured; in key). Grey 1956:251 (synonymy; distribution). Bussing 1965: 222 (misidentification, specimen here referred to *Pentherichthys atratus*). Pietsch 1974:31, 32, 89, table 23 (relationships; in key).

*Trematorhynchus multiradiatus* Beebe and Crane 1947: 166, text fig. 11 (original description; single male specimen; CAS-SU 46491). Bertelsen 1951:95, fig. 52B (redescription; comparison with all known material; figured).

*Material.* — Two females, 12.5 - 36.5 mm, two larval males, 4.5 - 5.0 mm, and a single adolescent male, 11.5 mm.

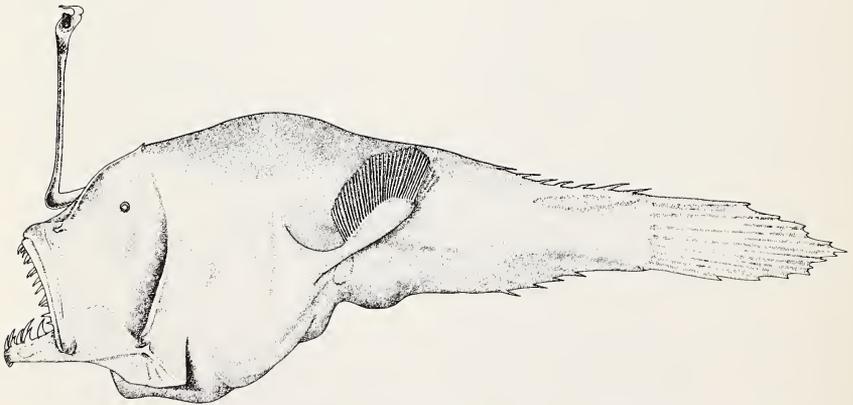


FIGURE 11. Paralectotype of *Ctenochirichthys longimanus*, BMNH 1932.5.3.20, 36.5 mm.

Lectotype of *Ctenochirichthys longimanus*.—ZMUC P9297, 12.5 mm; *DANA* Station 3548 (2); Gulf of Panama, 7° 06' N, 79° 55' W; 3000 m wire; 1030 hr; 3 September 1928.

Paralectotype of *Ctenochirichthys longimanus*—BMNH 1932.5.3.20, 36.5 mm; *DANA* Station 1206 (5); Gulf of Panama, 6° 40' N, 80° 47' W; 2500 m wire; 1845 hr; 14 January 1922.

Holotype of *Trematorhynchus multiradiatus*.—CAS-SU 46491, 11.5 mm; Eastern Pacific *ZACA* Expedition Station 225, Net No. T-1; 11 miles southwest of Jicaron Island, Panama, 7° 08' N, 81° 57' W; 1 m diameter conical ring net, 0-910 m; 20 March 1938.

*Non-type material*.—ZMUC P92795, 5.0 mm; *DANA* Station 3548(7); Gulf of Panama, 7° 06' N, 79° 55' W; 100 m wire; 2000 hr; 3 September 1928. ZMUC

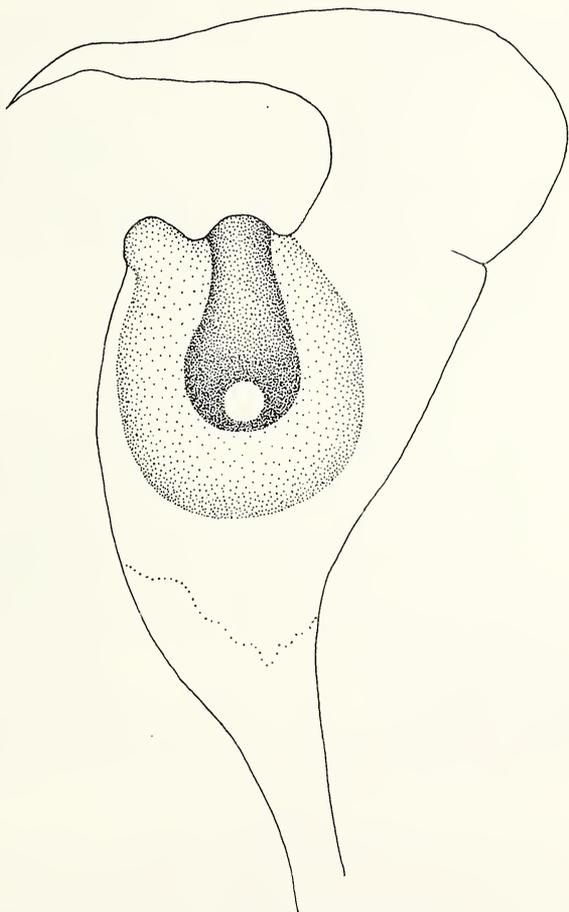


FIGURE 12. Esca of *Ctenochirichthys longimanus*, lectotype, ZMUC P9297, 12.5 mm.

P92794, 4.5 mm; *DANA* Station 1141(14); eastern north Atlantic, 34° 15' N, 16° 53' W; 300 m wire; 2355 hr; 14 October 1921.

*Description of females*.—Escal bulb with a short, rounded anterior appendage; a darkly pigmented, raised band of tissue extending over dorso-medial surface and down onto sides of bulb with a circular unpigmented area on each side; an unpigmented, compressed, tapering posterior appendage; lateral filaments absent (Fig. 12).

Operculum bifurcate, the two forks forming an acute angle of 38°; length of lower fork 21.9 per cent of SL, upper fork 52.5 per cent of length of lower fork; length of suboperculum 51.2 per cent of length of lower fork of operculum (Fig. 6C).

Teeth as described for family; pelvics absent; caudal fin 9 (2 unbranched-4 branched - 3 unbranched); branchiostegal rays 6 (2 + 4). Fin ray counts are given in Table 1, tooth counts and body measurement in Table 2.

*Distribution*.—*Ctenochirichthys longimanus* is known from five specimens, four of which were collected in the Gulf of Panama. The fifth specimen, a larval male, was taken in the eastern north Atlantic at 34° 15' N, 16° 53' W (Fig. 18).

#### *Chirophryne* Regan and Trewavas

*Chirophryne* Regan and Trewavas 1932:81-82, figs. 131-132 (type species *Chirophryne xenolophus* Regan and Trewavas 1932, by original designation).

*Diagnosis for females* (based on two metamorphosed specimens, 11.0 and 22.0 mm).—*Chirophryne* differs from other oneirodid genera in having the following combination of characters: snout moderate in length, dorsal profile of frontal bones convex; gape of mouth extending past eye; length of anterior maxillomandibular ligament greater than half length of premaxillary (Fig. 3C); hyomandibular with a double head; anterior end of pterygiophore of illicium exposed, its posterior end concealed under skin; illicium length 18.2 - 22.7 per cent of SL; lower jaw with a small symphyseal spine; sphenotic spines well developed; articular spines present, quadrate spine nearly six times length of mandibular spine; vomerine teeth present; pharyngobranchials II and III present and toothed; epibranchial teeth present; pectoral-fin lobe long and narrow, longer than the longest rays of pectoral fin; suboperculum short and broad, upper end rounded, lower end without anterior spine or projection (Fig. 6G); anal fin with 4 rays; skin presumably naked (bleached and stained skin not available for examination), covering caudal fin to some distance from fin base.

*Males and larvae*.—Unknown.

#### *Chirophryne xenolophus* Regan and Trewavas

Figures 3C, 6D, 13C, 14, 15, 18

Tables 1, 2

*Chirophryne xenolophus* Regan and Trewavas 1932:81-82, figs. 131-132 (original description; single specimen; holotype ZMUC P9296). Bertelsen 1951:75, 94, fig. 50 (redescription of holotype; opercular bone figured; in key). Grey 1956:250-251 (synonymy; distribution). Pietsch 1974:31, 32, 89, table 23 (relationships; in key).

*Material.*—Two adolescent females, 11.0 - 22.0 mm.

*Holotype.*—ZMUC P9296, 11.0 mm; *DANA* Station 3731(12); South China Sea, 14° 37' N, 119° 52' E; 2500 m wire; 0200 hr; 17 June 1929.

*Non-type material.*—SIO 70-306, 22.0 mm; ANTIPODES Expedition Station 4-51A, Trawl 1; 32° 10' N, 136° 05' E; 0-1400 m; 2355-0746 hr; 28-29 August 1970.

*Description of 22.0 mm female.*—Escal bulb with an unpigmented, tapering anterior appendage connected by a thin membrane to an internally-pigmented antero-

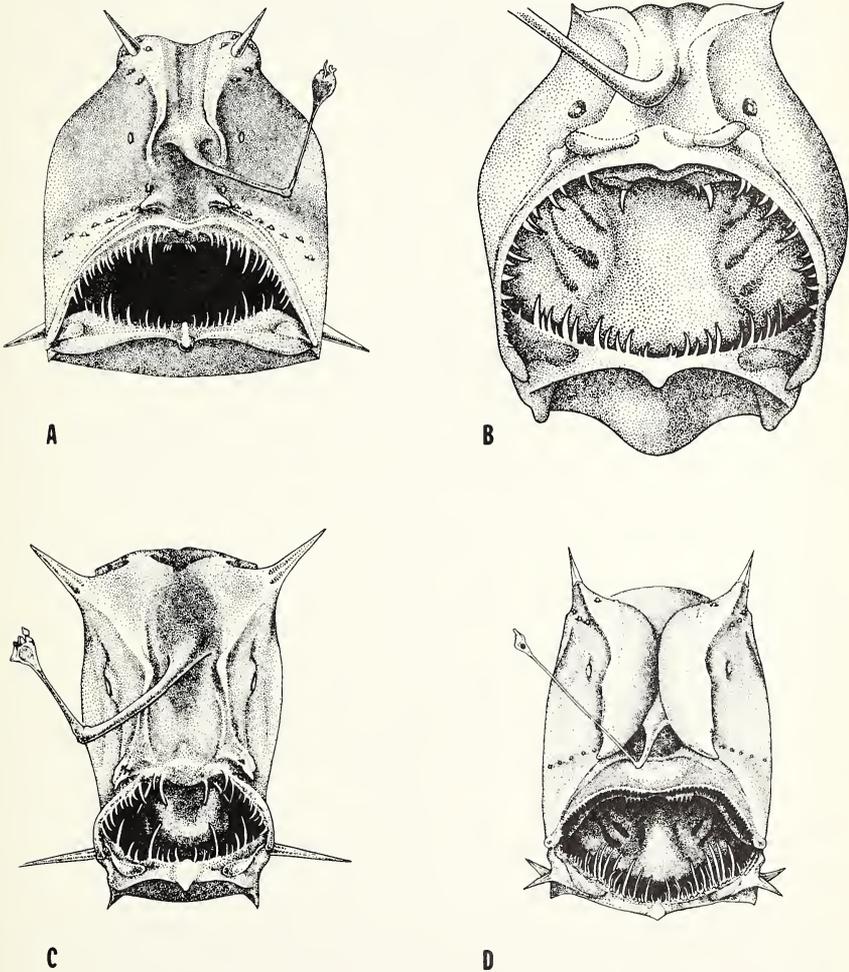


FIGURE 13. A. *Puck pinnata*, holotype, LACM 34276-1, 46.0 mm; B. *Ctenochirichthys longimanus*, paralectotype, BMNH 1932.5.3.20, 36.5 mm; C. *Chirophryne xenolophus*, SIO 70-306, 22.0 mm; D. *Leptacanthichthys gracilispinis*, LACM 33625-2, 56.0 mm.

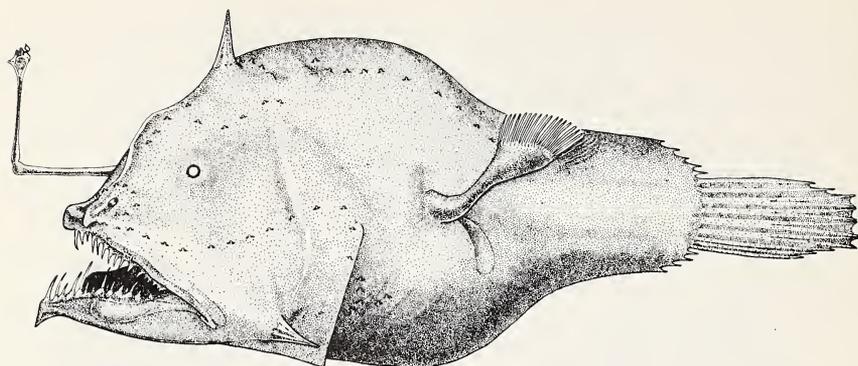


FIGURE 14. *Chirophryne xenolophus*, SIO 70-306, 22.0 mm.

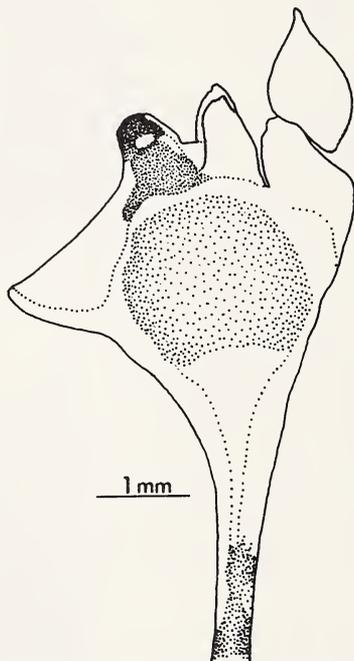


FIGURE 15. Esca of *Chirophryne xenolophus*, SIO 70-306, 22.0 mm.

dorsal appendage that is darkly pigmented on distal tip except for a small, circular, unpigmented area on each side; a pair of bilaterally placed, unpigmented medial appendages; an unpigmented, compressed, posterior appendage bearing distally a rounded lump of tissue that tapers to a point; lateral filaments absent (Fig. 15; Regan and Trewavas 1932:82 fig. 132).

Operculum bifurcate, the two forks forming an acute angle of 37°; length of lower fork 25.4 per cent of SL, upper fork 55.2 per cent of length of lower fork; length of suboperculum 32.5 per cent of length of lower fork of operculum (Fig. 6G).

Teeth as described for family; longest tooth in upper jaw 0.5 mm; in lower jaw 1.0 mm; pelvics absent; caudal fin 9 (2 unbranched - 4 branched - 3 unbranched); branchiostegal rays 6 (2 + 4).

Fin ray counts are given in Table 1, tooth counts and body measurements in Table 2.

*Distribution.*—*Chirophryne xenolophus* is known from two adolescent females: the holotype collected from the South China Sea and a second specimen from off Japan at 32° 10' N, 136° 05' E (Fig. 18).

#### *Leptacanthichthys* Regan and Trewavas

*Dolopichthys* (subgenus *Leptacanthichthys*) Regan and Trewavas 1932:66, 80, fig. 128 (genus *Dolopichthys* broadened to incorporate five subgenera, amended by Bertelsen 1951; type species *Dolopichthys gracilispinis* Regan 1925, by monotypy).

*Leptacanthichthys* Bertelsen 1951:74, 94, fig. 49 (subgenus *Leptacanthichthys* given generic status; type species *Dolopichthys gracilispinis* Regan 1925, by monotypy).

*Diagnosis for females* (based largely on osteological evidence presented by Pietsch 1974).—The genus *Leptacanthichthys* differs from other oneirodids by having a well-developed mandibular spine that is considerably longer than the quadrate spine (Fig. 5B). In addition, *Leptacanthichthys* is unique in having the following combination of characters: snout long, dorsal profile of frontal bones nearly linear; gape of mouth extending past eye; length of maxillomandibular ligament greater than half length of premaxillary (Fig. 3D) hyomandibular with a double head; anterior end of ptergiophore of illicium exposed, its posterior end concealed under skin; illicium length 19.2 - 24.1 per cent of SL; lower jaw with a small symphyseal spine; sphenotic spines well developed; angular spines absent; vomerine teeth present; pharyngobranchial I absent; pharyngobranchials II and III present and toothed; epibranchial teeth absent; hypobranchial II present; pectoral-fin lobe long and narrow, longer than the longest rays of pectoral fin; suboperculum short and broad, upper end rounded to bluntly pointed, lower end without anterior spine or projection (Fig. 6D-F) anal fin with 5 rays, rarely 6; skin naked (embedded dermal spines cannot be detected microscopically in bleached and stained skin), covering caudal fin to some distance from fin base.

*Diagnosis for males* (based on a single known male in late metamorphosis, parasitically attached to a sexually mature female, LACM 33625-2; Pietsch 1976 figs. 2-5).—Posterior nostril well separated from eye; upper end of suboperculum rounded; 6 lower denticles; gill cover pigmented with slightly darker pigmentation along posterior margin of suboperculum; dorsal pigment restricted to upper part of body extending beneath base of dorsal fin and just past anterior base of anal fin with a more heavily pigmented dorsal and ventral group of melanophores near hypural plate; peritoneum pigmented.

*Larvae.*—Unknown.

*Leptacanthichthys gracilispinis* (Regan)

Figures 3D, 5B, 6E-H, 13D, 16-18

Tables 1, 2

*Dolopichthys gracilispinis* Regan 1925:563 (original description; two specimens; lectotype designated by Bertelsen 1951, ZMUC P9295). Regan 1926:27, 30, pl. V, fig. 2 (brief description after Regan 1925; in key).

*Dolopichthys* (*Leptacanthichthys*) *gracilispinis* Regan and Trewavas 1932:66, 80 fig. 128 (genus *Dolopichthys* broadened to incorporate five subgenera, amended by Bertelsen 1951; description after Regan 1925, 1926; in key).

*Leptacanthichthys gracilispinis* Bertelsen 1951:74, 94, fig. 49 (subgenus *Leptacanthichthys* given generic status; description; in key). Grey 1956:250 (synonymy; distribution). Pietsch 1974:16-32, 82, 86-89, Figs. 22, 34, 39c, 42, 51c, 55, 59, 103, 104, tables 23, 24 (osteology; relationships, esca figured; in key).

*Material*.—Thirteen females, 10.5-56.0 mm, and a parasitic male in late metamorphosis, 7.5 mm.

*Lectotype*.—ZMUC P9295, 52.0 mm; *DANA* Station 1206(3); Gulf of Panama, 6° 40' N, 80° 47' W; 3500 m wire; 1845 hr; 14 January 1922.

*Paralectotype*.—BMNH 1925.8.11.14, 43.0 mm; *DANA* Station 1358(5); north Atlantic, 28° 15' N, 56° 00' W; 3000 m wire; 1530 hr; 2 June 1922.

*Non-type material*.—ROM 27284, 54.0 mm; *BRANDAL* Tow 20; 43° 23' N, 52° 30' W; Engel trawl, 0-1050 m; 25 July 1968. ROM 27293, 43.0 mm; *BRANDAL* Tow 22; 44° 00' N, 57° 52' W; Engel trawl, 0-1000 m; 26 July 1968. ROM 27274, 41.0 mm; *BRANDAL* Tow 14; 46° 00' N, 44° 30' W; Engel trawl, 0-1000 m; 18 July 1968.

LACM 33625-2, female, 56.0 mm, with parasitic male, 7.5 mm; *VELERO IV* Station 19009; 8° 10' N, 86° 00' W; 3 m IKMT, 0-750 m; 0625 hr; 24 May 1973. LACM 34275-1, 27.0 mm; *VITYAZ* Cruise 24, Station 3573, Sample 50; 38° 04' N, 144° 13' E; 1.6 m conical ring net, 0-3000 m; bottom depth 5660-5760 m; 0950-1530 hr; 4 May 1957. LACM 32776-1, 22.0 mm; *TERITU* Cruise Blood, Sweat, and Tears, Sample 70-7-6; 21° 20'-30' N, 158° 20-30' W; 2 m IKMT, 0-1250 m; 0746-1200 hr; 6 July 1970.

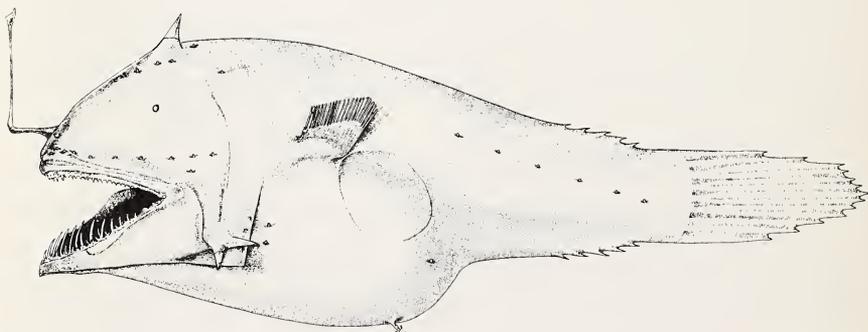


FIGURE 16. *Leptacanthichthys gracilispinis*, LACM 33625-2, 56.0 mm. Stalk of tissue protruding from belly bears embedded bones of upper jaw of a parasitic male (see Pietsch 1976).

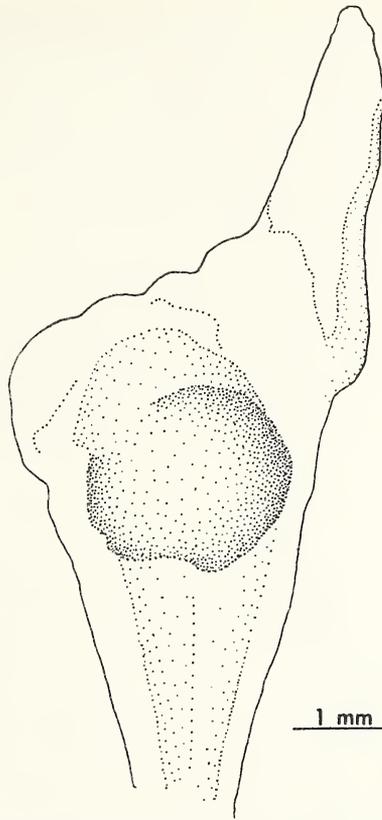


FIGURE 17. Esca of *Leptacanthichthys gracilispinis*, LACM 32776-1, 22.0 mm.

SIO 60-235, 13.0 mm; TETHYS Expedition;  $0^{\circ} 08.5' S$ ,  $138^{\circ} 50.9' W$ ; 0-2100 m; 3 - 4 July 1960. SIO 68-476, 10.5 mm; STYX Expedition VII-40;  $22^{\circ} 00' N$ ,  $171^{\circ} 40' E$ ; 3 m IKMT, 0-1250 m; bottom depth 3660 m; 0640-1300 hr; 15 September 1968.

CAS-SU 43423, 14.0 mm; GLADISFEN Net 874;  $32^{\circ} 12' N$ ,  $64^{\circ} 36' W$ ; 11 September 1930.

IOS uncatalogued, 12.5 mm; DISCOVERY II 8281-37;  $31^{\circ} 48' N$ ,  $63^{\circ} 37' W$ ; Rectangular Midwater Trawl with closing device, 1240-1265 m; 0200-0500 hr; 19 March 1973.

MCZ 50705, 12.5 mm; ATLANTIS II Cruise 49, RHB 1939;  $40^{\circ} 22' N$ ,  $58^{\circ} 51' W$ ; 3 m IKMT, 0-1040 m; 1235-1440 hr; 8 July 1969.

*Description of females.*—Escal bulb with a darkly pigmented streak on dorsal surface, and an unpigmented, compressed posterior appendage; anterior and lateral appendages absent (Fig. 17; Regan and Trewavas 1932:80 fig. 128).

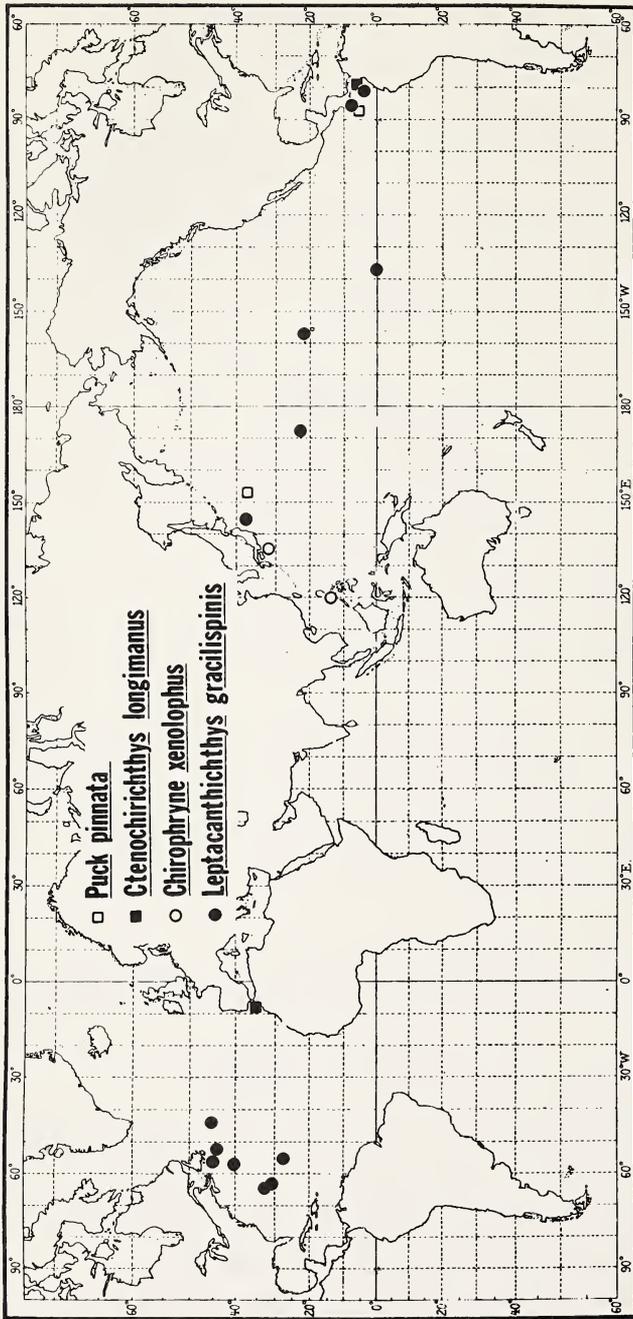


FIGURE 18. Distributions of "long-pectored" oneirodid genera. A single symbol may indicate more than one capture.

Operculum bifurcate, the two forks forming an acute angle of 18° to 27°; length of lower fork 18.1-19.5 per cent of SL; length of lower fork 64.4-70.5 per cent of length of lower fork; length of suboperculum 29.5-37.5 per cent of length of lower fork of operculum (Fig. 6D-F).

Teeth as described for family; D. 4-6, of 10 specimens counted one had D.4; A.5-6, P. 18-21, of 8 specimens counted, one had P.18; pelvics absent; caudal fin 9 (2 unbranched - 4 branched - 3 unbranched); branchiostegal rays 6 (2 + 4).

Fin ray counts are given in Table 1, tooth counts and body measurements in Table 2.

*Distribution.*—In the Atlantic Ocean, *L. gracilispinis* seems to be restricted to waters off the continental slope of North America where about one-half of the known material has been collected between 28° and 46° N, as far east as 44° W. The remaining material is from the north Pacific where it ranges from off Japan to the Gulf of Panama (Fig. 18). Ninety-two per cent of the known material was captured by gear fished below 1000 m; 62 per cent by gear fished below 1200 m.

## DISCUSSION

The ceratioid family Oneirodidae is by far the largest and most diverse of the 11 deepsea anglerfish families, but probably remains the least well known. With the addition of *Puck*, 15 oneirodid genera are now recognized. Eleven of these genera consist of a single species and of these, nine are based on only one or two adolescent or adult females. The addition of yet another monotypic genus based on two female specimens is justified, however, as this new form clearly cannot reasonably be placed within any previously described genus. *Puck*, *Ctenochirichthys*, *Chirophryne*, and *Leptacanthichthys* share an unusually elongate pectoral-fin lobe that bears the fin rays along its dorsal margin. A similar arrangement is not found in any other ceratioid; it is mainly because of the common occurrence of this derived character complex that these four genera are thought to form a natural assemblage. Within this group of four genera, *Puck* appears to be most closely related phylogenetically to *Ctenochirichthys*. These two genera share a modification of the jaw mechanism in which the gape of the mouth is considerably shorter, but at the same time, wider, relative to other oneirodids. In addition, *Puck* and *Ctenochirichthys* share an elongate suboperculum, unlike the short and broad suboperculum of *Chirophryne* and *Leptacanthichthys*.

*Puck* appears to be intermediate in many ways between more generalized oneirodid genera, especially *Danaphryne*, and the other three, more specialized "long-pectoral" genera. *Puck* is similar to *Danaphryne* and unlike *Leptacanthichthys* in the shape and relative size of the bones of the ethmoid region, in the shape and position of the frontals, and in the length and depth of the cranium and elements of the mandibular, palatine, and hyoid arches. *Puck*, on the other hand, shares the specialized pectoral lobe with *Ctenochirichthys*, *Chirophryne*, and *Leptacanthichthys* as well as the modification of the jaw mechanism of *Ctenochirichthys*.

Although apparently most closely related to *Puck*, probably the least derived of the four "long-pectoral" genera, *Ctenochirichthys* is considered the most derived

member of the group in having reduced sphenotic and articular spines, a reduced number of vomerine teeth, a considerably more elongate pectoral lobe, a secondarily derived increase in the number of pectoral-fin rays, and a more elongate illicium.

Little can be said concerning relationships of *Chirophryne*, known from only two small, adolescent females. It is perhaps intermediate between *Puck* and *Ctenochirichthys* on one hand, with which it shares convex frontal bones, and *Leptacanthichthys* on the other, with which it shares a similar jaw mechanism and similarly-shaped subopercular bones.

*Leptacanthichthys* is derived and unique among "long-pectoraled" oneirodid genera in having a nearly linear profile of the frontal bones; it is unique among oneirodids in having a well-developed mandibular spine that is considerably longer than the quadrate spine.

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I thank E. Bertelsen, Robert J. Lavenberg and Camm C. Swift for critically reading the manuscript. The following people and institutions provided study material: E. Bertelsen (ZMUC); Robert J. Lavenberg and Jerry W. Neumann (LACM); Richard H. Rosenblatt (SIO); Alwyne Wheeler (BMNH); Nigel Merrett and Julian Badcock (IOS); William N. Eschmeyer and Tomio Iwamoto (CAS); Thomas A. Clarke (Hawaii Institute of Marine Science); W. B. Scott (ROM); and Karsten E. Hartel (MCZ). Special thanks go to N. V. Parin, of the Institute of Oceanography of the Academy of Sciences of the USSR, Moscow, for his gift of the holotype of *Puck pinnata* to the Natural History Museum of Los Angeles County; and to Richard Rosenblatt for allowing me to clear and stain the second known specimen of *Puck*. Figures 9-11, 13-14, and 16 were made by Patricia Chaudhuri. The work was supported by a grant from the National Science Foundation, No. GB-40700. Partial assistance from the William F. Milton Fund of Harvard University and the Johannes Schmidt Fund of the University of Copenhagen is also gratefully acknowledged.

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REPRODUCTION IN *MACROGENIOGLOTTUS ALIPIOI* CARVALHO  
(ANURA, LEPTODACTYLIDAE)



By J. PAUL ABRAYAYA AND JAMES F. JACKSON

NATURAL HISTORY MUSEUM OF LOS ANGELES COUNTY

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REPRODUCTION IN *MACROGENIOGLOTTUS ALIPIOI* CARVALHO  
(ANURA, LEPTODACTYLIDAE)<sup>1</sup>

By J. PAUL ABRAVAYA<sup>2</sup> AND JAMES F. JACKSON<sup>3</sup>

ABSTRACT: Mating behavior, mating call, and larval morphology are described for the leptodactylid frog *Macrogenioglottus alipioi* Carvalho. The mating behavior is conducted in a way that would be advantageous in a species in which the number of eggs oviposited per female is great but the number of ovipositing females per pond is small. Feeding behavior is modified for the capture of slow moving prey such as snails and earthworms. The sonogram of the mating call of *M. alipioi* is similar to that of *Odontophrynus americanus*. The tadpoles of *Macrogenioglottus* are similar to those of *Odontophrynus*, having the same tooth row formula and similar arrangement of labial papillae. They differ, however, in the position of the spiracle and the vent. A review of the taxonomic history of *M. alipioi* combined with new data suggests a close relationship between *Macrogenioglottus* and *Odontophrynus*.

INTRODUCTION

Although *Macrogenioglottus alipioi* Carvalho was described 30 years ago (Carvalho 1946) and has been considered of no small interest to anuran phylogeny (Reig 1972; Duellman 1975), little on its biology has been published. We report our observations on reproduction of the species made in 1974 at the Reserva Biologica Nova Lombardia, Município de Santa Teresa, Espírito Santo, Brazil. The vegetation of the area was classified as Subtropical Lower Montane Moist Forest by the Holdridge (1967) system. Because of the extremely dissected topography, the only lentic water (other than that in tank bromeliads) is found in oxbow ponds along the valley streams. These ponds are empty much of the year and receive significant amounts of water only when their progenitory streams overflow after heavy rains characteristic of the wet season. Choruses of *Macrogenioglottus alipioi* were heard only after extremely heavy rains which resulted in such flooding.

Our observations were made at an oxbow pond 30 by 6 m and less than a meter deep. The water was stained by tannic acids and on the pond bottom was a deep layer of organic mud and decaying plant material. The elevation of the pond is 810 m.

The pond was visited several times a month between June 1973 and November 1974. No reproductive activity was noted on rainless days or nights, but activity was

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

ROBERT L. BEZY

W. RONALD HEYER

ROY W. MC DIARMID

JOHN W. WRIGHT

<sup>2</sup>Research Associate in Mammalogy, Natural History Museum of Los Angeles County, and Department of Biology, California State University, Northridge, California 91234.

<sup>3</sup>Department of Biology, University of Southwestern Louisiana, Lafayette, Louisiana 70504.

noted on the two visits we made during nights of substantial rain, and during one day after a heavy rain.

Specimens of adult *Macrogenioglottus alipioi* were deposited in the Museu de Biologia "Prof. Mello Leitão," Santa Teresa, Brazil. Eighteen tadpoles were deposited in the Natural History Museum of Los Angeles County (LACM 121739).

### REPRODUCTIVE BEHAVIOR

On the night of 4 January 1974 a chorus of 6 male *M. alipioi* was heard. All males were stationed on the bank within a meter of the water. No females were found at the pond, but a female was watched for an hour as she walked several hundred meters along a dirt road toward the chorus. When she reached the point on the road nearest the pond, she turned uphill and proceeded in the opposite direction from the pond.

On 10 February 1974 observations were made at the pond from 19:30 until 01:30 (local time) of the next day. Three calling males were stationed on the bank at the water's edge. One male once moved into the pond and called while standing in water 2-3 cm deep. An amplexed pair was located in the pond at 20:30. Amplexus is axillary, the male's forelegs clasped around the female one-third to one-fourth the distance between her fore- and hindlegs, and his forefeet placed in her axillae. Initially the pair floated quietly and moved only every five minutes; later they moved once or more each minute. The female initiated changes of location by swimming or walking one to several meters dragging the male behind. When they reached a new site, oviposition usually occurred. When she stopped, the male flexed his forelegs and pulled himself forward on top of the female. While in this position, he flexed his hindlegs and brought his hindfeet together at the female's vent. The hindfeet were then pushed directly backward in a single stroke that started slowly and then accelerated, as if the male were conducting eggs or sperm posteriorly. During or after this movement, the male slid backwards off the female. Then the male kicked several times rapidly; these kicks were sometimes between the female's hindlegs but usually lateral to them. Whether the male is distributing sperm over the eggs or whether he is distributing the eggs through the water, or both, was impossible to determine. The number of eggs oviposited at each site was not determined but probably is small, perhaps less than 20. Eggs were laid in short strands and small clusters, 2-eggs thick. They adhered to vegetable debris and did not float. The amplexed pair was collected at 23:30 and laid fertilized eggs in the plastic collecting bag. A second female that presumably had not oviposited was found walking toward the pond. She was collected and found to contain approximately 3650 eggs.

Although we have no data on tadpole vagility or survivorship, for heuristic purposes we hypothesize three possible adaptive functions of the multiple oviposition. The frequent changes of oviposition sites and the deposition of eggs in small batches could function to reduce the probability that all the eggs would be lost due to predation or desiccation. Spreading the tadpoles around the pond could possibly also function to minimize competition between siblings. Such a function would be advantageous in a species where the number of eggs oviposited per female is great but the

number of ovipositing females per pond is small, as it appears to be in *M. alipioi* judging from our observations and the fact that the type specimens were a single pair collected in amplexus (Carvalho 1946). In a species with numerous amplexing pairs per pond, there would be little advantage to such egg dispersal because tadpoles produced by other pairs would be hatching throughout the pond.

### MATING CALL

The call of *M. alipioi* sounds most like a fog horn. Figure 1 illustrates the sonogram of calls recorded on a Uher model 4000 at an ambient temperature of 17°-20°C on 10 February. The call is a series of pulsed notes, each note lasting 0.24-0.27 seconds. The number of notes in the call varies from one to several dozen. When repeated, the notes are separated by intervals of 0.54-0.58 seconds. Maximum sound energy of the moderately well-tuned note is spread over the frequency range 230-800 hz. In the frequency range 800-1180 hz exists a component of weaker intensity with a pulse rate of 195-230 pulses per second. The beginning and end of the note on the sonogram are slightly less dark than the middle, indicating weak intensity modulation. The low frequency-low intensity "echo" that appears between notes on the sonogram (Fig. 1) probably originated from another individual in the chorus. The males alternate their calls to form duets and triplets.

### NATURAL HISTORY

Fertilized eggs with their gelatinous envelopes averaged 2.2 mm in diameter. The tadpoles hatched 48-70 hours after fertilization. In the laboratory, tadpoles grew even when the only nutrient provided was organic muck from a pond bottom. They refused to eat meat but readily accepted fruit of avocado and papaya. The tadpoles stayed near the bottom of the aquarium and did not swim much. This inactivity may serve a protective function, since the pond had a high density of predaceous *Ceratotophrys* tadpoles. Three tadpoles transformed at ages of 86, 95, and 127 days. This rate of development is consistent with apparent ecological necessities, since the oxbow ponds are nearly dry by May. The snout-vent lengths of the transformed frogs were 19.9, 19.8, and 21.0 mm.

Stomachs of 5 adult *M. alipioi* were examined. Two were empty; one contained 2 earthworms; one contained a small snail shell; and one contained the central spiral of a snail shell and part of an earthworm. An adult maintained in the laboratory ate snails and earthworms, appearing to prefer the former. It attempted to eat roaches but was not often successful in picking them up. When a *M. alipioi* recognized a potential food item, presumably by its movement, it would walk close, open its mouth, and pick up the item through a slow extrusion of the tongue. Neither the very deliberate feeding movements nor the dentition and lingual morphology of *M. alipioi* appear adapted for capturing fast-moving prey. Consequently, we believe that our sample of stomach contents, although limited, accurately reflects the dietary habits of the species.

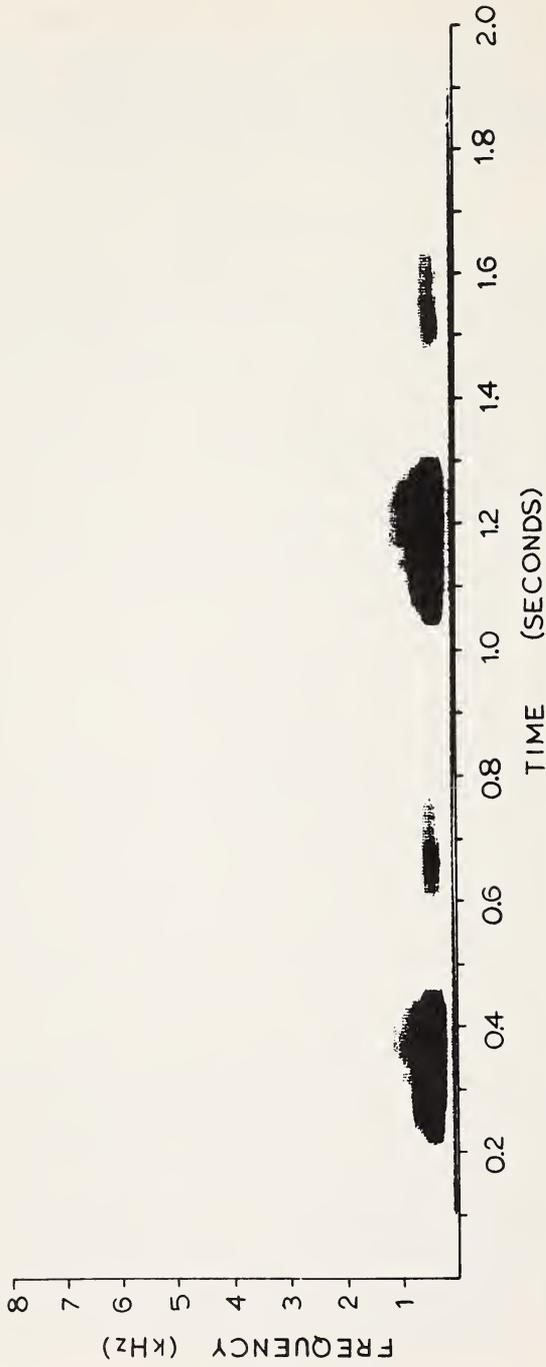


FIGURE 1. Sonogram of mating call of *Macrogenioglottus alipioi* Carvalho. 10 February 1974; Santa Teresa, Espírito, Santo, Brazil; ambient temperature 17-20 C.

## DESCRIPTION OF TADPOLE

The tadpole of *M. alipioi* is illustrated in figure 2. The tadpole is characterized as follows (terminology of Altig 1970): sinistral spiracle; dextral anus; complex mouthparts; labial papillae well developed laterally and complete along posterior labium, absent on median portion of anterior labium; labia strongly emarginate laterally; tooth rows  $\frac{2}{3}$ ; second anterior tooth row with a broad A-2 gap; first posterior tooth row with narrow P-1 gap; denticles fine and short; upper jaw narrow and smooth; lower jaw narrow and toothed laterally; eyes and nostrils dorsal, eyes directed dorsally; body elliptical in dorsal view; somewhat depressed dorso-ventrally, greatest depth .35-.43 of standard length; dorsal and lateral surface of body brownish-grey, reticulated with non-pigmented areas; venter transparent; tail musculature pigmented with a series of dark grey spots or bars along dorsal portion and with irregular dark grey reticulation on ventral portion; margins of tail fin spotted irregularly with dark grey; standard length 12-18 mm; tail relatively short, 1.24-1.40 of standard length. The tadpole in Figure 2 is at stage 30 (Gosner 1960); standard length 13.9 mm, tail 21.5 mm, body width 9.8 mm. Tadpoles at stage 25 show considerable variation in growth; four specimens examined ranged from 4.5 mm to 11.5 mm in standard length.

## EVOLUTIONARY RELATIONSHIPS

In the description of *Macrogenioglottus*, Carvalho (1946) assigned the genus to the Ceratophryidae (=Ceratophrydidae) and considered *Odontophrynus* its closest relative. Since then the relationship of *Macrogenioglottus* to *Odontophrynus* has been a subject of considerable disagreement. Lynch (1971) synonymized *Macrogenioglottus* with *Odontophrynus* in the leptodactylid subfamily Telmatobiinae which was separated from the subfamily Ceratophryinae. From the appendix of his paper one would assume that this synonymy was made without examination of specimens of *Macrogenioglottus*. This presumably is the reason that some of the characters in his diagnostic definition of *Odontophrynus* (sensu lato) actually exclude *Macrogenioglottus*. For example, *Macrogenioglottus* is considerably larger (Carvalho 1946) and falls outside Lynch's size range for *Odontophrynus*, and the inner metatarsal tubercle of *Macrogenioglottus*, though enlarged, is not spade-like. Reig (1972) on the other hand made a detailed anatomical comparison of *Macrogenioglottus*, *Odontophrynus*, *Ceratophrys*, and *Bufo*. He concluded that similarities between *Macrogenioglottus* and *Odontophrynus* are convergent and that *Macrogenioglottus* resembles a hypothetical taxon representing the ancestral bufonoid stock. He proposed elevating *Macrogenioglottus* to familial rank placing it together with the Bufonidae, Atelopodidae and Ceratophrynidae in the superfamily Bufonoidea, retaining *Odontophrynus* in the Leptodactyloidea.

Martin (1972) used evidence from laryngeal anatomy and function, and from karyotypes (Bogart 1967) to suggest that *Odontophrynus*, as well as *Macrogenioglottus*, are close to the base of the bufonid-*Atelopus* radiation. He felt that anatomical evidence (Reig 1972) actually supported this conclusion and that Reig's suggestion of convergence between *Macrogenioglottus* and *Odontophrynus* was untenable.

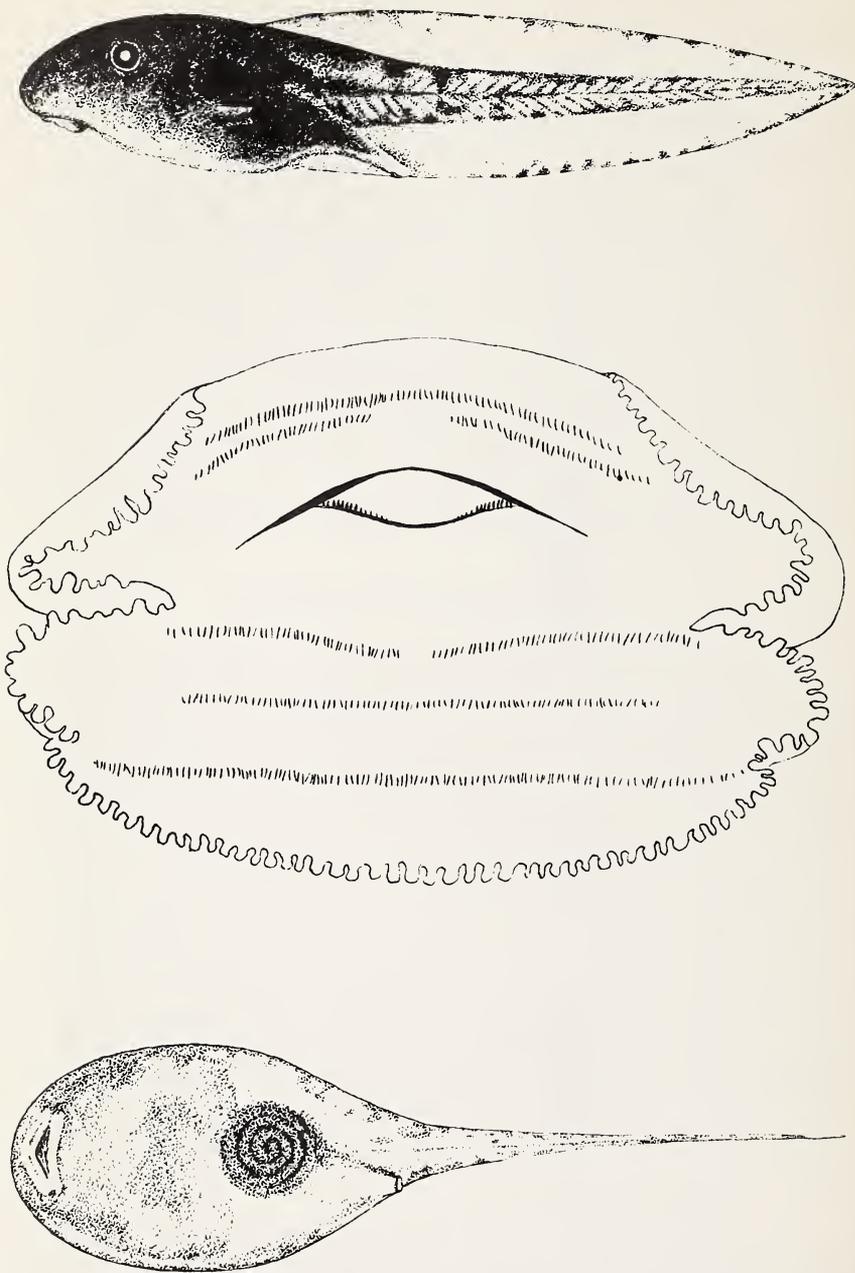


FIGURE 2. Stage 30 larva of *Macrogenioglottus alipioi* Carvalho (LACM 121739).

Heyer (1975) did not examine specimens of *Macrogenioglottus* but using the data provided by Reig (1972) suggested that within the New World Leptodactylidae *Macrogenioglottus* has affinities with *Ceratophrys*, *Lepidobatrachus*, *Odontophrynus* and *Proceratophrys*. He did not consider *Macrogenioglottus* and *Odontophrynus* to be congeneric.

The tadpole of *Macrogenioglottus* is quite similar to those of *Odontophrynus* examined by us and described by Savage and Cei (1965). It has the same tooth row formula, a similar arrangement of labial papillae and the labia are emarginate as in *O. occidentalis* and *O. americanus*.

It differs principally by having a shorter tail (1.24-1.40 standard length in *Macrogenioglottus* versus 1.30-2.15 in *Odontophrynus*) and finer denticles. Viewed laterally, the spiracle opening of *Macrogenioglottus* is clearly at a level dorsal to the mouth, whereas in *Odontophrynus* the spiracle opening is at the same level as the mouth. There appears to be confusion regarding the position of the vent in *Odontophrynus*. Savage and Cei (1965) stated that it is median. Lynch (1971:26) called the vent dextral for the genus *Odontophrynus* but gave a median vent as a character diagnostic for the tribe Odontophrynini (Lynch 1971:131). After examining tadpoles of *Odontophrynus americanus* (LACM 28060), *O. cultripes* (LACM 28059), and *O. occidentalis* (LACM 28068), we consider all to be weakly dextral. Regardless of whether the vent of *Odontophrynus* is considered median or dextral, it is clearly less extremely dextral than the vent of *Macrogenioglottus*.

The mating calls of *Odontophrynus americanus* and *O. occidentalis* have been described by Barrio (1964). These calls have similarities to that of *Macrogenioglottus* in consisting of several unmodulated notes repeated at regular intervals and in having a dominant frequency between 400-1200 hz. The call of *O. occidentalis* is least similar since it has a very short interval between the notes (about .04 seconds) and is thus a trill. The inter-note interval of *O. americanus* (about 0.4 seconds) is closer to that of *Macrogenioglottus*. Both *Odontophrynus* species differ from *Macrogenioglottus* in producing calls with complex harmonics. Of the two, *O. americanus* is again the closer to *Macrogenioglottus* by having a less accentuated harmonic structure, suggesting that the pulse rate is similar to that of *Macrogenioglottus*.

In summary, we feel that the weight of taxonomic evidence indicates a close relationship between *Macrogenioglottus* and *Odontophrynus* and that new evidence from larval morphology and mating call support this conclusion. However, to include *Macrogenioglottus* in the genus *Odontophrynus*, as presently known, would seem to violate the homogeneity traditionally expected of a genus of four or five species.

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## RESUMO

O comportamento nupcial, o grito nupcial e a morfologia larval são descritos para o anuro *Macrogenioglottus alipioi* Carvalho (Leptodactylidae). Na Reserva Nova Lombardia, Santa Teresa, Espírito Santo, Brazil, o cruzamento ocorre em pequenas lagoas formadas pelo transbordamento dos correços durante a estação chuvosa. O numero de pares que cruzam em cada lagoinha é baixo. Amplexus é axilário. Cada fêmea põe mais do que tres mil ovos, mas esses são distribuídos pela lagoinha em pequenas porções em lugares distintos. O grito nupcial é baixo (frequência 230-800 hz tem força sonora máxima) e é repetido várias vezes. A duração do grito é de .24-.27 segundos e o intervalo entre os gritos é de .54-.58 segundos. O girino é semelhante ao girino de *Odontophrynus*, mas existem diferenças na localização do espiráculo e do anus. Observações no laboratório e o exame de conteúdos estomacais indicam que os adultos alimentam-se de caracois e minhocas. Tanto o grito nupcial como a morfologia do girino de *Macrogenioglottus* são semelhantes aos de *Odontophrynus*, mas diferenças na morfologia adulta exigem que se os mantenham em gêneros separados.

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A NEOGENE SECTION  
NORTHEASTERN SAN CLEMENTE ISLAND, CALIFORNIA



By TAKEO SUSUKI AND CAROL J. STADUM

NATURAL HISTORY MUSEUM OF LOS ANGELES COUNTY

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# A NEOGENE SECTION, NORTHEASTERN SAN CLEMENTE ISLAND, CALIFORNIA<sup>1</sup>

By TAKEO SUSUKI<sup>2</sup> AND CAROL J. STADUM<sup>3</sup>

**ABSTRACT:** A discontinuous section of Miocene, Pliocene, Pleistocene, and Recent sediments overlies rhyolite 0.9 to 2.5 kilometers south of the Naval Ordinance Test Station Pier in the area of Randall Blockhouse, northeastern San Clemente Island, Los Angeles County, California. Poorly consolidated orange sandstone containing the Miocene mollusk *Pecten (Amussiopecten) lompocensis* Arnold and marine limestone lenses, grades upward into diatomaceous shale equivalent to the Miocene Monterey Formation. Unconformably overlying the Miocene units are Pliocene bioclastic sediments containing the mollusks (*Pecten*) (*P.*) *bellus* (Conrad) and *Pecten (Patinopecten) healeyi sanclementensis* n. subsp. Isolated outcrops of Pleistocene sand, containing a molluscan fauna, correlate with the Palos Verdes Sand of the Los Angeles Basin. An occurrence of a desmostylid tooth is reported and illustrated.

## INTRODUCTION

San Clemente Island, the southernmost Channel Island off the southern California coast, is approximately 96 km south and west of Long Beach. (Figs. 1,2) The elongate island, extending northwest to southeast, is 35 km long and 2 km to 6.4 km wide. Sediments cover the slightly tilted and gently domed block, which is composed of lava flows, tuffs, and breccias that have been dated at about 15.7 million years (Merifield and others 1971). More than twenty marine terraces are exposed on the western slope of the island, while the eastern flank rises steeply from the northwest trending San Clemente fault.

During a visit to the island in April, 1975, an outcrop of Pliocene biosediments was located in a discontinuous Neogene section by the junior author. The occurrence of these strata was reported by Stadum and Susuki (1976) as containing mullusks and brachiopods, interbedded in sediments composed predominantly of bryozoans, foraminifers and echinoid spines of Pliocene age and the authors' findings were subsequently confirmed in a later publication by Vedder and Moore (1976). The only Channel Island known to contain similar age strata is Santa Cruz Island (Weaver and Myer 1969). An extensive field investigation was undertaken in July and November, 1975, to determine the areal extent of the discontinuous Neogene section. The Neogene

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

WARREN O. ADDICOTT

JERE H. LIPPS

EDWARD C. WILSON

<sup>2</sup>Research Associate in Invertebrate Paleontology, Natural History Museum of Los Angeles County, and Department of Geology, University of California, Los Angeles, California, 90024.

<sup>3</sup>Huntington Beach High School, 1905 Main Street, Huntington Beach, California, 92648.

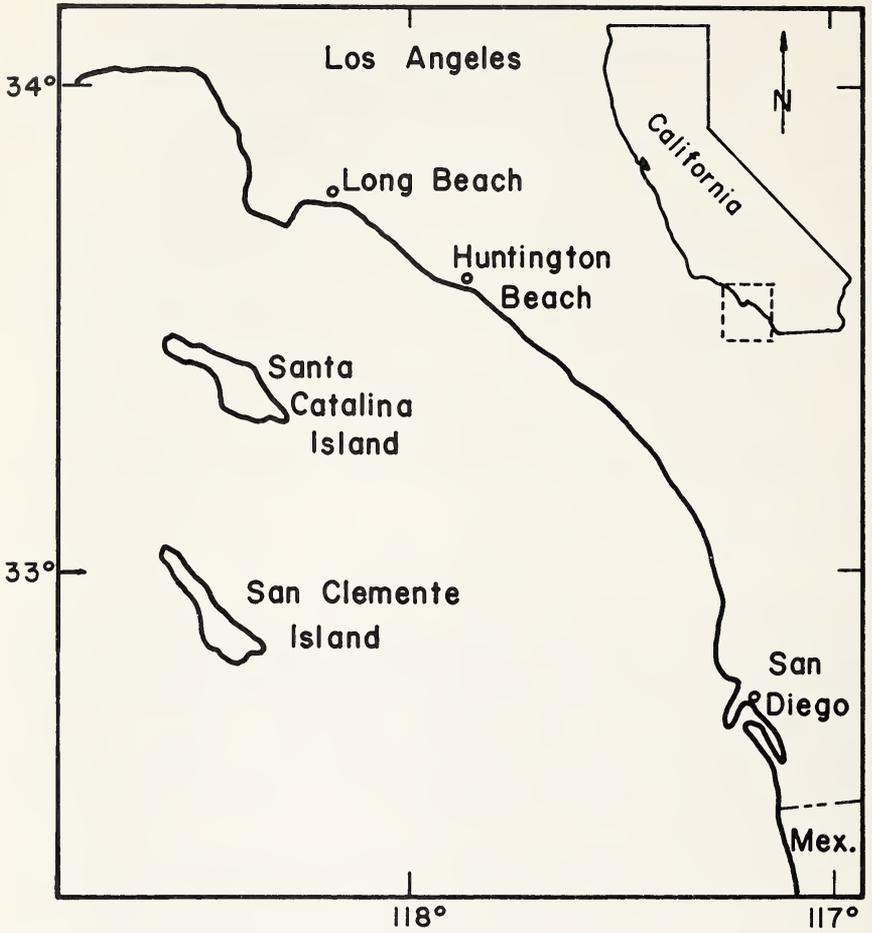


FIGURE 1. Index map showing general location of San Clemente Island.

marine mollusks from northeast San Clemente Island are summarized and a new Pliocene subspecies is described and illustrated.

The specimens are deposited in the paleontology collection, Department of Geology, University of California, Los Angeles.

## PREVIOUS GEOLOGIC INVESTIGATIONS

The earliest publication to describe the San Clemente Island lithology was Cooper (1865). This report stated that the "island form is that of a terraced table" and that the rocks are composed almost entirely of basalt. He implied that the scarcity of fossils was apparently due to lack of marine sediments. Lawson (1893) discussed the physiography in detail and mentioned fossiliferous white limestone which, he thought, was equivalent to the mainland Miocene coastal deposits. Smith (1898) recognized that a portion of the island was composed of Miocene sandstone, shale, and limestone with overlying sediments which were post-Pliocene in Age. Olmsted (1958) distinguished the lower sedimentary unit as middle Miocene and the unconsolidated sand deposits as Pleistocene (?).

Mitchell and Lipps (1965) collected numerous Miocene marine vertebrates, pelecypods, algae, and microorganisms from the Chalk Canyon area (Horse Cove) and two mid-island basins. They stated that an interval of geologic history "from about the end of the middle Miocene to about 500,000 years or so ago" is missing. Oceanographic surveys by Ridlon (1968; 1969; 1972) found middle Miocene sedimentary rocks, post-Miocene sediments of undetermined age, and Holocene surficial sediments offshore near Eel Point. Merifield and others (1971) emphasized the petrography and structure and volcanic rocks on the central part of the island, and noted the presence of Miocene sediments and Quaternary beach sand. Most recently, Vedder and others (1975), and Vedder and Moore (1976) discussed Miocene and Pliocene biostratigraphy and paleontology of the island. These publications did not include the Neogene sediments south of Randall Blockhouse in sections RS-2 and RS-3 of this paper.

## STRATIGRAPHY

### INTRODUCTION

The authors have used abbreviations for four sections of Neogene sediments exposed near Randall Blockhouse, an observation structure and lighthouse about 900 m south of NOTS (Naval Ordinance Test Station) Pier. Neogene sediments overlie rhyolite and are exposed in gullies northwest, west and south of Randall Blockhouse. The letters "RS" refer to "Randall Section", with the number indicating the location of outcrop (Fig. 3).

RS-1 = Pliocene sediments in roadcut above Randall Blockhouse and a ravine just to the west of the roadcut. (includes localities 6316, 6318 and 6320).

RS-2 = Miocene, Pliocene and Pleistocene in a steep gully about 213 m south of Randall Blockhouse. (includes localities 6321 and 6327).

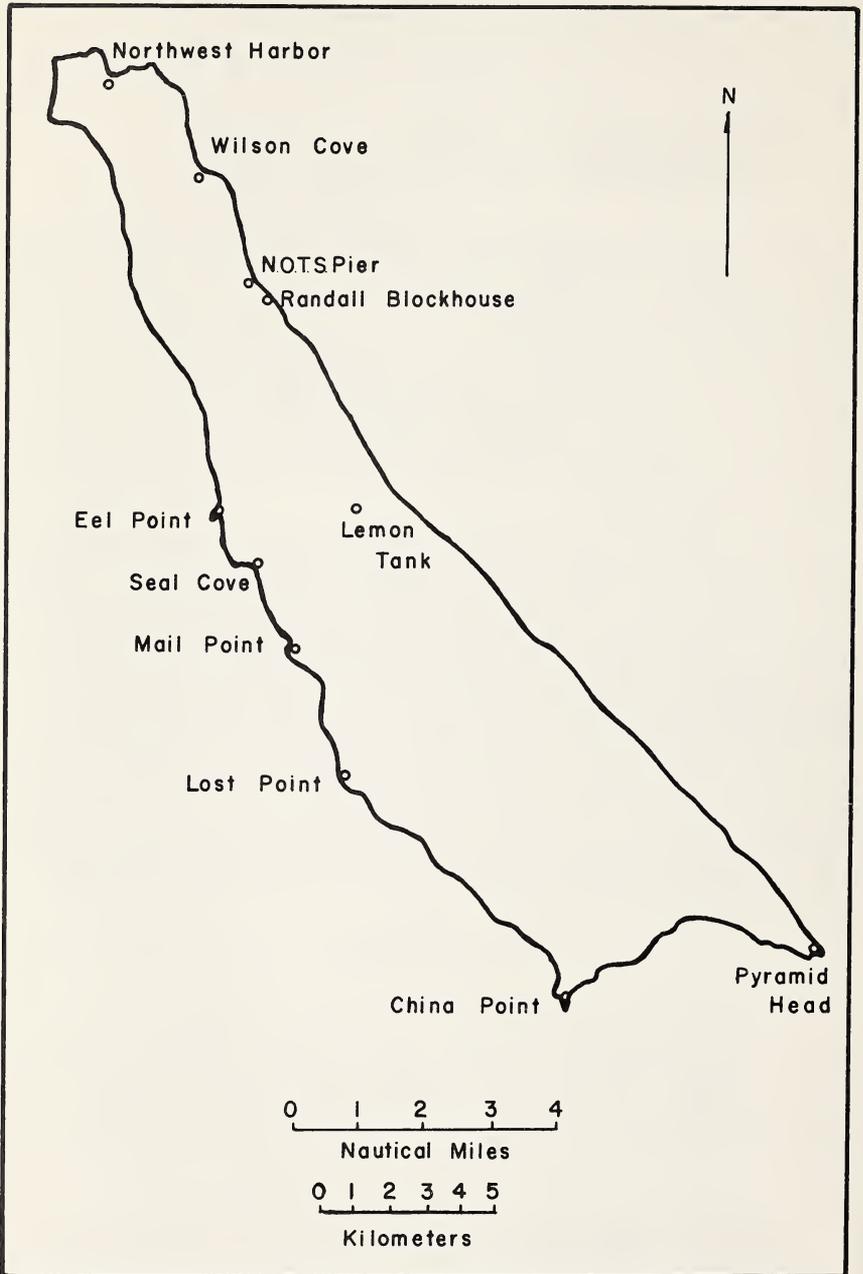


FIGURE 2. Index map of San Clemente Island showing some of the prominent landmarks.

RS-3 = Miocene beds about 1525 m southeast of Randall Blockhouse. (locality 6317).

RS-4 = Miocene strata about 1585 m north and slightly west of NOTS Pier.

#### MIOCENE SANDSTONE

The base of the Miocene sedimentary sequence is a coarse, poorly-consolidated, unfossiliferous, dark-gray volcanic sandstone overlying rhyolite flow lava. The basal sandstone is best developed at RS-3 (Fig. 6) with a maximum thickness of approximately 1.2 m which thins northward to about 0.3 m at RS-2, within a distance of about 660 m. This basal sandstone was not recognized by Vedder and Moore (1976) from the NOTS Pier area. They reported shale and claystone lying unconformably on the rhyolite.

Grading upward from the basal volcanic sandstone is a prominent marker bed of loosely-consolidated to well-indurated, medium to coarse grained, fossiliferous, orange sandstone. This unit is best exposed at RS-3 (4.5 m thick), where the basal 1.2 m has abundant *Pecten* (*Amussiopecten*) *lompocensis* Arnold (Figs. 12-17). Echinoid spines, rare gastropod nodes similar to those of the genus *Trophon*, marine mammal bones and teeth, shark teeth, and fish bones occur commonly throughout the sandstone. At section RS-4, where the orange sand is approximately 1.5 m thick, only a few diagnostic fragments of *P. (A.) lompocensis* were found. Other equivalent localities were reported by Olmsted (1958) from the central island area, including his locality F-3 which contains fragments of *Chlamys* (*Lyropecten*) *crassicardo* (Conrad), and his locality F-2 from which he reported "abundant shell fragments, chiefly pectinids, and scattered mammalian bones." Vedder and Moore (1976) reported *Lyropecten crassicardo* (Conrad), *Amussiopecten* cf. *A. vanvlecki* (Arnold), and *Crassostrea* cf. *C. freudenbergi* (Hertlein and Jordan) in equivalent beds from the China Canyon section, USGS loc. M6505.

Near the base of the orange sandstone are dense limestone lenses containing *Ostrea* sp. with other unidentifiable shell fragments. These lenses have been observed on the north wall of the most southerly exposure at RS-3, and near the pier at Wilson Cove. Olmsted (1958) reported limestone at his locality F-3, overlying "gritty andesitic sandstone about 2.5 m thick that in turn overlies a flow of platy-jointed andesite." Calcarene deposits overlying andesite flow in China Canyon (Vedder and Moore 1976) appear to be similar to limestone lenses at RS-3 and Wilson Cove. Bramlette (1946) established limestone "reef" structures at the base of the Monterey Formation, generally as a boundary between lower and middle Miocene sediments. Similar middle Miocene structures are found locally in the Palos Verdes Hills areas (Bramlette 1946) and in southwestern Orange County (Morton and others 1974).

The authors collected a large, shattered desmostyloid tooth (Figs. 27, 28, 29) from a grayish sandstone (loc. 6363) about a meter above beds containing *P. (A.) lompocensis* and stratigraphically below the silty diatomaceous shale. The tooth was examined by L. G. Barnes, Los Angeles County Museum of Natural History, who suggested that the specimen could be *Paleoparadoxia tabatai*, whose characteristic cingulae have been worn off (personal communication, Mar. 24, 1977).

## MIOCENE DIATOMACEOUS SHALE

The diatomaceous shale member is probably the most widespread sedimentary unit within the area investigated. Vedder and others (1975) and Vedder and Moore (1976) have correlated this unit with the middle Miocene Monterey Formation, locally found in the Palos Verdes Hills, San Joaquin Hills, and Capistrano syncline. The representative section is exposed at RS-3 with a thickness of about 18 m and conformably overlying orange sand which becomes finer and grades upward into diatomaceous shale. The shale is interbedded with several layers (about 7 cm thick) of gray, finely laminated chert with abundant fish scales. Above the chert layers, four phosphate nodule layers (each about 2.5 cm thick) are intercalated with the shale. A bluish, unaltered vitric ash layer (15 cm thick) occurs near the top of the unit. Fish remains, shark teeth, and marine mammal bones and teeth are common through the shale.

Elsewhere, the shale extends north and south of NOTS Pier, and is exposed at RS-2. More extensive sections, as much as 90 meters in thickness (Mitchell and Lipps 1965), are exposed on the southern part of the island. Vedder and Moore (1976) extensively examined the Horse Cove and China Canyon diatomaceous deposits, which they suggested resemble parts of the Monterey Shale exposed at Newport Bay and in the Capistrano syncline.

The depositional sequence of orange sand with limestone lenses overlain by diatomaceous shale containing chert, phosphate nodules, and vitric ash layers is equivalent to the depositional sequence of middle Miocene units in the El Toro and San Joaquin Hills area of Orange County (Morton and others 1974; Stadum 1975).

## PLIOCENE BIOGENIC SEDIMENTS

The Pliocene bioclastic outcrops appear to be restricted to the eastern flank of the central island region. The basal bed is an unsorted, thin, pebble to cobble conglomerate, composed of volcanic clasts unconformably overlying the Miocene diatomaceous shale. A complete section, exposed in a small ravine several hundred meters south of RS-1, is approximately 30 m thick. Although the bottom and top contacts are not visible, a better exposed section is in a roadcut to Randall Blockhouse (RS-1) (Fig. 9). Pliocene sediments are also present at Lemon Tank Reservoir (Vedder and Moore 1976) unconformably overlying Miocene sandstone on the northwest wall. Vedder and Moore (1976) collected well-preserved *P. bellus*, *P. healeyi*, moulds of minute gastropods *Alyania* and *Bittium*, and other fossils from a truncated calcarenite remnant at USGS loc. M6501 at Lemon Tank Reservoir. About one hundred m east of USGS loc. M6501, the authors found mixed Pliocene-Pleistocene sands containing the following species: *Glycymeris (Axinola) growingki* Dall, *Cyclocardia* cf. *C. ventricosa* Gould, *Pseudocardium* sp., *Calliostoma* cf. *C. gemmulatum* Carpenter, *Calliostoma* cf. *C. annulatum* Martyn, *Architectonica* cf. *A. nobilis* Röding, *Haliotis* sp., *Opalia (O.) wroblewskyi* (Mörch), *Terebratalia* cf. *T. occidentalis* Dall, *Laqueus vancouveriensis diegensis* Hertlein and Grant, and *Paracyathus* cf. *P. stearnsii* Verrill.

Biogenic detritus and shells compose 95% of the gently dipping, massive, coarse Pliocene strata. Where firmly cemented, the chalky-colored biolith forms noticeable

outcrops with rounded, wave-cut cavities (Fig. 11) greater than a meter in diameter. There are two significant conglomerate beds (Fig. 10), with a thickness of 0.30 to 1.0 M composed of dacite, andesite, and rhyolite clasts.

The poorly-sorted bioclastic sediments are predominantly bryozoans, foraminifers, and echinoid spines. Within this unit, there are four fossiliferous layers containing the Pliocene guide fossil *Pecten (P.) bellus* (Conrad) and a new subspecies of *Pecten (Patinopecten) healeyi* Arnold. Other species include *Pecten* cf. *P. (P.) lecontei* Arnold, *Chlamys (C.) opuntia* Dall, *Pododesmus macroschisma* Deshayes, *Mytilus* sp., *Anomia peruviana* d'Orbigny, *Hinnites* sp., *Opalia (O.) varicostata* Stearns, *Epitonium (Nitidiscala)* cf. *E. (N.) indianorum* (Carpenter), and distinctive layers of the brachiopods (Fig. 8) *Laqueus californianus* Koch, *L. vancouveriensis diegensis* Hertlein and Grant, and *Terebratalia hemphilli* Dall. All invertebrates are well-preserved. Brachiopods and pelecypods generally are articulated and faintly retain their original colors.

Although similar assemblages are found in Pliocene marine deposits throughout southern California (Pico Member of the Fernando Formation in the Ventura and Los Angeles Basins; Santa Barbara Formation in the Ventura Basin; "San Diego" Formation in the western Santa Monica Mountains; Fernando Formation in the Palos Verdes Hills and Orange County; and Niguel Formation in the San Joaquin Hills) the lithology and fossils of the San Clemente Island Pliocene strata appear to be most similar to the San Diego Formation in coastal San Diego County. Hertlein and Grant (1944) described the San Diego Formation as deposits containing layers of conglomerates and lacking fine sediments "which indicates a water depth from low tide to possibly fifty fathoms." They also noted the occurrence of pockets, seams, and rare beds of nearly pure white marl in exposures of the San Diego Formation suggesting lithologic similarity to the San Clemente Island Pliocene.

In a more recent report, Hertlein and Grant (1960) listed *Pecten (P.) bellus*, *Pecten (Patinopecten) healeyi*, *Chlamys (C.) opuntia*, *Laqueus californianus*, *L. vancouveriensis diegensis*, bryozoans, and echinoids from the San Diego Formation exposed at Pacific Beach. The report stated that species of the brachiopod genus *Laqueus* (which is abundant in San Clemente Island Pliocene sediments) "occur at moderate depths on clear sea bottoms free of mud, and a greater number occur in warm rather than cold water." By comparing the similar fauna and lithology of the San Diego Formation with San Clemente Island Pliocene sediments, the authors suggest that the strata were deposited in a clear, sublittoral environment that was slightly warmer than at present.

Olmsted (1958) separated the younger deposits into Older Sand (Pleistocene) and Younger Sand (Recent). He designated the older deposits as chiefly old dunes with beach sand and lagoonal deposits. He stated that the distinction between the flat-lying sandy Miocene beds overlain by older Pleistocene sand deposits "is difficult principally in the large area centered at 7 km south-southeast of Wilson Cove." This large area is the general location of the gently dipping Pliocene bioclastic sediments (RS-1, RS-2), which may be the "flat-lying sandy Miocene beds" mentioned by Olmsted.

## PLEISTOCENE MARINE SEDIMENTS

The Pleistocene consists of gray to buff color, fossiliferous sand with a basal conglomerate, that differs in its relationship with underlying beds from locality to locality. At RS-1 (loc. 6320) and RS-2 (loc. 6327), Pleistocene sand unconformably overlies Pliocene sediments; about 800 m west of Wilson Cove and at NOTS Pier, Pleistocene sand is unconformable on Miocene shale (loc. 6326); several hundred m south of Wilson Cove (loc. 6324), it rests unconformably upon volcanic rocks; east of Northwest Harbor near the northeast side of the new airfield, the underlying unit is a volcanic conglomerate of unknown age (loc. 6323). The mollusks, representing a littoral and a sublittoral environment, are found in loosely consolidated sand except at localities 6320, 6324, and 6327, where they occur between and attached to clasts in the basal conglomerate. *Codakia (Epilucina) californica* (Conrad) was the most commonly collected species from each locality.

The following is a list of Pleistocene fossils collected from six localities. This assemblage can be correlated with the late Pleistocene Palos Verdes Sand fauna of the Los Angeles Basin.

## UCLA locality 6320

- Codakia (Epilucina) californica* (Conrad)
- Tranzenella tantilla* (Gould)
- Acmaea (Acmaea) mitra* Eschscholtz
- Acmaea (Collisella) scabra* Gould
- Hipponix tumens* Carpenter

## UCLA locality 6323

- Codakia (Epilucina) californica* (Conrad)
- Glans subquadrata* (Carpenter)
- Acmaea (Collisella) digitalis* Eschscholtz
- Acmaea (C.) pelta nacelloides* Dall
- Acmaea (C.) scabra* Gould
- Acmaea (C.) scutum* Eschscholtz
- Fissurella volcano* Reeve
- Tegula funebris* (A. Adams)
- Littorina planaxis* Philippi
- Hipponix antiquatus* (Linnaeus)
- Hipponix tumens* Carpenter
- Serpulorbis squamigerus* (Carpenter)
- Bittium* sp.
- Amphissa versicolor* Dall
- Fusinus barbarentis* (Trask)
- Olivella biplicata* (Sowerby)
- Trimusculus reticulata* (Sowerby)
- Ischnochiton* sp.

## UCLA locality 6324

- Codakis (Epilucina) californica* (Conrad)
- Fissurella volcano* Reeve

*Tegula ligulata* Menke  
*Hipponix antiquatus* (Linnaeus)  
*Hipponix tumens* Carpenter  
*Thais (Stramonita) biserialis* (Blainville)  
*Mitra idae* Melvill  
*Hyalina californica* (Tomlin)  
*Conus californicus* Hinds

## UCLA locality 6325

*Codakia (Epilucina) californica* (Conrad)  
*Acmaea (Collisella) limulata* Carpenter  
*Acmaea (C.) scabra* Gould  
*Acmaea (C.) scutum* Eschscholtz  
*Haliotis cracherodii* Leach  
*Megathura crenulata* (Sowerby)  
*Fissurella volcano* Reeve  
*Tegula funebris* (A. Adams)  
*Norrisia norrisi* (Sowerby)  
*Littorina planaxis* Philippi  
*Hipponix antiquatus* Linnaeus  
*Hipponix tumens* Carpenter  
*Serpulorbis squamigerus* (Carpenter)  
*Bursa californica* Hinds  
*Amphissa versicolor* Dall  
*Mitra idae* Melville  
*Hyalina californica* (Tomlin)  
*Conus californicus* Hinds

## UCLA locality 6326

*Codakia (Epilucina) californica* (Conrad)  
*Fissurella volcano* Reeve  
*Astraea (Pomaulax) undosa* (Wood)  
*Tegula funebris* (A. Adams)  
*Hipponix tumens* Carpenter  
*Neverita reclusiana* (Deshayes)  
*Serpulorbis squamigerus* (Carpenter)  
*Bursa californica* Hinds  
*Thais (Stramonita) biserialis* (Blainville)  
*Mitra idae* Melvill  
*Olivella biplicata* (Sowerby)  
*Conus californicus* Hinds

## UCLA locality 6327

*Codakia (Epilucina) californica* (Conrad)  
*Transenella tantilla* (Gould)  
*Acmaea (Acmaea) mitra* Eschscholtz  
*Acmaea (Collisella) limatula* Carpenter  
*Acmaea (C.) scabra* Gould

*Acmaea (C.) scutum* Eschscholtz  
*Fissurella volcano* Reeve  
*Tegula funebris* (A. Adams)  
*Hipponix antiquatus* (Linnaeus)  
*Mitrella carinata gausapata* (Gould)  
*Thais (Stramonita) biserialis* (Blainville)  
*Olivella biplicata* (Sowerby)  
*Conus californicus* Hinds  
*Ischnochiton acrior* Carpenter

#### PLEISTOCENE NON-MARINE SEDIMENTS—RECENT DUNE SAND

Loose, wind-blown sand accumulations cover much of the northern half of the island and in many places contain calcareous and siliceous root sheaths or rhizoconcretions (Fig. 5). Johnson (1967) suggested that all the Channel Islands had supported more vegetation during the early Holocene than at the present. The authors found evidence of calcareous root sheaths forming around living sand-dune plants. Opaline silica seams were common within the sand deposits west of NOTS Pier and near the old airfield (Fig. 3). Numerous Indian midden remains and artifacts were observed in the dune sand.

Olmsted (1958) stated that the maximum thickness of the active and recently active sand dunes is approximately 19 meters, and that the older sand deposits are as much as 40 meters thick west of Wilson Cove (loc. 6326).

### PALEONTOLOGY

#### DESCRIPTION OF NEW SUBSPECIES

##### CLASS BIVALVIA LINNE

##### ORDER PTERIOIDA NEWELL

##### FAMILY PECTINIDAE RAFINESQUE

Type (by subsequent designation, Schmidt 1818): *Ostrea maxima* Linne 1758.

Subgenus *Patinopecten* Dall 1898

Type (original designation): *Pecten caurinus* Gould 1850.

***Pecten (Patinopecten) healeyi Arnold sanclementensis* NEW SUBSPECIES**

GENUS *PECTEN* MÜLLER 1776

*Diagnosis.*—Distinguishable by the much finer and greater number of closely and equally spaced ribs on the left valve; ribs narrow, flat, interspaces shallow and narrow on right valve; right valve gently but evenly convex; left valve slightly convex with anterior and posterior margins flat to somewhat concave; poorly developed ribbing on umbonal area of both valves.

*Description.*—Shell inequivalve, wider than high, right valve slightly more convex than left valve; *Right valve*—slightly but evenly convex; margins adjacent to ears ornamented by numerous fine radial ribs prior to beginning of primary ribs; approximately thirty, low rectangular, irregular radial ribs separated by narrower, primary



mens are found articulated, but complete specimens are difficult to collect. Each shell is fractured and it is necessary to coat the surface with an adhesive, prior to removing it from the coarse sandstone matrix.

*P. (A.) lomdocensis* is often confused with *Pecten (Amussiopecten) vanvlecki* Arnold, (Arnold 1907) and the two species are not readily separable unless the external and internal surfaces are well preserved. However, there are several helpful distinguishing features, which include the development of the external radial ribs and the spacing of the internal ribs. On the right valve of *P. (A.) lomdocensis*, the external radial ribs are poorly defined and the ribs are paired internally. On the left valve, the external ribs are better developed and the internal ribs are not paired but equally spaced with the interspaces. In *P. (A.) vanvlecki*, the external ribs on both valves are better developed but internally, the paired ribs occur on the left valve and they are equally spaced in the right valve.

Masuda (1971), in his study of *Amussiopecten*, stated that *P. (A.) vanvlecki* is easily distinguishable from the frequently confused species *P. (A.) lomdocensis* by "its rather thick shell, squarish, low, flatly round-topped radial ribs tending to become obsolete towards the ventral and lateral margins, paired internal ribs developed at lower part and larger and angulate auricles." Masuda (1971) did not make any distinction as to which valve is characterized by the paired internal ribs.

The occurrence of fragmentary specimens of *Amussiopecten* cf. *A. vanvlecki* is reported by Vedder and Moore (1976) from China Canyon in the southern end of San Clemente Island in association with *Lyropecten crassicardo* (Conrad) and *Crassostrea* cf. *C. freudenbergi* (Hertlein and Jordan), USGS loc. M6505. According to Vedder and Moore (1976), these fossils are imbedded in a fine-to coarse-grained calcarenite which differs considerably in lithology from the orange sandstone in which *P. (A.) lomdocensis* occurs so commonly (UCLA loc. 6317, which apparently has not been visited by previous investigators).

## CONCLUSIONS

Unusually well-preserved marine mollusca are found in Neogene sedimentary units on San Clemente Island. Miocene sands contain pecten beds and oyster lenses which suggest a shallow, near-shore environment. Diatomaceous shales, overlying these sands, have been correlated with the coastal Monterey Formation and are evidence of deep submergence during the middle Miocene. These Miocene deposits appear to have accumulated in the same depositional basin as the Monterey Formation in the southeastern Los Angeles Basin and represent a comparable environment.

The overlying Pliocene strata contain abundant brachiopods, bryozoans, and pectens with conglomerate layers which are indicative of shallow water and uplift of the island block. The small fauna includes diagnostic Pliocene species which correlate with the *Pecten (P.) healeyi* zone (upper Pliocene) throughout southern California.

Abundant collections of Pleistocene littoral and sublittoral mollusks in sand deposits and among volcanic boulders continue to denote elevation of the island. The formation of marine terraces and the deposition of dune sand with rhizoconcretions mark the emergence of the island during the Holocene.

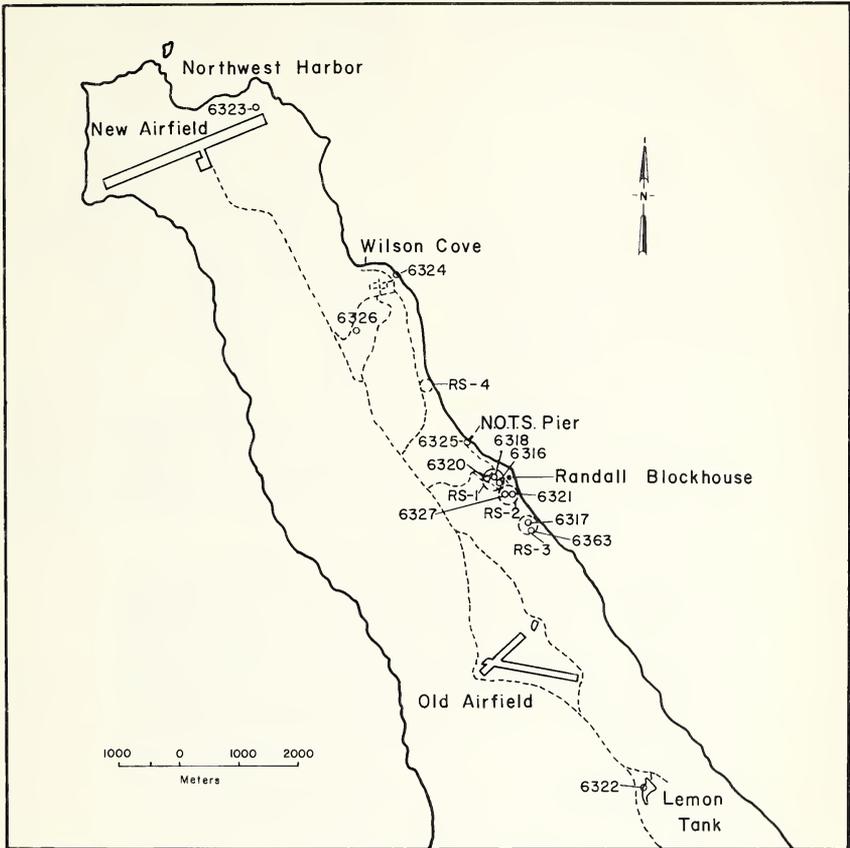


FIGURE 3. Map of northern and part of central San Clemente Island showing fossil localities and RS-sections.

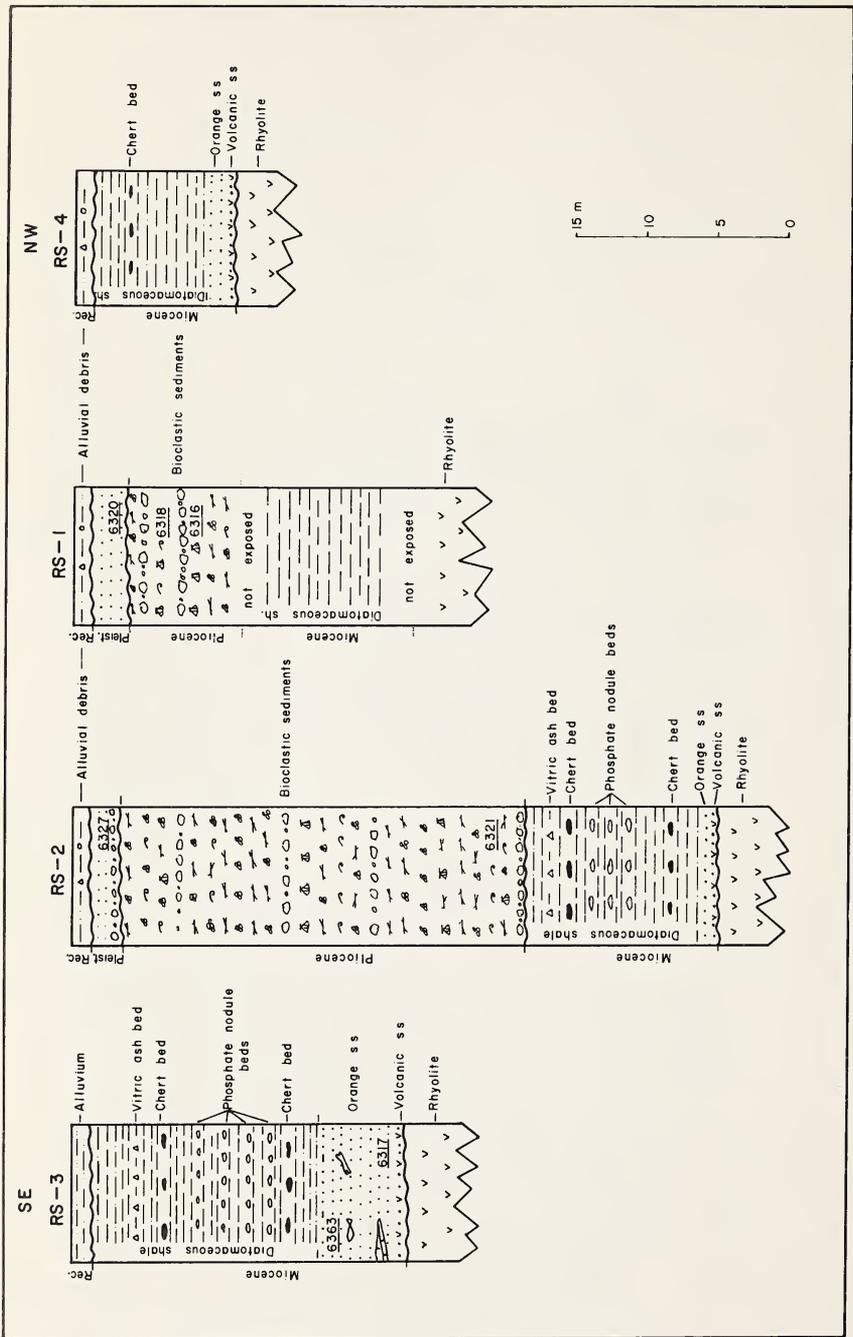


FIGURE 4. A comparison of generalized stratigraphic columns, Randall Blockhouse Area.



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FIGURES 5-8. (5.) Rhizoconcretions in post-Pleistocene sands. (6.) Miocene section at RS-3, the darker unit just above the collectors is the orange sandstone. (7.) *Pecten (Amussiopecten) lompoensis* occurring in the orange sandstone, UCLA loc. 6317. Icepick points to a bone. (8.) Brachiopod bed exposed in roadcut at RS-1.



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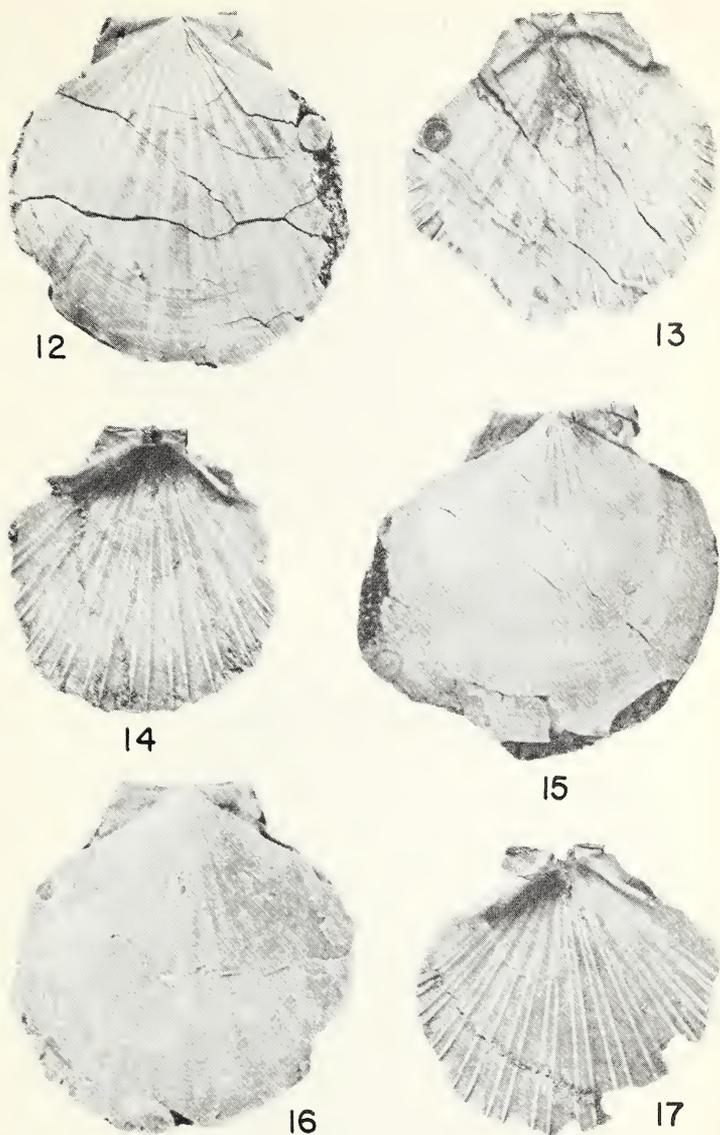


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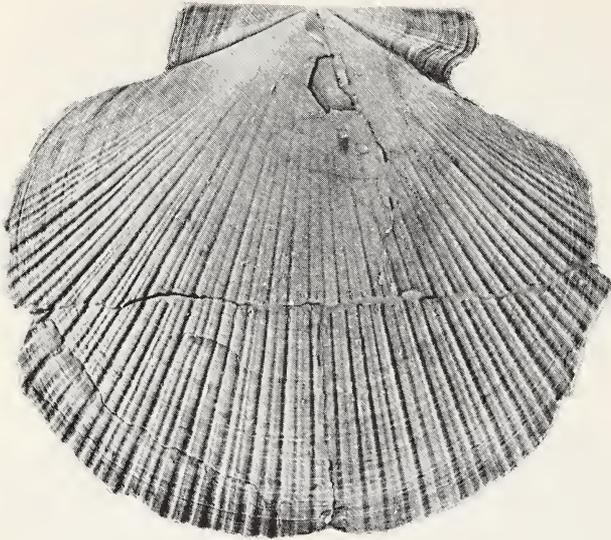


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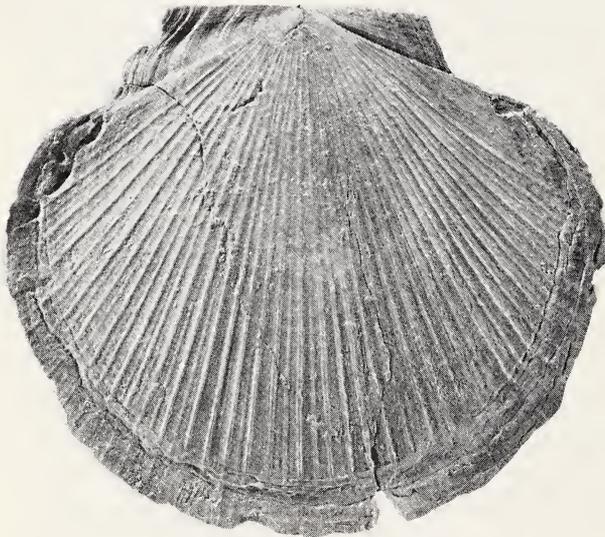
FIGURES 9-11. (9.) Soil-covered Pliocene sediments exposed in roadcut just above Randall Blockhouse, section RS-1. (10.) Characteristic conglomerate layer (middle of photograph) in Pliocene strata. (11.) Rounded, wave-cut cavities in Pliocene strata at RS-2.



FIGURES 12-17. (12.) *Pecten (Amusiopecten) lompocensis* Arnold. left valve. external view. height - 64 mm. length - 64 mm. UCLA cat no. 38788. UCLA loc. 6317. (approx.  $\times 7/10$ ). (13.) *Pecten (Amusiopecten) lompocensis* Arnold. left valve. internal view. height - 70 mm. length - 70 mm. UCLA cat no. 38896. UCLA loc. 6317. (approx.  $\times 3/5$ ). (14.) *Pecten (Amusiopecten) lompocensis* Arnold. right valve. internal view. height - 44 mm. length - 41 mm. UCLA cat no. 38895. UCLA loc. 6317. (approx.  $\times 4/5$ ). (15.) *Pecten (Amusiopecten) lompocensis* Arnold. right valve. external view. height - 95 mm. length - 100 mm. UCLA cat no. 38789. UCLA loc. 6317. (approx.  $\times 4/2$ ). (16.) *Pecten (Amusiopecten) lompocensis* Arnold. right valve. external view. height - 64 mm. length - 64 mm. UCLA cat no. 38788. UCLA loc. 6317. (approx.  $\times 7/10$ ). (17.) *Pecten (Amusiopecten) lompocensis* Arnold. right valve. internal view. height - 44 mm. length - 47 mm. UCLA cat no. 38897. UCLA loc. 6317. (approx.  $\times 4/5$ ).

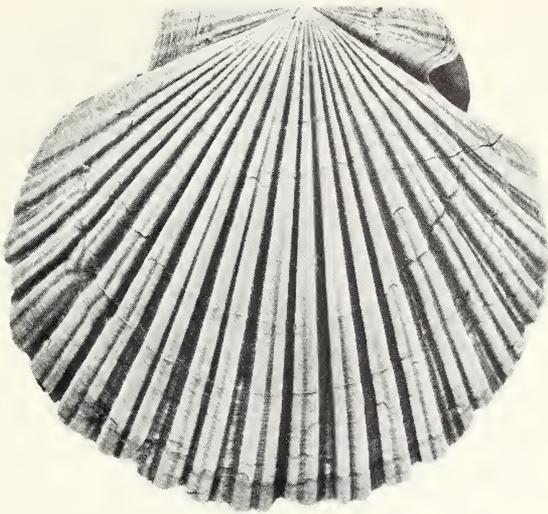


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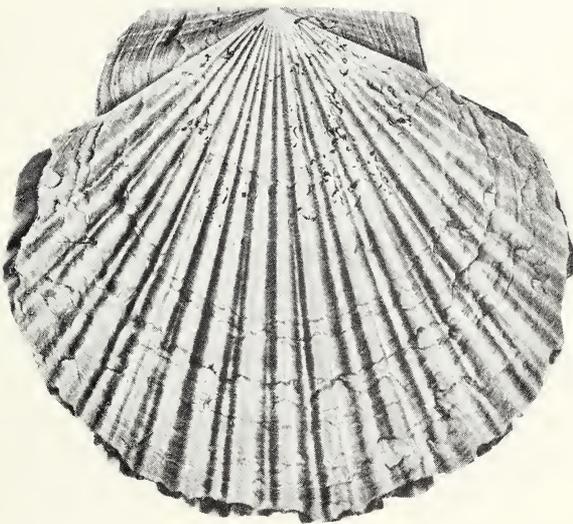


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FIGURES 18-19. (18.) *Pecten (Patinopecten) healeyi sanclementensis* n. subsp. Syntype. right valve. height - 170 mm. length - 190 mm. UCLA cat no. 38790. UCLA loc. 6316. (approx.  $\times 2/5$ ). (19.) *Pecten (Patinopecten) healeyi sanclementensis* n. subsp. Syntype. left valve. height - 137 mm. length - 150 mm. UCLA cat no. 38791. UCLA loc. 6316. (approx.  $\times 1/2$ ).

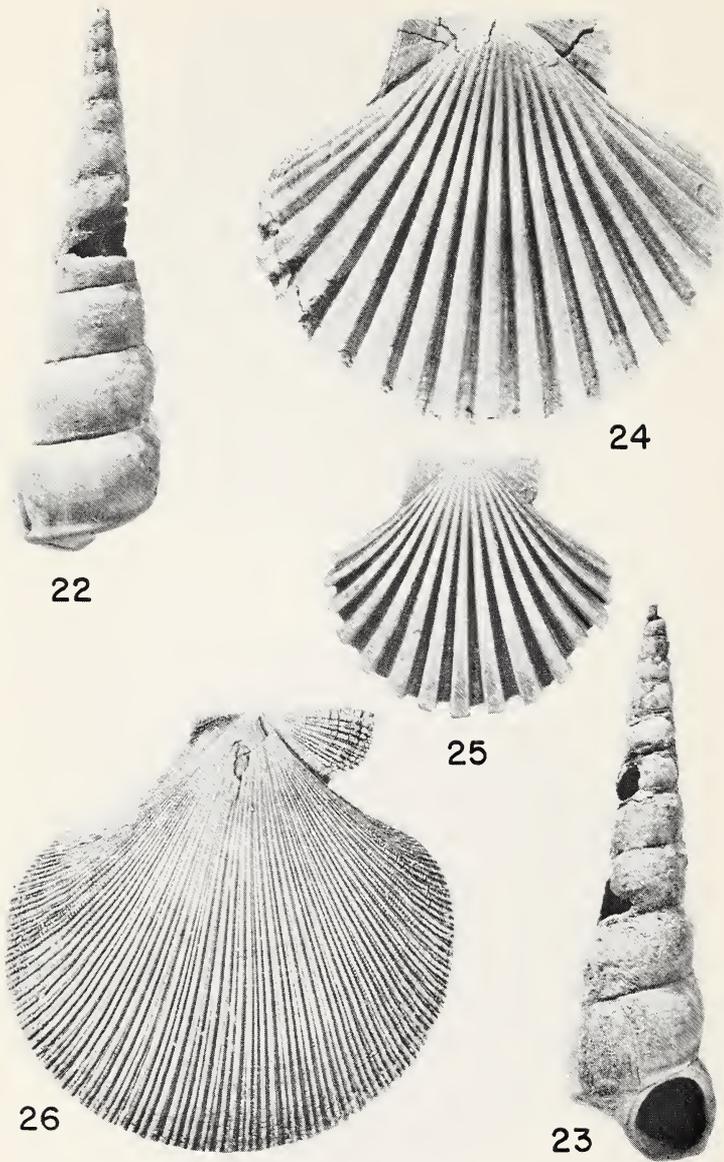


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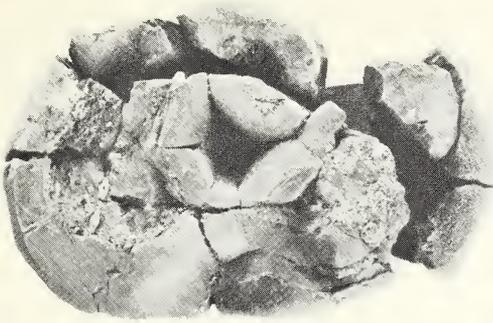


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FIGURES 20-21. (20.) *Pecten (Patinopecten) healeyi* Arnold. Hypotype. right valve. Figured by Hertlein & Grant. 1972 (text-fig. 9A, p. 184). height - 122 mm. length - 130 mm. UCLA cat no. 1950. Pacific Beach, San Diego, California (approx.  $\times \frac{1}{2}$ ) compare with fig. 18. (21.) *Pecten (Patinopecten) healeyi* Arnold. Hypotype. left valve. Figured by Hertlein & Grant. 1972 (text-fig. 9B, p. 184). height - 122 mm. length - 130 mm. UCLA cat no. 1950. Pacific Beach, San Diego, California. (approx.  $\times \frac{1}{2}$ ) compare with fig. 19.



FIGURES 22-26. (22.) *Opalia (Opalia) wroblewskyi* (Mörch), ab-aperture view, height - 81 mm. width - 22 mm. UCLA cat no. 38798. UCLA loc. 6322. (approx.  $\times 9/10$ ). (23.) Same specimen as fig. 22, aperture view. (approx.  $\times 9/10$ ). (24.) *Pecten (Pecten)* cf. *P. (P.) lecontei* Arnold, right valve, height - 60 mm. length - 67 mm. UCLA cat no. 38787. UCLA loc. 6316. (approx.  $\times 9/10$ ). (25.) *Pecten (Pecten) bellus* (Conrad), right valve, height - 39 mm. length - 43 mm. UCLA cat no. 38786. UCLA loc. 6316. (approx.  $\times 9/10$ ). (26.) *Chlamys (Chlamys) opuntia* (Dall), right valve, height - 66 mm. length - 66 mm. UCLA cat no. 38797. UCLA loc. 6316. (approx.  $\times 9/10$ ).



27



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FIGURES 27-29. (27.) Large desmostyloid tooth. occlusal view. UCLA cat no. 57531. UCLA loc. 6363. (approx.  $\times 2$ ) length - 33 mm. width - 22 mm. (28.) Same specimen as fig. 27. end view. (approx.  $\times 2$ ) height - 44 mm. (29.) Same specimen as fig. 27. labial view. (approx.  $\times 2$ ).

## ACKNOWLEDGMENTS

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All illustrations and photographs were prepared by the authors.

## FOSSIL LOCALITY REGISTER

The following locality numbers are those of the paleontology collection, Department of Geology, University of California, Los Angeles. They all were plotted on the U.S. Geological Survey topographic quadrangle of San Clemente Island North (7.5 min., 1950), unless otherwise indicated.

- 6316 - Sediments containing *Pecten (P.) bellus* and *Pecten (P.) healeyi sancllementensis* n. subsp. exposed in both sides of a roadcut, just before last turn to the end of road to Randall Blockhouse (RS-1), approx. 792 m S 42° E of NOTS Pier. (Upper Pliocene).
- 6317 - Loosely consolidated orange sandstone bed containing *Pecten (A.) lompocensis* exposed in a narrow, steep canyon approx. 1524 m S 35° E of NOTS Pier and about 1097 m N 58° E of BM-820 (RS-3). (Middle Miocene)
- 6318 - Well-indurated chalky-colored sediments cropping out on the south side of a narrow ravine containing *Pecten (P.) bellus*, about 213 m west of Randall Blockhouse (RS-1), (Upper Pliocene)
- 6320 - Pleistocene fossils attached to boulders and in the sand between the conglomerate on the southside of a narrow ridge about 427 m S 13° W of Randall Blockhouse (RS-1) and approx. 700 m S 18° W of NOTS Pier. (Upper Pleistocene)
- 6321 - Steep, small gully south of Randall Blockhouse (RS-2), Pliocene section exposed unconformably overlying Miocene shale and underlying Pleistocene conglomerate, about 213 m south of Randall Blockhouse. (Upper Pliocene)
- 6322 - Fossils collected from disturbed (by grading) beds overlying the brownish-orange sandstone on the northwest wall of Canyon (Lemon Tank) just below the top, 365 m east of

- Hill 1185, U.S. Geological Survey topographic quadrangle of San Clemente Island Central (7.5 min., 1950). (Upper Pliocene with some Upper Pleistocene)
- 6323 - Fossils collected from north of northeast end of new airfield, halfway down the slope between upper road to the first wide, flat terrace, 1280 m S 3° E of stream entering Northwest Harbor. (Upper Pleistocene)
- 6324 - Pleistocene along the top edge of sea wall in conglomerate, overlying volcanic rocks, about 455 m S 65° E from the end of Wilson Cove Pier. (Upper Pleistocene)
- 6325 - Pleistocene fossils in conglomerate and loose sand overlying Miocene shale, directly behind building by NOTS Pier. (Upper Pleistocene)
- 6326 - Fossiliferous Pleistocene bed in a shallow cut, lying unconformably on Miocene shale, 365 m S 68° E of Harbor triangulation station 648. (Upper Pleistocene)
- 6327 - Pleistocene fossils in conglomerate unconformably overlying Pliocene sediments in a gully 183 m due south of Randall Blockhouse (RS-2). (Upper Pleistocene)
- 6363 - A large desmostylid tooth collected from a gray sandstone approximately one hundred m south of UCLA loc. 6317, stratigraphically about a meter above beds containing *Pecten (Amussiopecten) lompocensis*.

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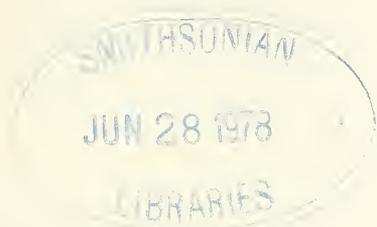
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JUNE 16, 1978

A SYSTEMATIC REVIEW OF THE MEXICAN FROG  
*RANA SIERRAMADRENSIS* TAYLOR

By ROBERT G. WEBB



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A SYSTEMATIC REVIEW OF THE MEXICAN FROG  
*RANA SIERRAMADRENSIS* TAYLOR<sup>1</sup>

By ROBERT G. WEBB<sup>2</sup>

ABSTRACT: The variation of *Rana sierramadrensis* Taylor is discussed. A previously unreported secondary sexual characteristic is the presence of white spinous excrescences on the non-enlarged thumbs, chest and lower jaw of males. The tadpoles are described. *Rana sierramadrensis* is compared with *R. sinaloae* Zweifel. The former is retained in the *R. palmipes* species group, while the latter is transferred to the *R. tarahumarae* group, which is proposed for the inclusion of the Mexican species, *R. tarahumarae*, *R. pustulosa*, *R. sinaloae*, *R. pueblae*, and *R. johni*. *Rana sierramadrensis* is confined to the Sierra Madre del Sur in the Mexican states of Guerrero and Oaxaca, and seems to be most closely related to *Rana maculata*.

INTRODUCTION

*Rana sierramadrensis* is an upland tropical species in southern Mexico that is little known except for a few published locality records. My interest in *R. sierramadrensis* is a by-product of a study of frogs of the *R. pustulosa-tarahumarae* complex and *R. sinaloae* in western Mexico. Zweifel included both *R. sierramadrensis* and *R. sinaloae* in the *R. palmipes* species group (1954), and the two species *R. pustulosa* and *R. tarahumarae* in the *R. boylei* group (1955). In view of speculation that *R. sinaloae* is related to the *R. pustulosa-tarahumarae* complex, most available specimens of *R. sierramadrensis* were examined in order to determine its relationship to *R. sinaloae*.

The "*Rana tarahumarae* group" is proposed for the first time to accommodate the Mexican species *R. tarahumarae*, *R. pustulosa*, *R. sinaloae*, *R. pueblae* and *R. johni*. Biochemical data (Case 1976 and personal communication) suggest that *R. tarahumarae* (only Mexican species studied by Case) is not closely related to the two United States members of Zweifel's *R. boylei* group (1955), *R. boylei* and *R. muscosa*. Those two species also differ from *R. tarahumarae* and the other Mexican species in having two metatarsal tubercles (instead of one), and the larvae having four or more lower rows of teeth (instead of three), and in lacking marginal teeth.

Specimens examined are deposited in the following collections: American Museum of Natural History (AMNH); Field Museum of Natural History (FMNH); Natural History Museum of Los Angeles County (LACM); University of Kansas Museum of

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

ROBERT L. BEZY  
ROY W. MCDIARMID  
JOHN W. WRIGHT  
RICHARD G. ZWEIFEL

<sup>2</sup>Research Associate in Herpetology, Natural History Museum of Los Angeles County, and Department of Biological Sciences, The University of Texas at El Paso, El Paso, Texas 79968

Natural History (KU); The Museum, Michigan State University (MSU); Texas Cooperative Wildlife Collection, Texas A&M University (TCWC); University of Illinois Museum of Natural History (UIMNH); University of Michigan Museum of Zoology (UMMZ); and, National Museum of Natural History (USNM). I thank Richard G. Zweifel for a kodachrome slide and a black-and-white photograph of *Rana maculata* here reproduced in figure 5.

*Rana sierramadrensis* TAYLOR

*Rana sierramadrensis* has always been considered a distinct, monotypic species. There are no known synonyms of *R. sierramadrensis*. In the original description, Taylor (1939:397-398) listed six specimens (3963A, 3963B, 6565, 6566, 6567, and 6568), designating 3963B as the holotype and the remainder as paratypes; these numbers refer to the Edward H. Taylor-Hobart M. Smith private collection (EHT-HMS). Later, Taylor (1944:140) reiterated data about the types. Of the six specimens in the type series, four were subsequently sent to the FMNH and two were donated to the UIMNH. The type material is briefly discussed below.

The holotype (Fig. 1, formerly EHT-HMS 3963B) from "near Agua del Obispo, between Rincón and Cajones, Guerrero, July 1, 1932" is now FMNH 100038. It is a female 88.2 mm SVL and was described in some detail by Taylor (1939:398-399). The other large frog (formerly EHT-HMS 3963A) with the same data of collection as the holotype is UIMNH 27053 (Smith, Langebartel, and Williams 1964:32); a photograph of this paratype, 69.7 mm SVL, was published in the original description (Taylor 1939: Pl. XXIX, Fig. 1). Four small paratypes do not exceed 40 mm SVL.



FIGURE 1. Holotype of *Rana sierramadrensis*, FMNH 100038, from near Agua del Obispo, between Rincón and Cajones, Guerrero, Mexico.

One of them (formerly EHT-HMS 6565 and UIMNH 27054), 38.9 mm SVL from "about 9 km. southwest of Mazatlán, Guerrero (km. 337), July 21, 1936," is now USNM 139724 (Cochran, 1961:76). A small paratype (formerly EHT-HMS 6566), 33.5 mm SVL, from "near Agua del Obispo (km. 350-351), July 24, 1936," is now cataloged as FMNH 102202. The other two paratypes (formerly EHT-HMS 6567 and 6568), 37.0 and 28.8 mm SVL, both from "Agua del Obispo, August 1, 1936," are now cataloged, respectively, as FMNH 102201 and FMNH 103917. Museum locality data associated with some paratypes are slightly different from the localities quoted (above) by Taylor (1939).

#### DESCRIPTION

*Color and pattern.*—The dorsal ground color is brown or bronze-brown. The narrow, dorsolateral folds are usually slightly paler (usually buff, not white) than the ground color, have distinct, but narrow, black, lateral borders, and extend to the sacral region. A prominent white supralabial stripe extends from near the tip of the snout to above the insertion of the forelimb; this white stripe is widest posteriorly (above forelimb insertion) where it is often interrupted forming a posteriormost, white spot. There is a black canthal stripe, black diagonal posttympanic bar, black barlike mark on the anterior surface of the humerus at the insertion of the forelimb, and often a black blotch or barlike mark in the groin. A posttympanic fold is absent; however, the region is often somewhat swollen and a partial fold is discernable in AMNH 52624. Ventrolaterally the body has black markings that form an irregular-bordered, continuous or interrupted band extending from axilla to groin. The femora have narrow, dorsal, dark crossbars (pale interspaces usually three to five times wider), and a coarse pale-dark marbling (mostly dark) on the posterior surfaces. The ventral surface of the legs also has coarse dark marbling resulting mostly from lateral encroachment of pattern. The top of the head, back, and usually the sides of the body are devoid of pattern; occasionally, a few small black dots occur on the back. The ventral surface of the head-body may lack dark marks or smudging (LACM 35054; UIMNH 32444, 52783), but usually the chin-throat, chest and anterior part of the abdomen are dark-smudged and often uniformly dark. The features of color and pattern are most contrasting in young and subadults (Fig. 5) and tend to become obscured in the largest frogs (Fig. 1).

*Sexual dimorphism.*—There seems to be no marked discrepancy in the maximum size attained by males (100 mm SVL, KU 87284) and females (98 mm SVL, TCWC 8546). My examination of large males does not reveal vocal sacs or slits. A previously unreported, secondary sexual character in males is the occurrence of whitish, spinous, nuptial excrescences on the thumb that, at maximal development, extend onto the chest and edge of the lower jaw. All frogs having these spinous excrescences were determined by dissection to be males. There is no pronounced enlargement of the thumb in large males. A cluster of nuptial spines first appears on the joint between the penultimate and antepenultimate phalanges. The white, spinous patch then spreads over the inner, medial surface of the thumb. With further development small excrescences appear on the medial surfaces of the second and third fingers. At maximum

development spinous excrescences also occur on the dorsal surfaces of the first two fingers (and part of the third finger), and on the edge of lower jaw and part of the chest; the excrescences are more dense on the thumb joint than elsewhere (Fig. 2). Spinous patches are not evident until males attain a body length of about 70 mm; thereafter, however, the development and extent of the excrescences does not seem to be directly correlated with size. The smallest male with spinous patches (covering only proximalmost joint of thumb) is 74.2 mm SVL (KU 87280). Two other males, both dissected, of 74.0 (UMMZ 125901) and 84.4 (KU 87283) mm SVL lack excrescences. In contrast, a male of 85.8 mm SVL (UIMNH 52782) shows the most extensive development with white, spinous excrescences on digits, chest and lower jaw (Fig. 2). This non-correlation of size with development of excrescences would seem to reflect a seasonal change with maximum development during the breeding season. If so, the breeding season is prolonged since the two males showing the most extensive development of white excrescences, UIMNH 52782 and KU 87284 of 100.3 mm SVL, were collected on 25 December 1962 and 3 June 1964, respectively.

*Body proportions.*—Four morphometric characters were utilized. The following measurements (mm) were recorded with a dial calipers (abbreviations used in parentheses): snout to vent length (SVL); tibia (tibio-fibula) length from heel to fold of skin on knee (TL); head length from posterior margin of tympanum to tip of snout (HL); head width at widest point, generally at level of posterior margin of tympana (HW). Six proportions of body parts (HW/SVL, HL/SVL, HL/HW, TL/SVL, HL/TL, HW/TL) were plotted against SVL; the resultant data thus reflect relative differences in width of head and length of leg. Ontogenetic variation is variable depending on the ratios utilized. Sexual dimorphism is lacking and the sexes are combined in the analysis of variation. The data are presented in Table 1. The size-group demarcation (60 mm) was initially determined by the inspection of scattergrams that depicted the most pronounced ontogenetic variation in the ratios TL/SVL, HL/TL, and HW/TL.

In the ratio HW/SVL, ontogenetic variation seems to be negligible or the HW increases at a slightly slower rate than the SVL. Ontogenetic variation is somewhat more pronounced in HL/SVL with the HL increasing at a slightly slower rate than the SVL. Heads are usually longer than broad (HL/HW exceeding 1.00). Although the data suggest much variation in small frogs, the heads tend to become relatively more broad with increasing size with some of the largest frogs having heads broader than long (two males). The ontogenetic variation in HL/HW thus seems to be reflected in the relatively slow rate of increase of HL (HW increasing at about same rate as SVL). There is more pronounced ontogenetic variation in TL/SVL with the TL increasing at a faster rate than the SVL; large frogs have on the average relatively longer legs than juveniles, with their TL averaging slightly more than half the body length. Ontogenetic variation is also expressed when the ratios HW/TL and HL/TL are plotted against SVL, with the variation most pronounced in HL/TL (owing to slow rate of increase of HL and fast rate of increase of TL relative to that of SVL).

In comparing ratios derived from body measurements in different kinds of frogs, it is necessary to determine the presence (if any) and degree of ontogenetic variation in each. The comparison of ratios may be taxonomically useful only when utilizing



FIGURE 2. Adult male of *Rana sierramadrensis* (UIMNH 52782, 85.8 mm SVL) showing white, spinous, excrescences on chest and lower jaw (above), and on dorsal surfaces of inner three digits of right forelimb (below).

TABLE I

Ontogenetic variation in six body proportions of *Rana sierramadrensis*. The upper set of values is for frogs less than 60 mm SVL, the lower set for frogs 60 mm SVL or larger. The data for each proportion are mean  $\pm$  its standard error, one standard deviation, and range (in parentheses).

Ratio	N	Variation
HW/SVL	14	0.357 $\pm$ 0.005, 0.018 (0.33-0.39)
	36	0.346 $\pm$ 0.002, 0.013 (0.31-0.37)
HL/SVL	14	0.383 $\pm$ 0.004, 0.016 (0.36-0.41)
	36	0.363 $\pm$ 0.003, 0.016 (0.33-0.41)
HL/HW	14	1.072 $\pm$ 0.001, 0.054 (0.97-1.15)
	36	1.043 $\pm$ 0.006, 0.035 (0.94-1.12)
TL/SVL	14	0.506 $\pm$ 0.008, 0.031 (0.44-0.54)
	36	0.568 $\pm$ 0.004, 0.025 (0.53-0.63)
HW/TL	14	0.708 $\pm$ 0.002, 0.057 (0.63-0.81)
	36	0.610 $\pm$ 0.004, 0.026 (0.56-0.66)
HL/TL	13	0.746 $\pm$ 0.001, 0.053 (0.67-0.84)
	36	0.638 $\pm$ 0.005, 0.030 (0.58-0.68)

restricted size groups. An on-going study of the *R. pustulosa-tarahumarae* complex, for example, indicates differences in ontogenetic variation between taxa in some ratios. The foregoing data for *Rana sierramadrensis* may be useful to future investigators in subsequent comparisons with related species.

*Larvae.*—The larvae or tadpoles of *Rana sierramadrensis*, not previously described, are discussed below and compared with larvae of sympatric and related ranid species in Mexico. Three tadpoles (KU 87660, N = 4) from 3.3 km north San Vicente, Guerrero, 920 m, collected on 8 June 1964 are assigned to *R. sierramadrensis* (see below). Another tadpole included in this lot of four tadpoles is smaller (24 mm total length) than the other three; the upper tooth rows are lacking (three lower rows present), the lateral margin of the oral disc is emarginate, and the dark-blotched tail fin has numerous filamentous melanophores. This small tadpole does not seem to be representative of *Rana sierramadrensis*. The description is based on the three larger larvae that exhibit the ranid features of sinistral spiracle, dextral anus, eyes more dorsal than lateral, and a papillate fringe along the lower lip; however, the lateral margins of the oral disc are not emarginate.

The three larvae measure 38, 41, and 50 mm in total length and correspond to limb bud stages I and V, and paddle stage X, respectively, according to the ranid staging system of Taylor and Kollros (in Rugh, 1962:70-71); corresponding stages of Gosner (1960) are 25, 30, and 35. The bodies of all three larvae have obscurely margined, broad pale dorsolateral areas. All three larvae either lack or have only sparse pigmentation on the tail and fins. The ventral tail fin is completely devoid of melanophores. The mostly clear dorsal fin has only a few small scattered dark pigment

patches (dendritic melanophores) and in some places the otherwise clear parts of the fin contain some scattered punctate (not filamentous) melanophores. The tail musculature is lightly and mostly uniformly pigmented, most dense on the dorsal half, and lacks definitive spots-blotching. The relatively streamlined tail with the reduced and not highly arched dorsal fin is illustrated (smallest larva of 38 mm) in figure 3D; however, the dorsal fin seems to be slightly more arched in the two larger larvae. The lateral margins of the oral disc are not infolded between the upper and lower tooth rows. There are submarginal papillae along the sides of the upper and lower lips. The fleshy flaplike lower lip with a papillate fringe seems unusually broad (especially larva of 38 mm) and may be folded down (Fig. 3C) or up against the lower tooth rows. The oral disc is large; the relative sizes of the oral discs of *R. sierramadrensis* and the sympatric *R. pustulosa* (stages X (35) and II (26), respectively; stages of Gosner, 1960, in parentheses) are compared in similar-sized larvae in figure 3A and 3B. The tooth row formula, modified from Altig's terminology (1970), is 7(2-7)/1-4/3(1); the numbers between diagonal lines indicate rows of marginal teeth. The edges of the horny beaks are pigmented and serrated. One of the larvae (41 mm) has irregular alignment of some upper tooth row segments that number eight when counted on the left side. Careful manipulation is required to discern the short seventh upper row of teeth on the right side of the largest larva. The first upper tooth row is continuous, all other upper tooth rows are separated, most by the upper beak. Larvae may have six upper tooth rows (and perhaps eight) owing to ontogenetic and/or individual vari-

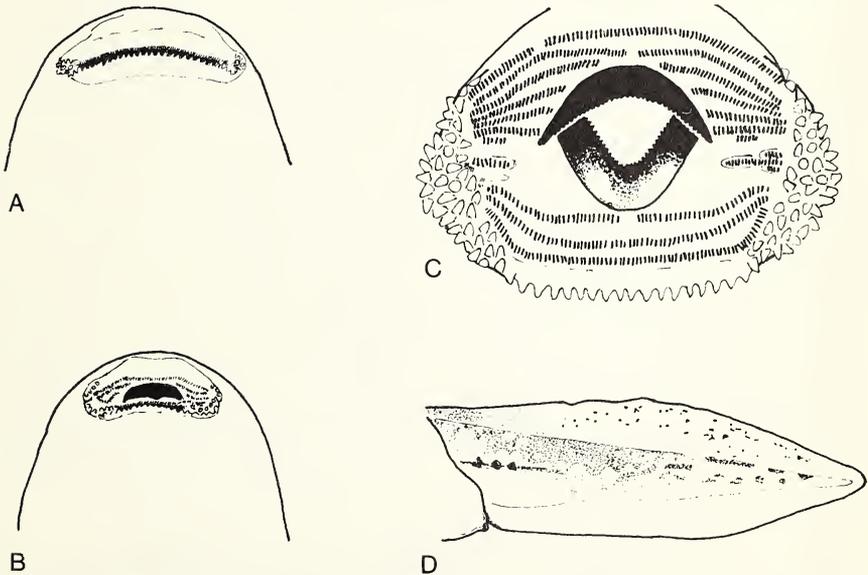


FIGURE 3. A, large oral disc or larva (50 mm total length) of *Rana sierramadrensis* (KU 87660, N = 3); B, small oral disc of larva (52 mm total length) of *Rana pustulosa*, compare with A; C, mouthparts of larva (38 mm) of *R. sierramadrensis*; D, shape and melanophore pattern of tail of larva (38 mm) of *R. sierramadrensis*.

ation. The A-2 gap is narrow (about equal to the width of five or six individual teeth) or the two lateral segments are nearly juxtaposed medially. The marginal teeth (corners of oral disc) may be scattered or arranged in rows; there are four small rows on the right side in the largest larva. The first lower tooth row is narrowly interrupted medially, the gap about equal in length to the medial gap in row A-2; the other two lower tooth rows are continuous. The oral disc and mouthparts are illustrated in figure 3C.

The three tadpoles assigned to *R. sierramadrensis* are not positively identified through direct association with metamorphosed individuals, although some such frogs (KU 87276-80) were collected at the same locality as the larvae. The three larvae are presumed to be of this species based on marked differences when compared with numerous larvae of the *R. pipiens* and *R. tarahumarae* groups from western Mexico. See subsequent section for comparison of larvae.

#### DISTRIBUTION

*Rana sierramadrensis* occurs along tropical-subtropical, foothill-montane, swift-flowing, often cascading, streams of the Sierra Madre del Sur in the Mexican states of Guerrero and Oaxaca (Fig. 4). A total of 70 specimens was examined (some of these are late-transforming frogs or are damaged and were not included in the data

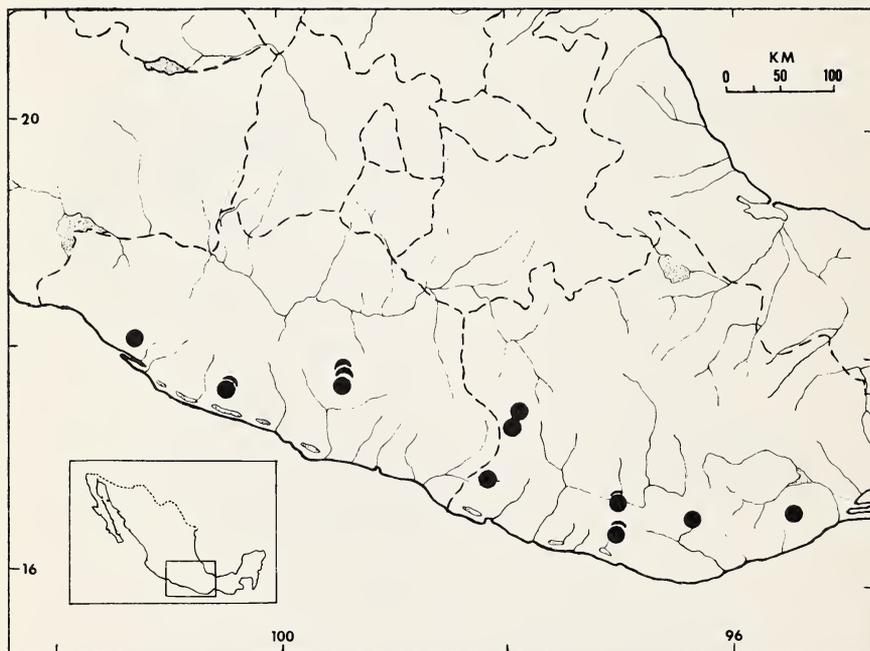


FIGURE 4. Map of southern Mexico showing localities (solid circles) for *Rana sierramadrensis* in the states of Guerrero and Oaxaca. Some localities a short distance apart share the same symbol.

analysis). The type-locality (Agua del Obispo) and other place-names in the Chilpancingo area of Guerrero were mapped by Davis and Dixon (1959).

*Guerrero*: near Agua del Obispo, between Rincón and Cajones (FMNH 100038, 102201-02, 103917; KU 87282; TCWC 10992; UIMNH 27053, 32442, 32444; UMMZ 115419, 125902-N = 5, 125903; USNM 114009-12; 9 km. SW Mazatlán, km. 337 (USNM 139724); 5.8 mi. S Mazatlán (UMMZ 115420); 3.7 mi. S Mazatlán (UMMZ 115421); 1 mi. SE San Andres de la Cruz (UMMZ 125901, N = 4); 3.3 km. N San Vicente (KU 87276-80); 37 km. S Chilpancingo (KU 87281); Acahuizotla (TCWC 8533-37, 8540-41, 10220-28, 26380; LACM 35054-55); 6 mi. NW San Jeronimito (UMMZ 125902, N = 5).

*Oaxaca*: 6 mi. N San Gabriel Mixtepec (MSU 10464); 6 km. NNW San Gabriel Mixtepec (KU 87283); 12 km. NNW San Gabriel Mixtepec (KU 87284); 14.8 km. N San Gabriel Mixtepec (KU 137539-40); Río Jalatengo, 0.8 km. S Jalatengo (KU 137538); 5.1 km. S Jalatengo (KU 137537); 13.1 km. N Juchatengo (KU 137541); 11 km. S Chicahuaxtla (MSU 12660); 3 mi. S Putla (UIMNH 52783-84); Cacahuau-tepec, at river (UIMNH 52782); Santa Lucía, near Tehuantepec (AMNH 52624).

#### COMPARISON WITH *RANA SINALOA*

*Rana sinaloa* shares some features of color and pattern with *R. sierramadrensis*—evidence of dark face mask bordered below by distinct white supralabial stripes; pale dorsolateral stripes; top of head, back and sides of body mostly devoid of pattern; narrow, dark, dorsal crossbars on femora; and black, irregular-bordered, and often interrupted, ventrolateral bands on body (see comparison in Fig. 5). *Rana sinaloa* is also similar to *R. sierramadrensis* in the body proportions affected by ontogenetic variation, especially HL/SVL and TL/SVL. The two species both have heads that in most specimens are longer than broad, and have relatively long legs (TL increasing at faster rate than SVL).

*Rana sinaloa* differs from *R. sierramadrensis* in having folds above and behind the tympana, in lacking distinct black posttympanic bars, in lacking distinct black lateral borders along the dorsolateral folds, and in having the dorsolateral folds (when present) terminating before the groin. Perhaps most important, the breeding males of *R. sinaloa* have swollen glandular thumb pads, instead of the non-enlarged thumbs and white, spinous excrescences of males of *R. sierramadrensis*. *Rana sinaloa* shares all these features with the other included species of the *R. tarahumarae* group. There are also corresponding differences in the larvae (see below). *Rana sinaloa* is considered to be a member of the *Rana tarahumarae* group and not a member of the *Rana palmipes* species group.

#### COMPARISON OF LARVAE

Since *R. sierramadrensis* is geographically sympatric with frogs of the *R. tarahumarae* group (currently referred to *R. pustulosa*) and *R. pipiens* group (hereafter referred to as *R. pipiens*), larvae of any one, or two, or all three, species could be expected to occur in a random sample. The larvae of *R. pipiens* are easily distinguished from those of *R. sierramadrensis* in having a maximum of three upper tooth rows

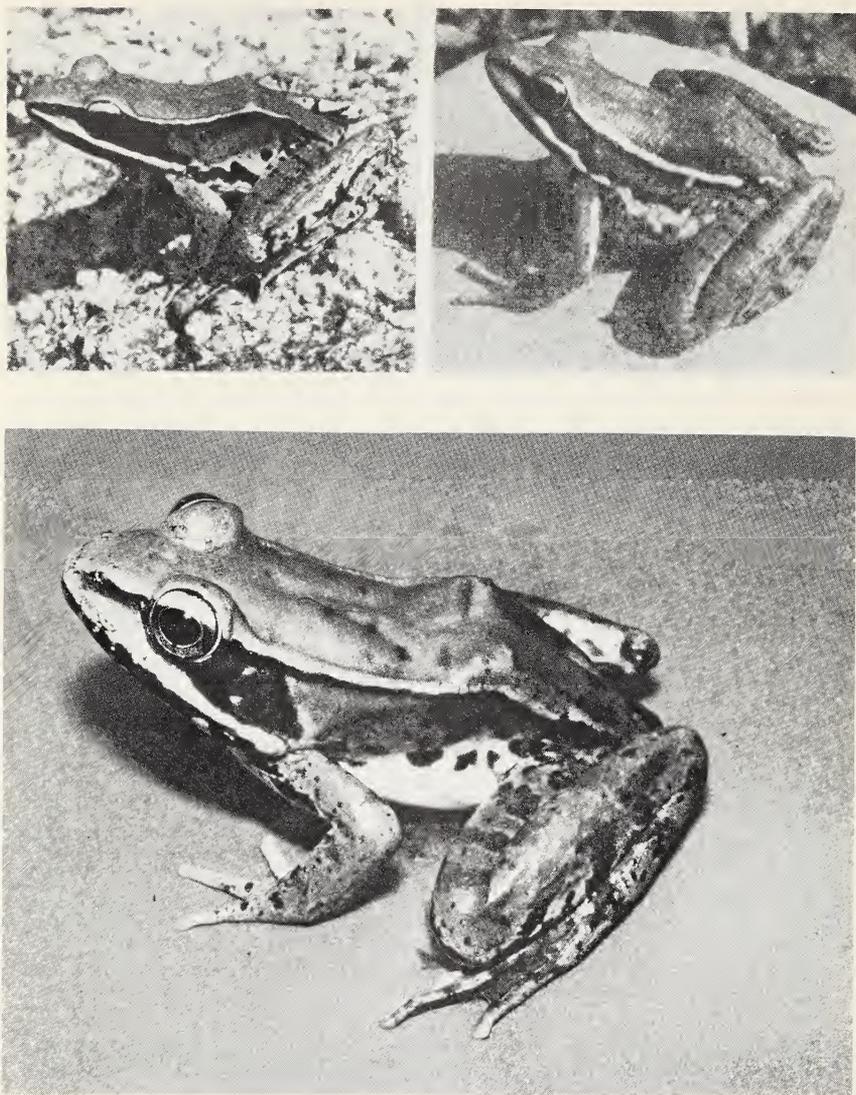


FIGURE 5. *Rana sierramadrensis* (upper left, MSU 12660, 51.3 mm SVL, 11 km. S Chicahuaxtla, Oaxaca), *Rana sinaloae* (upper right, MSU 12661, 75.8 mm SVL, 22 km. WSW Ameca, Jalisco), and *Rana maculata* (bottom, AMNH, 88 mm SVL, Finca El Rosario Vista Hermosa, ca. 7 km N Escuintla Guatemala, from kodachrome by Richard G. Zweifel), for comparison in pattern.

(but usually only two), no marginal teeth, more extensively pigmented dorsal tail fins, and in having the lateral margins of the oral disc emarginate. The larvae of *R. pustulosa* usually have some dark marks and blotches on the dorsal tail fins and musculature (mostly clear in *R. sierramadrensis*) and at least distally on the ventral fins (virtually lacking in *R. sierramadrensis*); in some larvae of *R. pustulosa* with relatively clear dorsal fins small punctate melanophores are more extensive than in *R. sierramadrensis*. The oral disc is relatively smaller in *R. pustulosa* (about two-thirds) than in *R. sierramadrensis*, and the lateral margins are infolded in larvae of *R. pustulosa* (see comparison in figure 3A, B). Less reliable is the number of upper tooth rows in distinguishing the two species, which is usually five (maximal at six) in larvae of *R. pustulosa*, and which is probably six but certainly seven in larvae of *R. sierramadrensis*. The larvae of *R. sinaloae* resemble those of *R. sierramadrensis* only in having a mostly clear dorsal tail fin; the larvae of *R. sinaloae* otherwise are not different from those of *R. pustulosa* and are distinguished from larvae of *R. sierramadrensis* by the same features that differentiate those two species.

The larvae of *R. sierramadrensis* are easily distinguished from larvae of both *R. maculata* (*macroglossa*) and *R. palmipes* (comparative data in Volpe and Harvey, 1958) in having only three lower tooth rows, and in the mostly clear tail fins. The larvae of *R. sierramadrensis* may have more highly arched dorsal fins than larvae of *R. maculata*. The larvae of *R. sierramadrensis* and *R. maculata* otherwise share several features that distinguish them from larvae of *R. palmipes*. The larvae of both species have a maximum of six or seven upper tooth rows (four or maximum of five in *R. palmipes*), have a narrow medial A-2 gap (wider in *R. palmipes*), have marginal teeth (lacking in *R. palmipes*), and have a suctorial oral disc that lacks infolded lateral margins (infolded in *R. palmipes*).

#### RELATIONSHIPS

*Rana sierramadrensis* is currently placed in the *Rana palmipes* species group (Zweifel 1954). So far as known the white, spinous excrescences in males of *R. sierramadrensis* are unique. One seemingly trenchant feature is shared with the member species of the *R. tarahumarae* group—three lower rows of teeth in larvae (the number may be variable in *R. sierramadrensis*, but is invariably three in *R. tarahumarae* group). All other member species of the *R. palmipes* group have larvae with four lower tooth rows (*R. palmipes*, *R. maculata*, *R. vibicaria*, *R. warschewitschii*); Lee (1976) referred some peculiar tadpoles from Belize with five lower tooth rows to *R. maculata*.

Variation in the two species *R. palmipes* and *R. maculata* (nearest geographically to *R. sierramadrensis*) has not been investigated in detail. In addition to other features distinguishing the two species, *R. palmipes* is especially distinctive from *R. sierramadrensis* in males having enlarged, glandular thumb pads; males of *R. palmipes* based on statements by Boulenger (1920:417), Taylor (1952:908), and Zweifel (1967:54) seem to have internal slits but lack external vocal sacs. *Rana maculata* differs from *R. sierramadrensis* in having well-developed vocal sac slits, but resembles *R. sierramadrensis* in having the thumbs "not larger than in females" (Smith 1959:216); presumably males of *R. maculata* lack the white, spinous excrescences of

*R. sierramadrensis*. *Rana sierramadrensis* seems to be most closely allied to, and the trans-isthmian counterpart of, *R. maculata*. Aside from the above-mentioned difference and those that readily distinguish the larvae (tail pigmentation and number of lower tooth rows), both species share general features of pattern (Fig. 5), occupy upland habitats, and have larvae with stream-adapted modifications. In pattern, *R. maculata* differs from *R. sierramadrensis* in having wider dark bars on the femora, in usually lacking a continuous black, ventrolateral band, and (at least in some specimens) in having a green dorsum (Kodachrome slide of R. G. Zweifel, Fig. 5).

#### RESUMEN

La variación de *Rana sierramadrensis* se discute. Los renacuajos son descritos por primera vez. Una característica secundaria sexual no conocida es la presencia de tuberculos espinosos blancos en los no engrandecidos pulgares, pecho, y mandíbulas inferiores de los machos. *Rana sierramadrensis* se retiene en el grupo *R. palmipes*. *Rana sinaloae* se traslada al grupo *R. tarahumarae*, qual se propone para inclusión de las especies *R. tarahumarae*, *R. pustulosa*, *R. sinaloae*, *R. pueblae*, y *R. johni*. *Rana sierramadrensis* ocurre solamente en la Sierra Madre del Sur en los estados Mexicanos de Guerrero y Oaxaca, y parece ser relacionada a *R. maculata*.

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