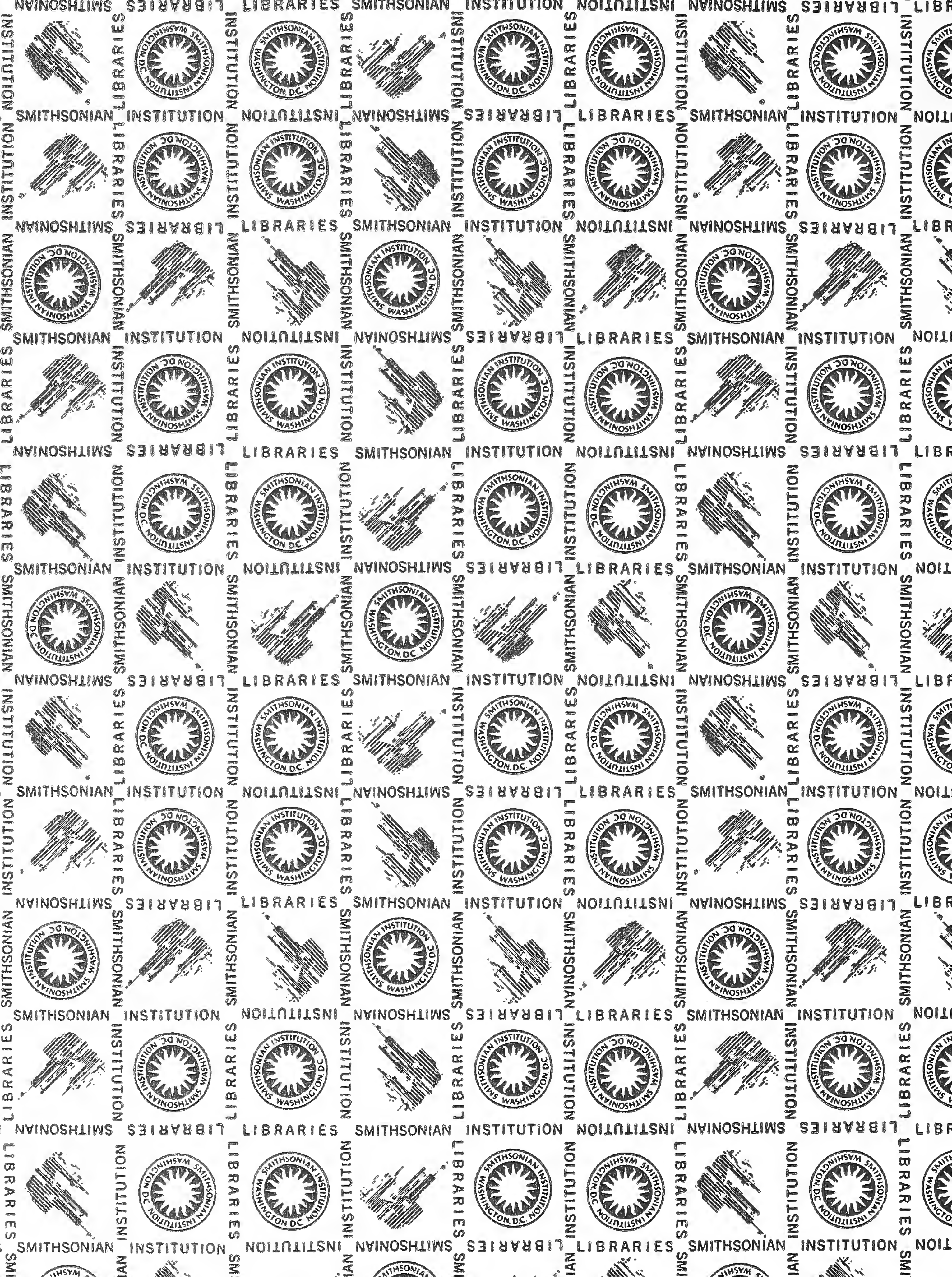

Number 301
March 16, 1979

CONTRIBUTIONS IN SCIENCE
NATURAL HISTORY MUSEUM OF LOS ANGELES COUNTY

A NEW FISH OF THE GENUS *PHALLICHTHYS* (FAMILY POECILIIDAE) FROM COSTA RICA

By William A. Bussing

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Edward Ostermeyer
Editor

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The *Science Bulletin* and *Contributions in Science* of the Natural History Museum of Los Angeles County were merged into a single imperial octavo serial, retaining the name *Contributions in Science* and beginning with Number 301.

This serial has been newly formatted for maximum use of typography and illustrations per page, and sized for maximum use of paper. All photography has been produced utilizing a 200-line screen for detail.

Since most institutions rebind *Contributions in Science* collectively into hardbound volumes, and many researchers using them desire to photocopy material, two new features have been incorporated into the new format. A suggested citation line provides the abbreviated serial title, year, number of publication, and total pagination, and appears in the lower left corner of each page; and pages of *Contributions in Science* have been printed off-center to provide a two-inch gutter between adjacent pages for easier accessibility in photocopying.

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Contributions in Science are articles in the earth and life sciences, presenting results of original research in Natural History. *Science Bulletin* (Numbers 1–30; 28 June 1965 to 10 April 1978) and *Contributions in Science* Numbers 1–300; 23 January 1957 to 16 June 1978) were merged into a single imperial octavo serial beginning with Number 301.

A NEW FISH OF THE GENUS *PHALLICHTHYS* (FAMILY POECILIIDAE) FROM COSTA RICA[1]

By William A. Bussing[2]

ABSTRACT: A new species, *Phallichthys quadripunctatus*, is described on the basis of 48 specimens from the Baja Talamanca lowlands of Costa Rica. The new form is shown to be closely allied to another congener, *P. tico*, of northern Costa Rica and southern Nicaragua. Both species are small, have sinistrally asymmetrical gonopodia, and each bears a curved membranous swelling on the terminal element of gonopodial ray 4a. *P. quadripunctatus* was collected only in shallow streams and standing waters of the Río Sixaola basin. Four species now comprise the Central American genus *Phallichthys*.

Phallichthys and four other genera with much in common morphologically and geographically, were placed in the tribe Heterandriini by Rosen and Bailey (1963). Most members of the tribe occur in Middle America, a few are found in western South America, one in southwestern United States and one in Florida. The species of *Phallichthys* are largely restricted to the Atlantic versant of Middle America (Fig. 1), although *P. amates* (Miller) was apparently introduced by man to the Valle Central (Río Tárcoles headwaters) and was recently collected at four sites on the Pacific slope in the Tempisque and Bebedero drainages of northwestern Costa Rica (Bussing and López 1977). Shortly after Rosen and Bailey (1963) revised the family Poeciliidae, Bussing (1963) described *Phallichthys tico* from northern Costa Rica, and subsequently reported on Nicaraguan material of the same species (1976). The present description of *P. quadripunctatus*, also from the Atlantic slope, increases the number of Costa Rican forms to three species. A fourth member of the genus, *P. fairweatheri*, inhabits northern Guatemala and part of Beliz (Rosen and Bailey 1959).

Phallichthys quadripunctatus NEW SPECIES

Figures 2, 3, 4

HOLOTYPE: LACM 36018–1; a mature male 14.6 mm SL, collected by William, Myrna and Eric Bussing in a small tributary of the Rio Sixaola, 0.5 km NE of Chase on road between Puerto Viejo and Bratsi, Limón Province, Costa Rica, on 4 October 1975.

PARATYPES: LACM 36018–2; 9 males 12.8–15.5 mm SL and 7 females and immatures 12.5–20.7 mm SL, same data as the holotype. USNM 216559; 3 males 11.7–15.0 mm SL and 2 females 14.6 and 15.9 mm SL, same data as the holotype. UCR 897–2; 10 males (2 cleared and stained) 10.3–15.4 mm SL and 8 females and immatures 8.8–21.0 mm SL, same data as the holotype. UCR 1017–1; 8 females and immatures 7.2–32.7 mm SL, collected by William Bussing and ichthyology class in a small tributary of the Río Sixaola, 1.2 km SW of Cruce Bribrí on road between Puerto Viejo and Bratsi, Limón Province, Costa Rica, on 18 September 1976.

MATERIAL AND METHODS: The type specimens are deposited in the Natural History Museum of Los Angeles County (LACM), the Museo de Zoología, Universidad de Costa Rica (UCR), and the National Museum of Natural History (USNM).

All body measurements refer to standard length (SL) in millimeters (mm), and were made according to the methods described in Rosen and Bailey (1959). All proportional measurements in the text are expressed as times in SL or times in head length. Body proportions as thousandths of SL and meristic counts appear in Table 1. The nomenclature of the gonopodial system is that used in Rosen and Bailey (1959).

DIAGNOSIS: This small *Phallichthys* is distinguished from its congeners by the presence of typically four conspicuous spots on each side of the body (Fig. 2), and an intermediate number of gill rakers on the first gill arch (11–17, usually 13–16 on large adults). Males of both the new species and *Phallichthys tico* differ from other *Phallichthys* in possessing a very long terminal segment of gonopodial ray 4a (4 or 5 times longer than wide and 3 or 4 times longer than wide, respectively), which extends beyond the other gonopodial elements, and bears a fleshy pad dorsally and a membranous hook at a right angle to its axis (Fig. 3).

DESCRIPTION: Body moderately robust, laterally compressed. Body depth greatest at pelvic-fin origin, and less in mature males than in mature females; greatest body depth in SL 3.2–3.6 times in males and 2.8–3.4 times in females. Predorsal profile slightly convex in both sexes; profile angular at dorsal-fin origin. Postdorsal profile slightly concave. Ventral profile of body rounded anteriorly; postanal profile straight. Caudal peduncle depth in SL 5.2–5.7 times in males and 5.5–6.0 times in females.

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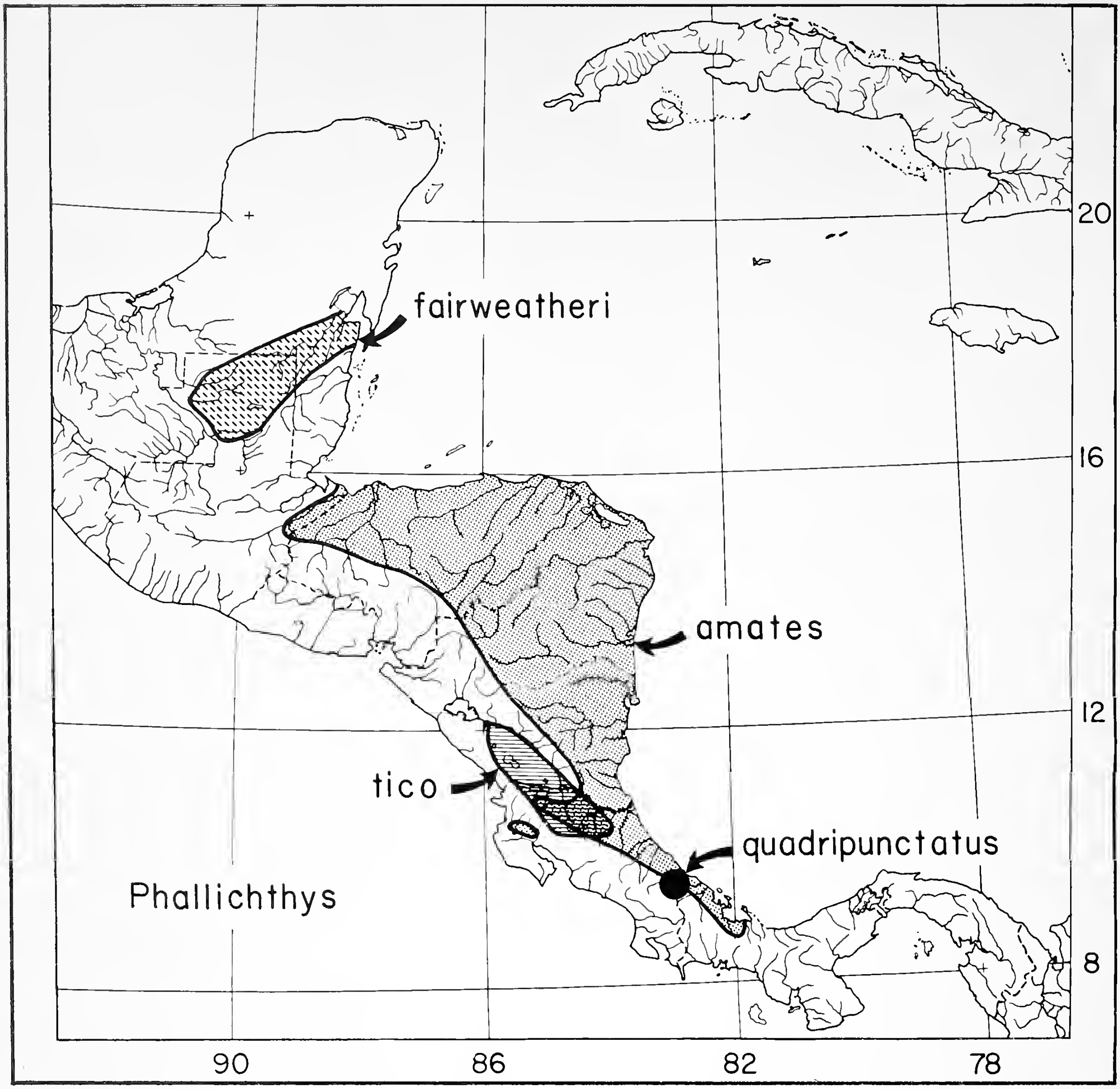

FIGURE 1. Map of Central America showing known distributions of the species of *Phallichthys*. Range of *P. fairweatheri* and Guatemalan distribution of *P. amates* from Rosen and Bailey (1963). Honduran distribution of *P. amates* after Martin (1972).

Head length 3.1–3.7 times in SL; head width 4.1–4.7 times in SL. Eyes slightly below dorsal head profile; horizontal orbit diameter 2.3–3.3 times in head length. Least width of bony interorbital 1.9–2.6 times in head length. Snout length always shorter than orbit diameter, 2.9–3.7 times in head length. Postorbital distance 2.2–2.5 times in head length.

Mouth opening dorsally; overall width 2.1–2.9 times in head length. Two rows of incurved teeth on each jaw. Teeth of outer row of each jaw spatulate, that is, with expanded flattened tips, apparently adapted to scraping surfaces. Teeth of inner series sharp-pointed and conical, much shorter than teeth of outer series. Teeth of both series gradually reduced in length toward lateral edges of jaws; premaxillary teeth of outer series not present at extreme edges of jaw.

Dorsal-fin origin at highest point on body; directly over anal-fin origin in females, slightly posterior to origin of gonopodium of males. Predorsal distance in SL 1.8–1.9 times in males and 1.7–1.8 times in females. Distance from dorsal-fin origin to caudal-fin base in SL 2.0–2.1 times in males and 2.1–2.2 times in females. Depressed length of dorsal fin in SL 3.2–3.6 times in males and 3.6–4.0 times in females. Dorsal-fin rays usually 9, range 8 (1) and 9 (21), frequency in parentheses.

TABLE 1

Meristics and proportions in thousandths of standard length of the holotypes and 10 male and 10 female paratypes each of *Phallichthys quadripunctatus* and *Phallichthys tico*.

	P. quadripunctatus			*P. tico*		
	Holotype	Paratypes		Holotype	Paratypes	
Dorsal rays	9	8-9		8	7-9	
Anal rays	10	9-10		10	9-10	
Pectoral rays	11	11-12		11	10-12	
Pelvic rays	6	5-6		6	6	
Caudal rays	13	12-14		13	12-14	
Scales in lateral series	27	26-27		26	26-27	
Total gill rakers	13	11-17		—	10-12	
		males	females		males	females
Standard length (mm)	14.6	12.0-15.2	17.3-32.7	17.4	13.7-17.6	17.7-32.9
Body, greatest depth	301	275-316	298-352	298	255-294	282-343
Caudal peduncle, least depth	185	175-191	167-182	183	154-180	158-173
Dorsal origin to snout tip	548	540-559	563-598	528	470-573	571-602
Anal origin to mand. symphysis	548	525-558	590-638	557	496-580	621-671
Dorsal origin to caudal base	493	483-507	464-481	465	422-483	431-458
Anal origin to caudal base	541	517-560	416-459	522	446-528	395-432
Head length	301	293-320	269-306	298	267-309	264-305
Head width	219	212-230	214-281	195	174-198	192-215
Snout length	89	87-99	92-99	97	83-105	88-107
Orbit length	116	113-133	83-116	109	96-111	75-101
Postorbital length of head	130	119-133	119-139	137	113-141	115-141
Interorbital, bony width	144	117-145	138-155	143	109-148	136-157
Mouth, over-all width	123	108-121	116-138	114	96-129	103-132
Dorsal fin, depressed length	288	275-309	249-280	264	244-271	224-257
Anal fin, depressed length	445	431-483	231-267	408	375-457	203-237
Caudal fin length	384	358-392	300-376	321	285-341	249-331
Pectoral fin length	267	263-280	229-262	224	193-228	181-235
Pelvic fin length	260	225-268	182-214	183	145-194	136-171

Anal-fin rays usually 10, range 9 (1) and 10 (10). Preanal distance in SL 1.8–1.9 in males and 1.6–1.7 times in females. Distance from anal-fin origin to caudal-fin base in SL 1.8–1.9 in males and 2.2–2.4 times in females. Depressed length of anal fin of females 3.8–4.1 times in SL; depressed length of gonopodium in males 2.1–2.3 times in SL. Posterior border of anal fin in females truncate.

Pectoral-fin rays usually 11, range 11 (21) and 12 (1). Tip of fins extending posteriorly to origin of pelvic fins of females and beyond origin of gonopodium of males; length of pectoral fin in SL 3.6–3.8 times in males and 3.8–4.3 times in females.

Pelvic-fin rays usually 6, range 5 (1) and 6 (21). Tip of fins in both sexes extending posterior to origin of anal fin. Length of pelvic fin in SL 3.7–4.4 times in males and 4.7–5.8 times in females. Caudal-fin rays usually 13, range 12 (1), 13 (19) and 14 (2). Length of caudal fin in SL 2.6–2.8 times in males and 2.7–3.3 times in females.

Total number of gill rakers increasing ontogenetically. Eleven specimens of 12–16 mm SL, including all males examined, with 11 (1), 12 (1), 13 (5) and 14 (4) gill rakers on first arch. Eleven larger specimens (17.0–32.7 mm SL), all females, with 15 (3), 16 (6) and 17 (2) gill rakers on first arch. Scales in lateral series usually 26, range 26 (20) and 27 (2). Vertebrae 29 on two cleared and stained paratypes. Long, pointed urogenital (?) papilla present on about 50 percent of large females; apparently non-tubular, but serving to divide genital and urinary apertures.

GONOPODIAL SYSTEM: Gonopodium of mature males sinistral, i.e. rays 3, 4 and 5 of anal fin forming a shallow groove opening to left side of body. Ray 3 deep and compressed; proximal segments sinistrally incurved to form ventral border of trough; six subdistal segments of ray 3(l) forming long thin spines; two minute terminal segments without spines (Fig. 3). Three or four corresponding segments of ray 3(r) also produced into spines.

Right and left halves of ray 4 symmetrical. Ray 4a slender, tapering to tip; terminal segment much longer than subterminal ones (4 or 5 times longer than wide). Terminal segment of ray 4a forming tip of gonopodium; a fleshy swelling on dorsal border of last segment from which hangs a pointed membranous knob. Distal portion of ray 4p also slender; subterminal segments of each half bearing long retrorse serrae; terminal two segments without serrae.

Ray 5 symmetrical and composed of an anterior half which forms bottom, and posterior half which forms sides, of a square-bottomed groove on posterior surface of gonopodium. Both halves of ray tapering at tip, terminal segments of ray 5a extending beyond end of ray 5p. Right and left halves of rays 6 to 10 symmetrical; rays 6, 7 and 8 constricted near middle of ray and split into anterior and posterior elements distally; rays 9 and 10 split only into right and left halves.

Ligastyle of moderate length. Gonapophysis I curved anteroventrally, tip lying between lateral wings of primary gonactinostal complex; a pair of long, slender uncini arising near center of gonapophysis and curving posteroventrally (Fig. 4). Gonapophysis II projecting anteroventrally between preceding uncini, and bearing a pair of posteroventrally projecting uncini. Gonapophysis III projecting anteroventrally, shorter and stouter than others; a pair of short, pointed uncini arising near center of gonapophysis and directed posteriorly.

Gonactinost 1 free, pointed tip directed anterodorsally. Primary gonactinostal complex (gonactinosts 2, 3 and 4) with lateral flanges along entire length of gonactinost 4; these lateral processes flaring broadly and curving posteriorly on distal third of primary complex. Gonactinost 5 lying between lateral processes of primary complex. Gonactinosts 6 to 9 free and slender with symmetrical or dextral lateral processes. Gonactinosts 6 and 7 slightly expanded laterally at tips, gonactinost 7 also with a dextral lateral flange subterminally; gonactinosts 8 and 9 with tri-

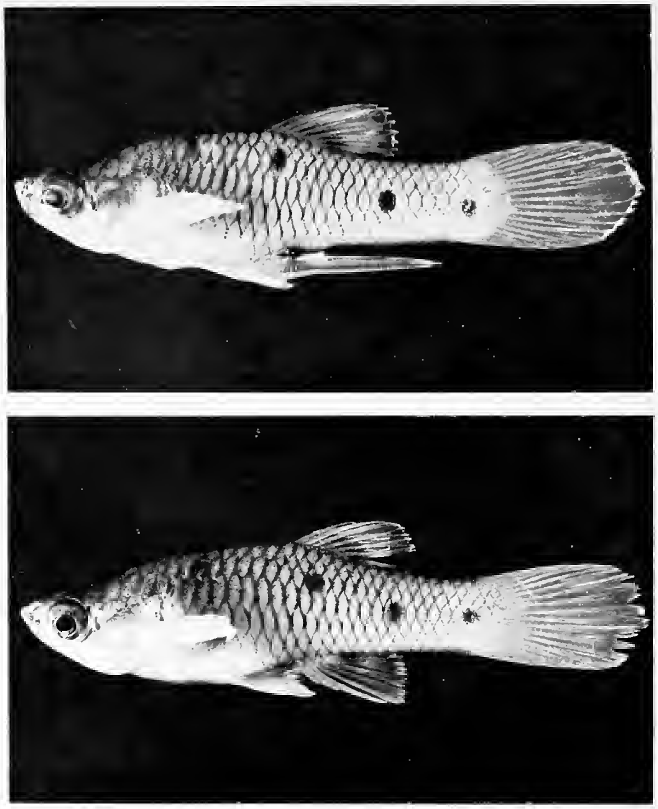

FIGURE 2. *Phallichthys quadripunctatus*, new species from the Rio Sixaola drainage, Costa Rica. Above, the holotype (LACM 36018–1), a mature male, 14.6 mm SL. Below, a young female paratype (UCR 897–2), 20.1 mm SL.

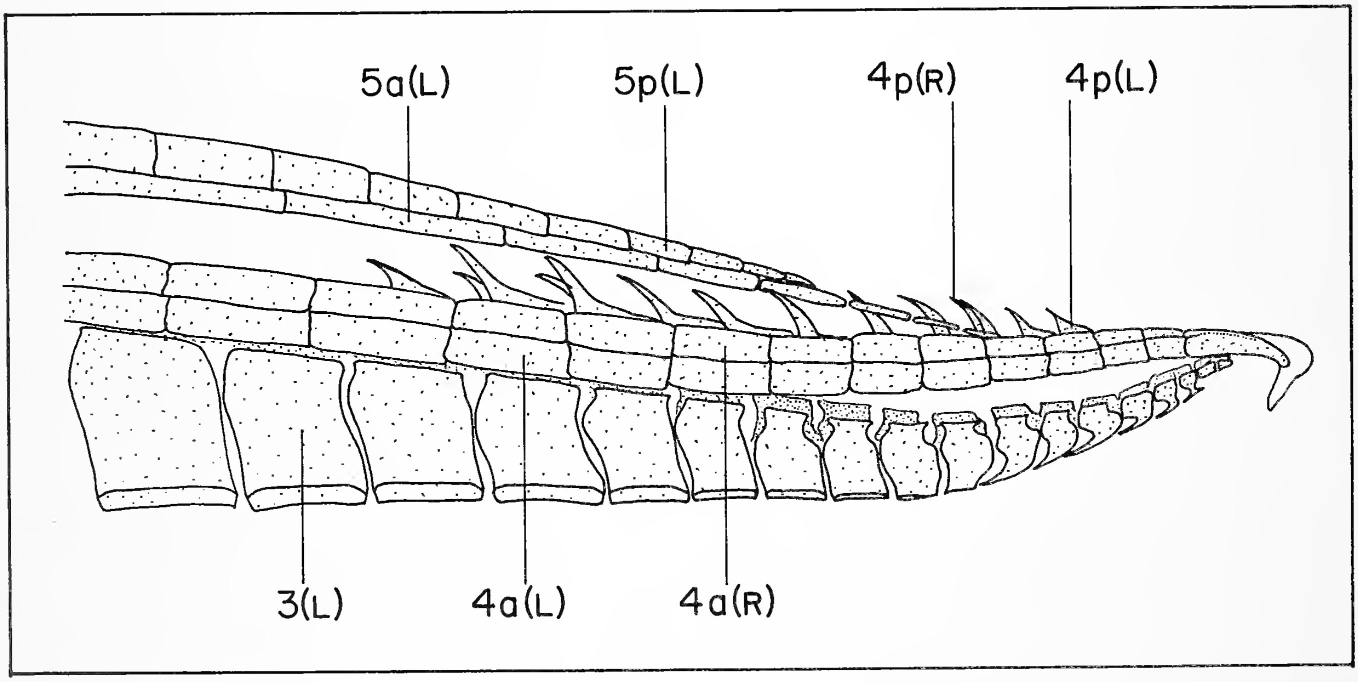

FIGURE 3. Distal tip of gonopodium of *Phallichthys quadripunctatus*, new species (UCR 897–2), a male paratype, 14.9 mm SL.

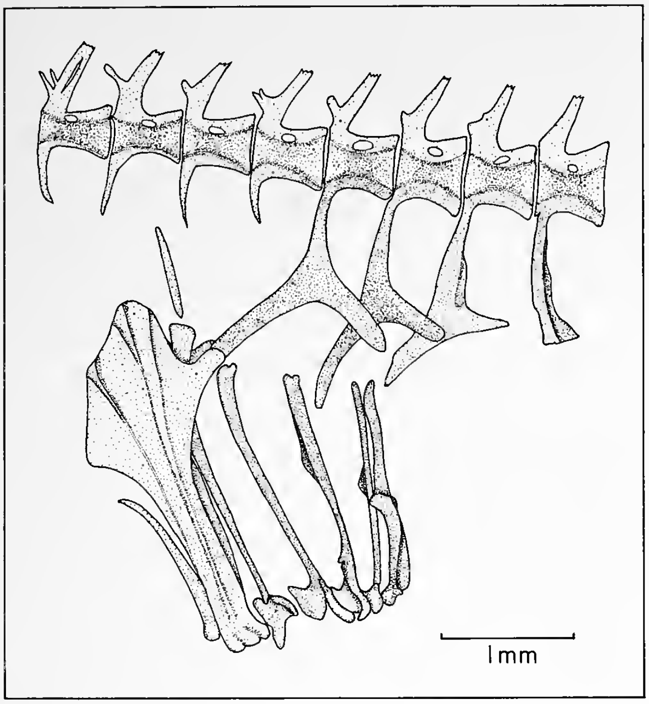

FIGURE 4. Gonopodial suspensorium of *Phallichthys quadripunctatus*, new species (UCR 897–2), a male paratype, 14.9 mm SL.

angular dextral flanges on distal halves; gonactinost 10 short, directed dextrally, and incorporated into gonactinost 9.

SENSORY CANALS: Sensory canals of head poorly developed. Supraorbital canal consisting of an open groove between pores 3 and 4 (Gosline 1949) and a closed tube uniting pores 6 and 7; an indistinct groove between pores 2 and 3 and between pores 5 and 6 visible on some specimens. Preopercular canal with 6 pores connected by closed tube. Preorbital canal with two pores connected by closed tube; a shallow groove below lower pore on some specimens.

COLORATION: In live material a tenuous light blue iridescence sometimes apparent on posterior margin of dorsal fin of both sexes, and anal fin of females. Other color traits similar in live and preserved examples. Generally four conspicuous subcircular spots along horizontal axis of body (Fig. 2). Anterior spot one scale row above fourth or fifth scales of lateral series; slightly closer to dorsal-fin origin than posterior margin of eye. Second spot one scale row above eleventh or twelfth scale of lateral series, and below fourth dorsal-fin ray. Third spot centered on nineteenth or twentieth scale of lateral series; slightly anterior to posterior margin of dorsal fin. Fourth spot over twenty-fifth or twenty-sixth scale of lateral series; usually centered between dorsal and ventral margins of caudal peduncle or slightly displaced ventrally. Individual variants (21 percent of specimens collected) with three or five spots on one or both sides of body. Three-spotted variants with first spot (4 cases) or second spot (1 case) missing. Five-spotted variants with extra spot between spots 2 and 3 (2 cases) or between spots 3 and 4 (8 cases); in these specimens adjacent spots slightly displaced to accommodate extra spot. Holotype normal on left side (Fig. 2), with five spots on right side. Four-spot pattern present as vertically elongated blotches on newborn specimens.

Scale pockets edged in black, contrasting sharply with pale yellow-gray ground color; belly and ventral half of head white. Dorsal fin dark at base and posterior margin, clear between; large melanophores on interradial membranes of proximal third of fin and along distal one-fifth or one-sixth of fin. Anal fin with black interradial membranes; a conspicuous spot at posterior base of anal fin produced by melanophores on base of last two rays and adjoining urosome. Gonopodium of male with small melanophores along rays 3 and 5; an intense black spot at base, and along most of length of last three anal rays and extending onto urosome. Pectoral, pelvic and caudal fins clear.

ETYMOLOGY: The specific name, *quadripunctatus*, refers to the four distinctive spots on the body of this species.

ECOLOGY: The species was collected only in two shallow rivulets and a roadside ditch. Collection UCR–897 was made in a clear, shaded brook (0.5 m wide by 0.1 m deep, temperature 26°C, sand and gravel substrata), which also formed a stagnant, turbid ditch (0.1 m deep, temperatures 26° to 40°C, sand substrata). The fish were collected in the strongly insolated ditch in areas where bottom temperatures reached as high as 34°C. Only one other fish species was taken at this site, a species of *Rivulus* from the running-water habitat.

Collection UCR–1017 was made in shaded and unshaded portions of a small stream (2.0 m wide by 0.2 to 0.5 m deep, temperature 20°C, sand and rock substrate). At this station the new species was not common, or perhaps just difficult to collect with dip nets. Other species taken at this site were *Phallichthys amates*, *Alfaro cultratus* and a species of *Rivulus*.

In an aquarium *P. quadripunctatus* is shy unless kept with small, less timid species in a heavily planted tank. It readily accepts small entomostracans (*Ceriodaphnia* spp.) and prepared dry foods.

GEOGRAPHIC DISTRIBUTION: *P. quadripunctatus* is only known from two tributaries of the Rîo Sixaola in extreme eastern Costa Rica (Fig. 1). It should also occur to the south in Panamanian tributaries of the Sixaola. The species has not been taken at apparently suitable habitats in adjoining drainages to the north. In their respective ranges, this form and *Phallichthys tico* are sympatric, and often syntopic, with *Phallichthys amates*.

REMARKS

Phallichthys quadripunctatus presents the diagnostic characteristics of the genus (Rosen and Bailey 1959; Bussing 1963). In general physiognomy, size, and characteristics of the gonopodial system, *P. quadripunctatus* and *P. tico* share a number of similarities which distinguish them from their congeners: maximum size (largest *quadripunctatus*, 32.7 mm SL and *P. tico*, 32.9 mm SL vs. *P. fairweatheri*, at least 44 mm SL and *P. amates*, 67 mm SL); terminal segment of gonopodial ray 4a several times longer than wide (omitted from original description of *P. tico*) and with a membranous pad at the tip; right and left halves of gonopodial ray 4 symmetrical; and a widely expanded primary gonactinost complex.

Dr. Donn E. Rosen *(in litt.)* has pointed out the similarity of the fleshy pad at the tip of the gonopodium of *P. fairweatheri* and *P. quadripunctatus*. A similar membranous swelling is present in *P. tico*. Dr. Rosen suggests that if the pad is a derived character for the group, then *P. quadripunctatus* and *P. tico* may be the sister-group of *P. fairweatheri*, and these three the sister-group of *P. amates*. The fact that *P. fairweatheri*, unlike its congeners, has dextral gonopodial asymmetry, may not be a strong objection to this hypothesis. Rosen and Bailey (1959) noted that a simple genetic change may determine the direction of gonopodial asymmetry and thus, would not necessarily signify a fundamental divergence between *P. fairweatheri* and its congeners.

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RESUMEN

Se describe un nuevo poecilido, *Phallichthys quadripunctatus*, de Baja Talamanca en la vertiente atlántica de Costa Rica. La especie nueva es de parentesco muy cercano a otra especie diminuta, *Phallichthys tico*, que habita el norte de Costa Rica y el sur de Nicaragua. La nueva especie, tanto como *P. tico*, se encuentran simpátricos con *Phallichthys amates* dentro de sus respectivas distribuciones geográficas. Una cuarta especie habita el norte de Guatemala y parte de Belice.

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A REVIEW OF THE SERRANID FISH GENUS *ANTHIAS* OF THE HAWAIIAN ISLANDS, WITH DESCRIPTIONS OF TWO NEW SPECIES

By John E. Randall

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CONTENTS

The *Science Bulletin* and *Contributions in Science* of the Natural History Museum of Los Angeles County were merged into a single imperial octavo serial, retaining the name *Contributions in Science* and beginning with Number 301.

This serial has been newly formatted for maximum use of typography and illustrations per page, and sized for maximum use of paper. All photography has been produced utilizing a 200-line screen for detail.

Since most institutions rebind *Contributions in Science* collectively into hardbound volumes, and many researchers using them desire to photocopy material, two new features have been incorporated into the new format. A suggested citation line provides the abbreviated serial title, year, number of publication, and total pagination, and appears in the lower left corner of each page; and pages of *Contributions in Science* have been printed off-center to provide a two-inch gutter between adjacent pages for easier accessibility in photocopying.

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Contributions in Science are articles in the earth and life sciences, presenting results of original research in Natural History. *Science Bulletin* (Numbers 1–30; 28 June 1965 to 10 April 1978) and *Contributions in Science* (Numbers 1–300; 23 January 1957 to 16 June 1978) were merged into a single imperial octavo serial beginning with Number 301.

A REVIEW OF THE SERRANID FISH GENUS *ANTHIAS* OF THE HAWAIIAN ISLANDS, WITH DESCRIPTIONS OF TWO NEW SPECIES[1]

By John E. Randall[2]

ABSTRACT: The serranid fish genus *Anthias* is represented in the Hawaiian Islands by three species: *thompsoni* (Fowler), which is distinctive in lacking prolonged dorsal spines, usually having 16 dorsal soft rays and 7 anal soft rays, and 50 to 58 lateral-line scales; *bicolor*, new species, with the second and third dorsal spines of adults prolonged, usually with 17 dorsal soft rays, 7 anal soft rays, 57 to 64 lateral-line scales, and males with a thickened and pointed upper lip; and *ventralis*, new species, with no prolonged dorsal spines, usually with 17 dorsal soft rays, 9 anal soft rays, and 39 to 46 lateral-line scales. *A. ventralis* is divided into two subspecies, the Hawaiian *A. v. hawaiiensis*, and *A. v. ventralis* from other localities in Oceania.

In their *Handbook of Hawaiian Fishes* Gosline and Brock (1960) listed ten species of serranid fishes, of which six belong in the subfamily Anthiinae. Recent collections in the islands have resulted in six additions to the subfamily, and adjustment is needed of some of the anthiine names in the *Handbook*. In a revision of *Plectranthias* Bleeker, Randall (in press) will describe two new species of this genus from Hawaii, one of which was reported as *Pteranthias longimanus* Weber by Gosline and Brock. In addition he will record *P. winniensis* (Tyler) from the islands. *Pseudanthias kelloggi* (Jordan and Evermann 1905), which is only subspecifically distinct from *azumanus* (Jordan and Richardson 1910) from Japan, also belongs in the genus *Plectranthias*. A collection of ten postlarval specimens of *Luzonichthys* Herre (BPBM 19926, 26–30.6 mm SL) taken by midwater trawl off Oahu in 1971 by Thomas A. Clarke appears to represent an undescribed species. Description of this form is delayed in the hope of obtaining adults of the species. Katayama (1975) described *Caprodon unicolor* from Midway. The other species of this genus in Hawaii, which has been identified as *C. schlegelii* (Günther) (type locality, Japan), appears to be undescribed. The species described as *Caesioperca thompsoni* by Fowler (1923) should be classified in the genus *Anthias*, subgenus *Pseudanthias*. Two new species of *Anthias*, one in subgenus *Pseudanthias* and one in subgenus *Mirolabrichthys*, are described herein. A paper on *Anthias pleurotaenia* (Bleeker), the type species of *Pseudanthias* Bleeker 1873, and the distinction of *Anthias* and *Pseudanthias* is in progress by P.C. Heemstra and Randall. The subgenus *Mirolabrichthys* Herre 1927 has been revised by Randall and Lubbock (in press). Although both new species of *Anthias* were first collected in the Hawaiian Islands, they were later taken at other Indo-Pacific localities.

The holotypes and some paratypes of the new species and subspecies are deposited in the Bernice P. Bishop Museum, Honolulu (BPBM). Other paratypes have been sent to the Australian Museum, Sydney (AM); British Museum (Natural History), London [BM(NH)]; California Academy of Sciences, San Francisco (CAS); Muséum National d'Histoire Naturelle, Paris (MNHN); Natural History Museum of Los Angeles County (LACM); and National Museum of Natural History, Washington, D.C. (USNM).

Data in parentheses in the descriptions below apply to the paratypes if different from the holotype. Tables 1 to 3 present the meristic data of the three species of *Anthias*. Tables 4 to 6 consist of the proportional measurements of the type specimens of the new taxa. More measurements are given in these three tables than are summarized in the text.

KEY TO THE HAWAIIAN SPECIES OF *ANTHIAS*

1a. Second and third dorsal spines prolonged in adults (especially in males); front of upper lip of males thickened and moderately pointed; lateral-line scales 57 to 64; mandible naked; subopercular margin smooth in adults ....*bicolor* new species

1b. No dorsal spines prolonged; front of upper lip not thickened; lateral-line scales 39 to 58; mandible scaled; lower subopercular margin serrate..2

2a. Anal soft rays 7; dorsal soft rays usually 16; pectoral rays 20 to 22; lateral-line scales 50 to 58; margin of posterior half of orbit rimmed with fleshy papillae...................*thompsoni*

2b. Anal soft rays 9; dorsal soft rays usually 17; pectoral rays 15 (rarely 16); lateral-line scales 39 to 46; margin of posterior half of orbit smooth......................*ventralis* new species

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Anthias (Mirolabrichthys) bicolor

NEW SPECIES

Figures 1–3; Tables 1–4

HOLOTYPE: BPBM 10146, 99.2 mm SL, male, Hawaiian Islands, Oahu, Waianae coast off Pokai Bay, small area of live coral with holes and ledges, 33.5 m, quinaldine, J. E. Randall, P. M. Allen and E. S. Helfman, 7 September 1970.

PARATYPES: BPBM 10141, 1(99.9 mm SL), Hawaiian Islands, Oahu, off Pokai Bay, patch of coral rubble with some live coral, 27.5 m, quinaldine, J. E. Randall, 31 August 1970; BPBM 10142, 4(76.5–99.2 mm SL), same data as preceding; CAS 35678, 1(94.5 mm SL), same data as holotype; USNM 215284, 1(63.8 mm SL), same data as holotype; BPBM 10145, 1(34.3 mm SL), Hawaiian Islands, Oahu, off Lahilahi Point, cave in 27.5 m, quinaldine, J. E. Randall, 7 September 1970; BPBM 19924, 2(26–26.9 mm SL), Hawaiian Islands off Oahu (21° 20–30′ N; 158° 20–30′ W), 200 m, 3.05-m Izaacs-Kidd midwater trawl, R/V *Teritu*, T. A. Clarke, 16 September 1970; BPBM 10173, 4(82.2–111 mm SL), Hawaiian Islands, Oahu, off Kahana Bay, W side at edge of channel, cave in 26 m, rotenone, J. E. Randall, 27 September 1970; ANSP 134235, 1(83.4 mm SL), same data as preceding; LACM 35579-1, 1(81 mm SL), same data as preceding; MNHN 1974–48, 1(76 mm SL), same data as preceding; BPBM 13344, 3(27.5–57.5 mm SL), Hawaiian Islands, Oahu, off Makapuu Point, collected from salvaged vessel raised from 68 m, W. D. Madden, 14 October 1970; BPBM 15498, 1(29 mm SL), Hawaiian Islands, Oahu, off Makaha, ledge in 44.5 m, rotenone, J. E. Randall, L. Taylor, P. M. Allen and A. Nahacky, 16 June 1973; BPBM 15877, 4(45.6–63 mm SL), New Guinea, Madang, Rausch Pass, S side, isolated coral block on sloping sand bottom, 34 m, quinaldine, J. E. Randall, 18 August 1973; BPBM 19930, 1(82 mm SL), Mauritius, W coast, Medine, off La Fouche, 32 m, quinaldine, J. E. Randall, 19 November 1973; BPBM 17959, 1(66.1 mm SL), Marshall Islands, Enewetak Atoll, Lagoon off Japtan (David) Island, small low-profile patch reef on sand in 18 m, rotenone, J. E. Randall, P. Lamberson and R. McNair, 13 December 1974; BPBM 18833, 1(72 mm SL), Maldive Islands, Villingili Island, lagoon reef, cave in 35 m quinaldine, J. E. Randall, 18 March 1975; MNHN 1975–1139, 1(74.5 mm SL), Hawaiian Islands, Oahu, off Makaha, ledge in 36.5 m, rotenone, J. E. Randall, P. S. Lobel, J. Culp and J. L. Earle, 3 May 1975; BPBM 19916, 1(72.3 mm SL), Loyalty Islands, Maré Island, 55 m, P. Laboute and Y. Magnier, 20 November 1975; AM I.18721–001, 1(65 mm SL), same data as preceding; BM(NH) 1976.3.15.1, 1(66.5 mm SL), same data as preceding.

DIAGNOSIS: Dorsal rays X,16 to 18 (usually 17); anal rays III,7 or 8 (rarely 8); pectoral rays 19 to 21 (rarely 21); lateral-line scales 57 to 64; gill rakers 11 or 12 + 26 to 28; depth of body 2.74 to 3.04 in SL; third dorsal spine prolonged in adult females, and second and third spines prolonged in adult males; front of upper lip of males thickened and moderately pointed; no papillae along hind margin of orbit; margins of subopercle and interopercle smooth in adults; pelvic fins long, reaching at least to anus (generally to or beyond origin of anal fin); teeth on vomer large; patch of teeth on palatines broad (about 10 irregular rows of teeth at broadest place); no auxiliary scales on body; mandible naked; dorsal and anal fins naked; upper half of body yellow-orange in life, lower half lavender-pink; males with fleshy tips of elongate second and third dorsal spines yellow.

DESCRIPTION: Dorsal fin X,17 (17 or 18, usually 17; two of 27 paratypes with XI, one of these with 16 soft rays); anal fin III,8 (26 paratypes with 7, one with 8); pectoral rays 20 (19 or 20; one of 27 paratypes with 21 rays on one side), upper two unbranched; pelvic fin I,5; principal caudal rays 15 (upper and lower unbranched); lateral-line scales 63 (60 on other side of holotype) (57–64); scales above lateral line to origin of dorsal fin 9 (8–9); scales below lateral line to origin of anal fin 23 (21–23); circumpeduncular scales 33 (31–33); gill rakers 12+27 (11–12 + 26–28); pseudobranchial filaments 20 (16–20); branchiostegal rays 7; vertebrae 26.

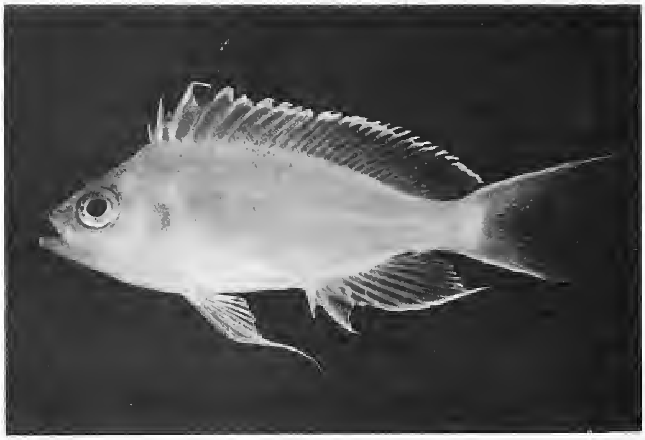

FIGURE 1. *Anthias (Mirolabrichthys) bicolor*, juvenile, 29 mm SL, Oahu, Hawaii, BPBM 15498.

Body somewhat elongate, the depth 2.82 (2.74–2.96) in SL (a little more elongate on non-Hawaiian specimens, the depth 2.84–3.04 in SL); body moderately compressed, the width 2.08 (1.97–2.36) in depth; head length 3.21 (2.81–3.23) in SL; snout 3.54 (3.36–4.27) in head, the front of upper lip of males thickened, somewhat pointed, and freely movable dorso-ventrally; diameter of orbit 4.34 (3.08–4.5) in head; posterior edge of orbit without fleshy papillae; interorbital space convex, the bony width 4.17 (3.86–4.4) in head; least depth of caudal peduncle 2.15 (2.15–2.84) in head.

Mouth oblique and moderately large, the maxilla reaching to or posterior to a vertical at rear edge of pupil; mouth terminal except on large males where it is slightly inferior due to hypertrophy of upper lip. Posterior end of maxilla rounded, its greatest depth 1.2 in orbit of holotype; no supplemental maxillary bone. Upper jaw with a band of villiform teeth which is broader anteriorly, the teeth at front enlarged; two large canine teeth anteriorly on each side of upper jaw (one laterally at front of jaw which is perpendicular in jaw and not curved, and a larger slightly curved one which lies nearly flat at posterior edge of the anterior band of villiform teeth); an outer row of enlarged teeth (13 to 15 on holotype) on side of jaw, the more posterior ones inclined forward and outward; lower jaw with a patch of villiform teeth anteriorly, the front ones enlarged; two large curved canine teeth on each side of lower jaw (one laterally at front of jaw which points outward and the other about one-third back in jaw which curves slightly posterior); a row of moderate-sized canines (14 to 17 on holotype) along jaw posterior to second large canine. Vomer with unusually large teeth (11 on holotype); palatines with a patch of villiform teeth in approximately 10 irregular rows at broadest place. Tongue pointed; upper surface with scattered very small papillae. Gill membranes free from isthmus. Gill rakers slender and long (largest 1.17 in orbit of holotype), notably longer than gill filaments (longest gill filament of first gill arch of holotype contained 1.5 in longest raker).

Opercle with three flattened spines, the central one the largest and most posterior, the upper one obtuse and indistinct, slightly anterior to lower; two lower spines acute; distance between tips of two lower spines about two-thirds the distance between central and upper spines; margins of subopercle and interopercle smooth

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(except some juveniles that may have a few small serrae on these bones); lower margin of preopercle smooth; rounded corner and upper edge serrate (25 on holotype); serrae increase in number with size (12 in a 34-mm specimen, 15 in a 47-mm specimen, 22 in a 57.5-mm specimen, 23 to 30 in four specimens from 81 to 88 mm, and 36 in a 104-mm specimen). The 27.5 and 29-mm paratypes have 9 serrae on the preopercle, the lower two at the corner enlarged, especially the lowermost, which extends slightly beyond posterior margin of operculum; in addition, there are two spines on the interopercle (the one at upper edge large), one on the subopercle, and for the smaller specimen, two on the lower edge of the preopercle. These two specimens are similar morphologically to the two post-larvae (BPBM 19924, 26–26.9 mm SL) and clearly are transforming from the postlarval form. The postlarvae have the same spination on the opercular bones, although the two enlarged spines at the corner of the preopercle exhibit a distinct serration.

Anterior nostril in a short membranous tube (higher dorsoposteriorly) directly anterior to middle of eye about half the distance from edge of orbit to edge of groove separating upper lip from snout; posterior nostril large, situated diagonally dorsoposteriorly to anterior one, with little or no rim; greatest diameter of opening about equal to distance between nostrils, 6.5 in orbit of holotype.

Scales ctenoid; no auxiliary scales on body; head scaled except mandible, throat and gill membranes, extreme front of snout and a broad zone on side of snout anterior to center of eye, which includes nostrils in its upper part. Small juveniles clearly show five diagonal rows of scales on cheek between orbit and corner of preopercle (plus a single scale just above upper posterior corner of maxilla); in larger individuals small scales, which become progressively larger, develop between the orbit and the larger scales and near the margin of the preopercle; spinous portions of dorsal and anal fins naked, the soft portions scaled basally (scales extending farther out on interradial membranes than on rays); caudal fin with small scales covering more than three-fourths distance to posterior margin; pectoral fins with small scales on basal third or more of fin; pelvic fins with small scales on medial surface.

Lateral line a smooth curve following contour of back; last pored scale slightly anterior to end of hypural plate. Some pores of cephalic lateralis system obscured by scales; prominent are: a pore in front of anterior nostril, one between nostrils, one medial to nostrils, two close together in interorbital space above front of eye, a series near edge of orbit around posterior half of eye, six on suborbital and preorbital region anterior to a vertical through center of eye, and six in a mandibular series beginning at end of lower margin of preopercle (last two on chin close together).

Origin of dorsal fin nearer a vertical at upper end of preopercular margin than upper end of gill opening; third dorsal spine prolonged in adult females, the length 4.85 to 5.82 in SL, more prolonged in males, 2.42 (2.65–3.21) in SL; second dorsal spine of females 7.51 to 8.28 in SL; second dorsal spine of males prolonged, 3.39 (2.63–2.93) in SL; tips of prolonged second and third dorsal spines of males with a short fleshy cirrus; longest dorsal soft ray 1.77 (1.79–2.02) in head; third anal spine 2.38 (2.12–2.37) in head; longest anal soft ray 1.23 (1.15–1.44) in head; caudal fin lunate, the lobes filamentous, caudal concavity 3.22 (3.47–3.8) in SL; longest rays of pectoral fins (tenth or eleventh) 3.77 (2.9–3.61) in SL; pelvic fins long, 2.49 (2.42–3.09) in SL, reaching to or beyond anus, and well beyond spinous portion of anal fin in males and small juveniles.

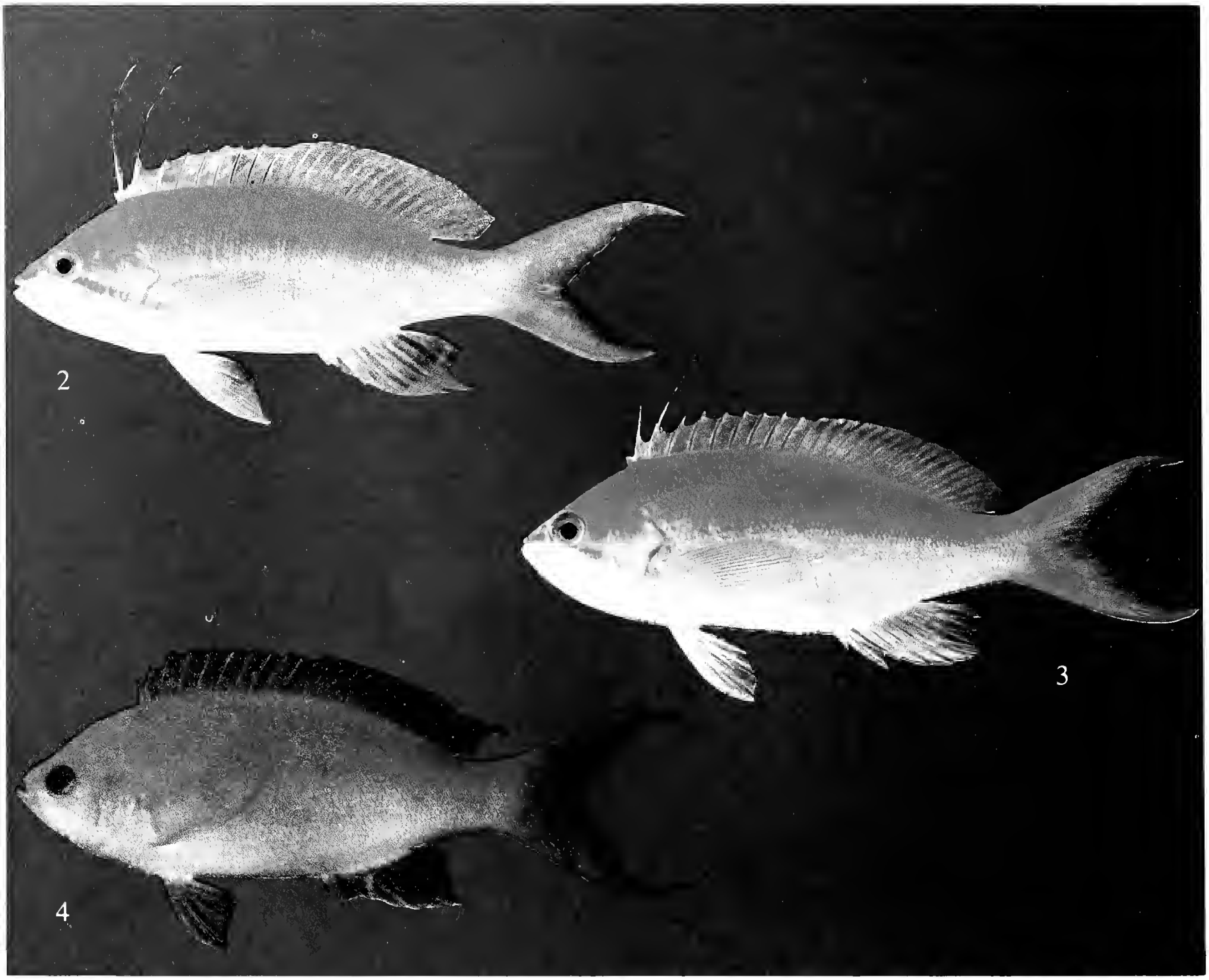
Color of adults and large juveniles in alcohol pale with no dark markings. Color of male holotype when fresh: upper half of body salmon, lower half lavender-pink; an orange-yellow band faintly edged in lavender running from lower part of eye to mid-pectoral base, lavender line continuing anterior to lower part of eye as a demarcation between orange-yellow color of most of snout and pale pinkish ventral part of head; indistinct pale red streak from beneath lower part of pectoral fin to above anus. Narrow red area basally at front of dorsal fin; dorsal fin mainly yellow with indistinct blotches of pale blue in middle, margin lavender, outer part of second and third and nearly all of fourth interspinous membranes red; fleshy cirri at tips of second and third spines bright yellow. Anal fin with pale blue membranes, shading outwardly to light red, rays pink, and margin pale bluish. Caudal fin with a broad zone of light red with a slight wash of yellow in lobes, shading on central and posterior part of fin to pale yellow with pink rays; pectoral fins pale pink. Pelvic fins colored much like anal fin, the lateral edge with pale bluish margin.

Color from field notes of a 99.9-mm female paratype (BPBM 10104) when fresh: upper half of body orange-yellow, lower half lavender pink (more lavender on abdomen and thorax); scales in zone of integradation of color on mid-side with yellow centers and pink edges; some irregular streaks of scales with yellow centers extending a short distance into pink lower half of body; head above lower edge of eye orange-yellow, below lavender with a wash of orange, especially on maxilla and rest of head below and anterior to eye; horizontal lavender line between orange-yellow and lavender colors on snout; tip of lower jaw lavender; orange band nearly as broad as pupil and narrowly edged with lavender, running from lower posterior portion of orbit to pectoral base. Dorsal fin primarily pale red, irregularly yellow at base (yellow limited to first five interspinous membranes); margin lavender, and an indistinct submarginal zone of yellow; rays of fin rose red. Anal fin light lavender-pink with some yellow areas, rays slightly darker, margin

TABLE 1

Fin-ray counts of *Anthias*

species	Dorsal Rays					Anal Soft Rays				Pectoral Rays							
	X	XI	16	17	18	7	8	9	10	15	16	17	18	19	20	21	22
bicolor	26	2	1	21	6	26	2							10	17	1	
thompsoni	33		32	1		33									7	25	1
ventralis																	
ventralis	11			11				11		11							
hawaiiensis	19	1	1	17	2			19	1	19	1						



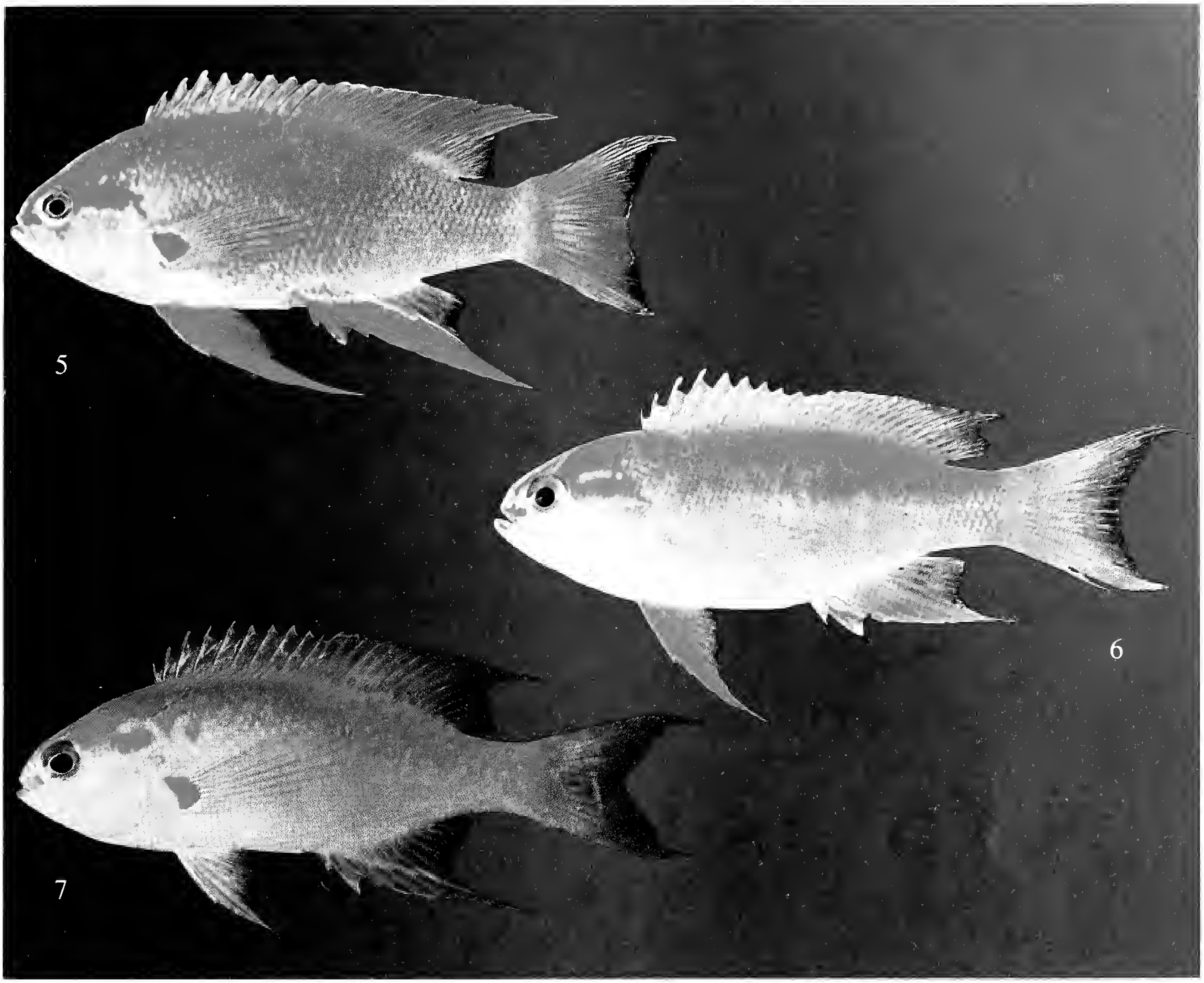
FIGURES 2–4. *Anthias* from Oahu, Hawaii. **2,** Upper, *Anthias (Mirolabrichthys) bicolor,* holotype, male, 99.2 mm SL, BPBM 10146. **3,** Middle, *Anthias (Mirolabrichthys) bicolor,* female, 83.5 mm SL, BPBM 10173. **4,** Lower, *Anthias (Pseudanthias) thompsoni,* female, 126 mm SL, BPBM 11290.

lavender. Caudal lobes rose red; upper and lower edges narrowly lavender, with traces of yellow submarginally; centro-posterior part of fin light red-orange. Pectoral fins pale magenta, the membranes pale. Pelvic fins pale yellowish, the rays light lavender.

Color from an ektrachrome transparency of 29-mm paratype (BPBM 15498; Fig. 1): upper half of body yellow, lower half lavender; dorsal fin pale yellow with violet margin. Pectoral fins lavender; remaining fins pale with a lavender cast, upper and lower margins of caudal fin, filamentous tip of pelvic fins, and tips of longest anal rays violet. In preservative, this fish shows a faint concentration of black pigment on the third interspinous membrane, a smaller spot of the same density on the second membrane, and a large but more diffuse one at the rear base of the spinous portion of the fin, extending in about equal area onto the body. In the 27.5-mm paratype these same dark areas are more evident. They are even more conspicuous on the two postlarvae (26–26.9 mm SL); in addition, the postlarvae have a blackish spot on the pelvic fins between the spine and the third ray about one-third distance from the base (only a faint remnant of this spot may be seen on the 27.5 and 29-mm specimens) and three less distinct blackish spots on caudal peduncle (dorsally, ventrally and at mid-base of caudal fin).

REMARKS: Adult and juvenile specimens of *A. bicolor* have been collected in the Hawaiian Islands, Marshall Islands, Loyalty Islands (kindly supplied by Pierre Fourmanoir of ORSTOM, New Caledonia), New Guinea, Maldive Islands and Mauritius in a depth range of 18 to 68 m. However, I have observed the species in 8 m in Hawaii, and aquarium fish collector Anthony Nahacky has seen it in as little as 5 m off Makua, Oahu. This fish usually is found in the vicinity of caves or ledges, but not infrequently it is encountered on small patch reefs where shelter seems minimal (even here an unexpected crevice generally will account for its presence). Typically it occurs in aggregations, though these may consist of only a few individuals. It feeds on zooplankton, and may rise as much as 3 or 4 m above the bottom in feeding. Although it may intermingle with feeding aggregations of *A. thompsoni,* it tends to maintain itself apart from this abundant Hawaiian species.

As in many other species of the subfamily Anthiinae, males are consistently larger than the females, probably as a result of sex reversal; also, they are notably less abundant than females. Although the differences in color between the sexes are not as marked as in some anthiines, the greatly prolonged second and



FIGURES 5–7. Species of the subgenus *Anthias (Pseudanthias)*. **5,** Upper, *Anthias ventralis hawaiiensis,* holotype, male, 76.9 mm SL, Oahu, Hawaii; BPBM 10560. **6,** Middle, *Anthias ventralis hawaiiensis,* female, 51.8 mm SL, Oahu, Hawaii; BPBM 10159. **7,** Lower, *Anthias ventralis ventralis,* male, 51.5 mm SL, Pitcairn Island; BPBM 16883.

third dorsal spines with a yellow cirrus at each tip clearly differentiates the male.

Two postlarvae (BPBM 19924) were collected in 200 m with a midwater trawl off leeward Oahu by Thomas A. Clarke of the University of Hawaii who kindly made them available as paratypes. The tow was made at 2006–2222 hours. The net remained open during descent and ascent, thus one cannot be certain of the depth of capture; however, the lowering and raising of the net required only 16 minutes of the 136-minute towing time.

The species appears to attain a larger size in the Hawaiian Islands than elsewhere. Four males in Hawaii range from 99.2 to 111 mm SL. Six males from outside Hawaii measure 63 to 82 mm SL. This difference may be due, at least in part, to the cooler water of the Hawaiian region. The largest non-Hawaiian specimen, however, is the 82-mm one from Mauritius, also a cool subtropical locality.

Named *bicolor* in reference to the salmon pink of the upper half and lavender pink of the lower half of the body. When viewed underwater in its usual moderately deep habitat (hence with shades of red subdued), the back appears more yellow and the lower side more blue, thus enhancing the bicolored effect and making this species easily distinguished from *A. thompsoni*. Anticipating the scientific name, some fish fanciers in Hawaii already have begun to use the common name "Bicolored Bass" for this species.

Anthias (Pseudanthias) thompsoni Fowler 1923

Figure 4; Tables 1–3

Caesioperca thompsoni Fowler 1923. B. P. Bishop Mus., Occ. Pap. 8(7):379 (type locality, Honolulu).

DIAGNOSIS: Dorsal rays X,16 (one of 33 specimens with 17); anal rays III,7; pectoral rays 20 or 21 (usually 21, one of 33 with 22); lateral-line scales 50 to 58; gill rakers 10 to 12 + 25 to 28; depth of body 2.7 to 3.3 in SL; no dorsal spines prolonged (fifth spine usually the longest, but fourth to tenth spines nearly equal); front of upper lip of males not thickened and not pointed; posterior edge of orbit with a row of fleshy papillae; margins of subopercle and interopercle smooth; pelvic fins short, usually not reaching anus (just reaching anus in large males); caudal fin lu-

TABLE 2

Lateral-line scale counts of *Anthias*

species	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64
bicolor																			2	5	4	6	6	2	2	1
thompsoni												1	1	2	6	8	7	4	2	2						
ventralis																										
ventralis	1	1	1	2	2	3		1																		
hawaiiensis		2	2	6	6	1	2	1																		

nate, the caudal concavity of large males up to 1.85 in SL; small villiform teeth on vomer forming a broad V-shaped (nearly triangular) patch; band of teeth on palatine narrow, consisting of only two irregular rows; anxiliary scales present over entire body; mandible scaled; dorsal and anal fins naked.

Color in alcohol pale with no dark markings. Color of an adult female when fresh: body red-orange dorsally, with a yellow spot basally on each scale; laterally the yellow has shifted to the edges of the scales, and the red-orange color is more magenta; ventrally the yellow fades to light lavender, and the scale centers to pale heliotrope. A double band, yellow above and magenta below, from lower edge of eye to lower opercle, then turning upward along margin of opercle to level of upper base of pectoral fin; a similar but faint double band extending onto snout from front of eye; a narrow yellow rim on posterior half of eye. Dorsal fin red; membranes mottled with yellow; margin of soft portion lavender. Anal rays salmon; the membranes light yellow; margin of anterior half of soft portion lavender (to tip of acute angle of margin). Caudal fin yellow-orange; upper and lower edges red, shading outwardly to lavender. Pectoral rays salmon, membranes transparent; base of fin yellowish with faint lavender marking in approximate V-shape. Pelvic rays salmon, membranes light yellow. Color of a large adult male is similar but the magenta streak on the head is broader with a wide band of yellow on either side; and the pectoral fin base more yellow with the lavender V more evident; large area of yellow on the basal rayed part of fin, with a faint broad outer margin of lavender; maxilla pale yellow, with a broad pale magenta border; lavender upper and lower margins of caudal fin and red submarginal lines are more pronounced, with a faint posterior margin of lavender and red submarginal line in central part of fin.

REMARKS: *A. thompsoni* is known only from the Hawaiian Islands. It is common near rocky vertical discontinuities in the bottom. Brock and Chamberlain (1968) commented on its abundance in loose schools on near-shore escarpments from submarining observations off the Waianae coast of Oahu. Strasburg, Jones and Iversen (1968) also observed it from a research submarine, in the depth range of 55 to 110 m, as did Clarke (1972:311) who noted that it was "seen frequently down to about 150 m, but never deeper."

Bishop Museum collections of this species have come from 26 to 157 m. It occurs in water at least as shallow as 10 m; however, it is not common in the lesser depths.

The stomach contents of six specimens, 98 to 119 mm SL, from three different lots, were examined. This material consisted entirely of zooplankton, primarily copepods. Also, shrimp larvae frequently were eaten. Adults feed up to several meters above the bottom (exceptionally as much as 9 m).

On April 25, 1972 I speared a jack *(Caranx melampygus)* 410 mm fork length off Barber's Point, Oahu that had three *A. thompsoni* in its stomach measuring 75 to 85 mm SL.

Females are much more numerous than males. Males have been observed in courtship; they elevate the dorsal fin during the display, which appears to take on a deeper red color; also, there is a red band along the back and a red border behind the operculum.

The holotype (BPBM 3376, 122 mm SL) is in the Bishop Museum and is in good condition. Corrections are in order for some of the counts given by Fowler in the description. The fish has 21 (not 22) pectoral rays, 54 (not 58) lateral-line scales, and 28 (not 27) lower-limb gill rakers. Fowler described *thompsoni* in *Caesioperca* Castelnau, a genus otherwise known only from temperate waters of Australia and New Zealand. A specimen of the type species of the genus, *C. rasor* (Richardson), was examined. It clearly is divergent from *thompsoni,* having a supplemental maxillary bone (absent in *thompsoni*), 21 dorsal soft rays, 14 pectoral rays, and a shallowly forked caudal fin.

The largest specimen of *A. thompsoni* (BPBM 15443) measures 149 mm SL. The Natural History Museum of Los Angeles County has specimens in two series (LACM 32242–1, 15:89–144

TABLE 3

Gill-raker counts of *Anthias*[3]

species	Upper Limb						Lower Limb							
	7	8	9	10	11	12	21	22	23	24	25	26	27	28
bicolor					13	15						6	15	7
thompsoni				2	14	7					3	9	15	6
ventralis														
ventralis	2	9					1	4	3	3				
hawaiiensis	1	14	5					4	7	6	3			

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[3] Gill-raker counts were made on the first arch and include all rudiments; the raker at the angle is included in the lower-limb count.

TABLE 4

Measurements of type specimens of *Anthias (Mirolabrichthys) bicolor* expressed as a percentage of the standard length

	HOLOTYPE	PARATYPES				
	BPBM 10148	BPBM 15498	BPBM 13344	BPBM 10142	BPBM 10173	BPBM 10173
Standard length (mm)	99.2	29.0	47.0	67.6	88.3	104.3
Depth of body	35.4	33.8	35.5	36.5	34.5	35.7
Width of body	17.0	15.5	15.0	17.0	17.5	18.2
Head length	31.2	35.5	32.0	33.9	31.0	31.9
Snout length	8.8	8.6	7.5	8.7	8.2	9.5
Diameter of orbit	7.2	11.5	10.2	8.5	7.8	7.1
Bony interorbital width	7.5	8.3	8.3	7.7	7.8	8.1
Length of maxilla	16.4	15.6	15.1	15.8	15.9	16.9
Least depth of caudal peduncle	14.5	12.5	13.6	15.1	14.4	14.8
Length of caudal peduncle[4]	21.0	20.0	21.3	20.7	21.5	21.3
Predorsal length	26.9	29.9	26.2	27.2	25.6	26.5
Preanal length	62.2	62.4	63.5	65.2	62.7	64.2
Prepelvic length	33.3	36.2	33.7	35.3	33.3	35.4
Length of first dorsal spine	4.3	6.5	—	4.7	5.1	5.1
Length of second dorsal spine	29.5	13.3	12.1	13.3	12.3	38.0
Length of third dorsal spine	31.2	15.5	—	20.6	17.2	41.3
Length of tenth dorsal spine	10.5	14.5	14.3	13.9	11.4	11.9
Length of longest dorsal ray	17.6	17.5	17.6	17.9	17.0	17.8
Length of dorsal fin base	65.4	63.2	65.8	63.6	65.6	66.6
Length of first anal spine	7.0	8.9	8.5	7.1	6.9	8.0
Length of second anal spine	—	19.7	17.6	16.6	14.2	14.1
Length of third anal spine	13.1	15.2	15.1	14.6	13.1	13.7
Length of longest anal ray	25.2	31.0	25.0	23.4	24.7	26.9
Length of anal fin base	18.5	20.7	19.5	19.6	18.7	19.0
Length of pectoral fin	26.5	34.4	30.2	31.2	28.1	27.7
Length of pelvic spine	16.1	21.0	18.2	18.1	16.4	16.2
Length of pelvic fin	40.1	41.4	33.4	32.9	32.4	41.2
Length of caudal fin	44.4	52.4	51.7	44.7	40.3	47.5
Caudal concavity[5]	31.0	28.9	34.9	29.6	26.3	33.7

[4] Measured diagonally from rear base of anal fin to mid-base of caudal fin.

[5] Measured horizontally between verticals at tips of shortest and longest caudal fin rays.

mm SL; LACM 32668–14, 17:83–148 mm SL), which are nearly as large. These were taken by trawl off Haleiwa, Oahu in 120 m.

John E. Fitch of the Department of Fish and Game, State of California, examined the otoliths from these LACM specimens. He detected one presumed annular ring in the otoliths of four specimens 83–95 mm, two in 14 specimens 93–112 mm, three in three specimens 112–127 mm, four in four specimens 137–140 mm, and five in a 145-mm specimen. He wrote me, ". . . While they (the otoliths) are not the best in the world for reflecting ages, I feel reasonably certain of my readings."

Five postlarval specimens of *A. thompsoni* (BPBM 19925, 23.4 to 24.3 mm SL) were collected off leeward Oahu by Thomas A. Clarke of the University of Hawaii from the R/V *Teritu* in a 3.05-m midwater trawl at a depth of 225 m on 11 June 1971. The time of the tow was 0200–0416 hours; the lowering and raising of the net required 18 minutes of this time. These fish have a very long serrate spine at the corner of the preopercle (nearly as long as diameter of orbit), with 7 to 9 smaller spines on upper limb of preopercle (adjacent spine somewhat enlarged and serrate), and three spines on lower limb (middle spine somewhat enlarged and serrate); also, there is a spine on the subopercle and 2 to 5 on the interopercle. There are no distinctive large blackish spots as on the postlarvae of *A. bicolor,* but there is a concentration of dark pigment basally on the third interspinous membrane of the dorsal fin and lesser dark blotches may be found on the lower part of the second membrane and basally on the fourth to seventh spines. Also a small amount of dark pigment may be seen on some specimens on the membranes behind the tips of the second to seventh spines and near the base of the pelvic fins centered on the first and second soft rays. As in many postlarvae, there are some fine dots of melanin over the occipital region of the head.

Anthias (Pseudanthias) ventralis hawaiiensis

NEW SPECIES AND SUBSPECIES

Figures 5–6; Tables 1–3, 5

HOLOTYPE: BPBM 10560, 76.9 mm SL, male, Hawaiian Islands, Oahu, Moku Manu; off N side at base of drop-off, 49 m, rotenone, J. E. Randall, W. J. Baldwin and A. Stark, 9 October 1968.

PARATYPES: BPBM 10561, 7(38.3–71.1 mm SL), same data as holotype: ANSP 134236, 1(62.5 mm SL), same data as holotype, AM I.18720–001, 1(49 mm SL), same data as holotype; BM(NH) 1976.3.15.2, 1(65.1 mm SL), same data as holotype; LACM 35578–1, 1(69.4 mm SL), same data as holotype; BPBM 10159, 3(36.3–62.2 mm SL), Hawaiian Islands, Oahu, off Kahana Bay, NW side of channel at entrance to bay, ledges and caves in 26 m, quinaldine, J. E. Randall and P. M. Allen, 12 September 1970; MNHN 1974–17, 1(60.2 mm SL), same data as preceding; BPBM 10172, 1(52.9 mm SL), same locality as

TABLE 5

Measurements of type specimens of *Anthias (Pseudanthias) ventralis hawaiiensis* expressed as a percentage of the standard length

	HOLOTYPE	PARATYPES				
	BPBM 10560	BPBM 15058	BPBM 10159	BPBM 10159	BPBM 10159	BPBM 10561
Standard length (mm)	76.9	24.0	36.3	51.8	62.2	71.1
Depth of body	37.8	35.8	35.4	34.7	34.0	38.4
Width of body	18.6	17.4	15.8	16.4	15.6	18.4
Head length	29.7	34.5	33.6	31.4	30.5	30.0
Snout length	7.4	7.5	7.4	7.2	7.3	7.7
Diameter of orbit	7.8	11.6	11.0	9.9	8.8	8.3
Bony interorbital width	8.9	9.2	9.1	8.9	8.9	9.0
Length of maxilla	14.8	15.8	15.4	14.2	14.4	14.5
Least depth of caudal peduncle	15.0	14.1	15.1	14.9	14.5	15.1
Length of caudal peduncle	20.7	19.7	19.6	18.7	20.2	19.2
Predorsal length	32.4	32.1	33.1	32.6	32.7	32.8
Preanal length	60.2	63.3	62.0	63.1	61.7	62.5
Prepelvic length	33.2	35.3	33.1	33.7	32.1	33.7
Length of first dorsal spine	5.8	5.6	5.5	5.6	5.0	5.3
Length of longest dorsal spine	12.9	16.0	15.7	15.3	13.4	13.2
Length of longest dorsal ray	32.3	18.8	23.8	21.8	26.2	30.0
Length of dorsal fin base	62.6	54.5	61.1	59.9	60.0	60.8
Length of first anal spine	6.2	7.9	7.7	7.1	6.4	6.1
Length of second anal spine	12.9	16.3	17.2	15.2	12.9	12.7
Length of third anal spine	13.6	15.8	16.6	14.3	12.9	12.8
Length of longest anal ray	40.2	30.8	30.3	32.4	37.5	39.4
Length of anal fin base	23.4	22.9	22.9	22.3	22.3	21.6
Length of pectoral fin	30.9	33.3	32.5	31.4	30.2	32.1
Length of pelvic spine	16.0	19.1	19.8	17.2	15.8	15.5
Length of pelvic fin	49.7	37.0	28.5	37.6	43.2	—
Length of caudal fin	32.7	48.0	36.3	35.5	34.6	37.0
Caudal concavity	11.8	24.1	14.0	13.7	12.5	16.2

preceding, rotenone, J. E. Randall, 27 September 1970. CAS 35679, 1(41.8 mm SL), Hawaiian Islands, Oahu, off Makapuu Point, collected from salvaged vessel raised from 68 m, W. D. Madden, 14 October 1970; USNM 215285, 1(43.8 mm SL), same data as preceding; BPBM 15058, 1(24 mm SL), Hawaiian Islands, Hawaii, South Point, large boulders and adjacent sand, 28 m, rotenone, L. Taylor and P. M. Allen, 21 May 1973.

DIAGNOSIS: Dorsal rays X,16 to 18 (usually 17); anal rays III,9 (rarely 10); pectoral rays 15 (rarely 16); lateral-line scales 40 to 46; gill rakers 7 to 9 + 22 to 25; depth of body 2.37–2.94 in SL; no dorsal spines prolonged (fifth spine usually the longest, but fourth to tenth nearly as long); front of upper lip of males not thickened and pointed; no papillae along rim of posterior half of eye; margin of subopercle serrate, and a few serrae may be present on upper posterior edge of interopercle; pelvic fins long, reaching well beyond origin of anal fin (entirely beyond base of fin in adult males); a few small teeth on vomer in an approximately triangular patch; band of teeth on palatines narrow, consisting of two or three irregular rows; a few auxiliary scales dorsally on body; mandible scaled; dorsal and anal fins scaled except distally. Color as in figures 5 and 6, the most conspicuous feature being the yellow of the upper half of the head with a few short lines of violet or magenta behind and above the eye.

DESCRIPTION: Dorsal fin X,17 (X,17 except one paratype with XI,18, one with X,18, and one with X,16); anal fin III,9 (one of 19 paratypes with 10); pectoral rays 15 (one of paratypes with 16), upper one or two and lowermost unbranched; pelvic fin I,5; principal caudal rays 15 (upper and lower unbranched); lateral-line scales 42 (40–46); scales above lateral line to origin of dorsal fin 5; scales below lateral line to origin of anal fin 19 (18–20); circumpeduncular scales 22; gill rakers 8 + 25 (17–9 + 22–25); pseudobranchial filaments 11 (10–12); branchiostegal rays 7; vertebrae 26.

Body depth variable, 2.65 (2.37–2.94) in SL; body moderately compressed, the width 2.03 (2.04–2.25) in depth; head length 3.37 (2.9–3.33) in SL; snout 4.02 (3.9–4.6) in head; front of upper lip of males not thickened and not pointed (contour of front of upper lip when viewed from above varying from slightly convex to flat); diameter of orbit 3.81 (2.97–3.6) in head; posterior edge of orbit without fleshy papillae; interorbital space smoothly convex, the bony width 3.34 (3.33–3.75) in head; least depth of caudal peduncle 1.98 (1.98–2.44) in head.

Mouth oblique and moderately large, the maxilla reaching posterior to a vertical at center of eye and often to or slightly beyond a vertical at posterior edge of pupil; lower jaw projecting slightly when mouth closed; upper posterior corner of maxilla more broadly rounded than lower; greatest depth of maxilla 2 in orbit of holotype; no supplemental maxillary bone. Upper jaw with inner row of villiform teeth of moderate size broadening to a maximum of about 4 rows anteriorly, the innermost and most medial of these teeth notably enlarged, lying nearly flat, and directed inward; a canine laterally at front of upper jaw, followed by a row of 13 teeth along side of jaw, which are about as long as front canine but more slender; posterior ones pointing forward;

TABLE 6

Measurements of type specimens of *Anthias (Pseudanthias) ventralis ventralis* expressed as a percentage of the standard length

	HOLOTYPE	PARATYPES			
	BPBM 16883	BPBM 13530	BPBM 13530	BPBM 13530	BPBM 19895
Standard length (mm)	51.5	20.4	31.8	50.8	54.3
Depth of body	35.1	32.9	32.0	33.4	33.4
Width of body	16.5	15.7	15.7	16.7	16.2
Head length	31.5	36.8	33.4	31.8	33.0
Snout length	7.8	7.9	7.6	7.7	7.7
Diameter of orbit	10.3	12.5	11.3	9.6	9.6
Bony interorbital width	8.8	9.0	8.5	8.9	8.7
Length of maxilla	14.5	15.7	14.1	14.9	14.9
Least depth of caudal peduncle	14.4	13.7	14.6	14.3	14.2
Length of caudal peduncle	18.9	19.4	20.4	19.2	18.6
Predorsal length	33.2	34.8	33.1	33.2	32.3
Preanal length	61.0	63.7	63.1	60.3	61.7
Prepelvic length	33.2	36.6	34.0	33.0	33.2
Length of first dorsal spine	6.2	6.3	5.8	6.1	6.2
Length of longest dorsal spine	13.4	16.2	15.7	13.9	13.1
Length of longest dorsal ray	27.0	18.1	17.7	29.7	29.5
Length of dorsal fin base	60.2	53.9	56.8	61.0	58.2
Length of first anal spine	7.4	7.8	7.7	7.3	7.1
Length of second anal spine	14.4	15.7	15.7	13.8	14.0
Length of third anal spine	13.8	15.7	15.4	13.8	13.3
Length of longest anal ray	35.4	21.5	25.1	32.6	40.8
Length of anal fin base	21.4	22.5	22.1	22.0	21.8
Length of pectoral fin	32.4	30.6	32.1	33.4	32.6
Length of pelvic spine	16.7	19.7	17.9	17.1	16.4
Length of pelvic fin	39.3	29.4	29.2	44.7	54.3
Length of caudal fin	38.3	—	37.8	—	43.7
Caudal concavity	17.8	—	15.7	—	21.5

a pair of moderate canines anteriorly in lower jaw that project slightly forward; two to three rows of smaller, incurved teeth medial to anterior canines; four or five strongly retrorse canines along side of anterior third of lower jaw; posterior to these are a series of uniformly large teeth (six on one side of holotype, nine on other) that point forward strongly, these closely associated with an outer row of smaller more slender teeth. Teeth on vomer small, in a patch of approximately triangular shape; a narrow band of two or three rows of small teeth on palatines. Tongue pointed. Gill membranes free from isthmus. Gill rakers slender and long, about as long as longest gill filaments; length of the longest contained 1.6 times in diameter of orbit of holotype.

Opercle with three flattened spines; the central one the largest and most posterior; the upper spine obtuse and indistinct, slightly anterior to lower; two lower spines acute, distance between their tips generally about three-fourths distance between central and upper spines. Lower edge of preopercle smooth; upper edge finely serrate (25 serrae on holotype; number of serrae variable, but tending to increase with size; paratypes from 24 to 42 mm SL have 16 to 23 serrae whereas those over 50 mm have 22 to 36); ventral edge of subopercle with 14 (4 to 14) serrae; interopercle with 4 (0–4) serrae near upper end.

Anterior nostril in a membranous tube (higher dorsoposteriorly) directly anterior to middle of eye and about halfway between edge of orbit and groove separating upper lip from rest of snout; posterior nostril large, dorso-posterior to anterior one, roughly semicircular, and without a rim; its greatest diameter nearly equals its distance from anterior nostril (about 6 in diameter of orbit of holotype).

Scales ctenoid; some auxiliary scales may be present on nape and body dorsal to lateral line. Head scaled except throat, gill membranes, extreme front of snout, and a broad zone of snout from level of lower edge of eye to above nostrils. Dorsal and anal fins with scales on about basal half (ignoring prolonged rays and associated membranes); caudal fin with small scales extending about three-fourths distance to posterior margin; pectoral fins scaled on about basal third; pelvic fins scaled on medial surface, the scales on first ray extending slightly beyond the pelvic spine.

Lateral line a little more strongly arched than upper contour of body, reaching highest point below posterior half of spinous portion of dorsal fin; last pored-scale of lateral line just anterior to posterior edge of hypural plate. Pores of cephalic lateralis system similar to those of *A. bicolor*.

Origin of dorsal fin above (or slightly anterior or posterior) to upper end of gill opening; no dorsal spines prolonged; fifth dorsal spine usually the longest, 2.3 (2.05–2.28) in head; a small cirrus behind tip of each dorsal spine; twelfth dorsal soft ray (and to a lesser extent adjacent rays) prolonged (except in small juveniles), its length 3.1 (3.33 to 4.2) in SL; third anal spine 2.18 (2.02–2.36) in head; fourth anal soft ray (and to a lesser extent adjacent rays) greatly prolonged, its length 2.49 (2.54–3.3) in SL; caudal fin deeply emarginate, the caudal concavity 2.52 (1.43–2.44) in head; longest ray of pectoral fins (ninth) 3.24 (3.0–3.31) in SL; second pelvic ray (and to a lesser extent adjacent rays) greatly prolonged, reaching beyond spinous portion of anal fin and often posterior to base of fin, the ray length 2.01 (2.17–3.51) in SL.

Color in alcohol pale with no dark markings. Color of holotype and other large males when fresh (from field notes): anterior part of body orange, dotted with magenta, shading to light yellowish with a lavender wash on thorax and abdomen, and to violet posteriorly. Upper half of head yellow with dotted lines of magenta as follows: from snout in front of eye through upper edge of eye and passing dorsally to nape, from behind eye along upper edge of opercle, from in front of lower part of eye through lower edge of eye and across middle of operculum to middle opercular spine; lower half of head varying from light yellowish to pale lavender. Dorsal fin orange, edged with magenta (except posteriorly); rear basal part nearly colorless; anal fin with anterior part (including prolonged rays) orange, posterior portion yellow, the two regions separated by a magenta line; caudal fin yellow-orange, shading to magenta in broad median posterior part of fin; pectoral fins pale orangish with a large magenta-edged orange spot on base; pelvic fins orange with a little magenta on leading edge of spine; isthmus yellow-orange (see Fig. 5).

Color of females when fresh similar but body mostly yellow instead of orange, the yellow unmarked dorsally, over posterior part of caudal peduncle and most of caudal fin; ventral half of body lavender; magenta lines on head more solid (and hence more evident) on females than males; anal fin almost entirely yellow, lacking the striking two-tone coloration with magenta division of the male; yellow spot at base of pectoral fin not as conspicuous as the orange basal spot on the fin of the male (see Fig. 6).

REMARKS: The Hawaiian population of *Anthias ventralis* is sufficiently distinct to warrant subspecific recognition, hence *hawaiiensis*. See "Remarks" of *A. v. ventralis* for discussion of differences.

The Hawaiian subspecies was collected in the depth range of 26 to 68 m. Nearly all specimens were taken from caves or beneath well-formed ledges. They are more closely tied to the substratum than the other two *Anthias* in Hawaii and are often seen swimming upside down near the roof of caves. They venture out for feeding on zooplankton (mainly copepods, but also other crustacean larvae, fish eggs, mollusk larvae, polychaete larvae, etc.).

This species is a good aquarium fish, though not often caught due to its deep-dwelling habits. It is hardier than the other two Hawaiian *Anthias* in aquaria.

Named *ventralis* in reference to the striking prolongation of the pelvic and anal fins.

The common name "Longfin Bass" is proposed for this species.

Anthias (Pseudanthias) ventralis ventralis

NEW SUBSPECIES

Figure 7; Tables 1–3, 6

HOLOTYPE: BPBM 16883, 51.5 mm SL, male, Pitcairn Island, patch reef on N side off Gannet Ridge, 40 to 44 m, rotenone, J. E. Randall, D. B. Cannoy, J. R. Haywood, R. R. Costello, J. D. Bryant and S. Christian, 6 January 1971.

PARATYPES: BPBM 13530, 8(18.2–50.8 mm SL), Tuamotu Archipelago, Gambier Group, Temoe Atoll, outside reef on N side, isolated dead coral block on sand near fringing reef, 41.3 m, rotenone, J. E. Randall, D. B. Cannoy, R. McNair and R. R. Costello, 16 December 1970; BM(NH) 1973.3.5.1, 1(29.4 mm SL), same data as preceding; LACM 35586-1, 1(21 mm SL), same data as preceding; USNM 215289, 1(29.8 mm SL), same data as preceding; BPBM 19895, 1(54.3 mm SL), New Caledonia, false pass Uitoe (about 3 km N of Dumbéa Pass), 55 m, bottom mainly coral rubble, rotenone, P. Laboute and Y. Magnier, 5 November 1975.

DIAGNOSIS: As in *Anthias ventralis hawaiiensis*, except for slightly lower gill-raker counts (see Table 3), more interopercular serrae, smaller size and color (see below).

DESCRIPTION: Dorsal rays X,17; anal rays III,9; pectoral rays 15 (upper one or two and lower one or two unbranched); pelvic rays I,5; principal caudal rays 15 (upper and lower unbranched); lateral-line scales 44 (39–46); scales above lateral line to origin of dorsal fin 5 (4 or 5); scales below lateral line to origin of anal fin 19 (18–19); circumpeduncular scales 22 (20–22); gill rakers 8 + 24 (7–8 + 21–24); pseudobranchial filaments 10 (9–10); branchiostegal rays 7; vertebrae 26.

Body depth 2.85 (2.86–3.13) in SL; width of body 2.13 (2.0–2.09) in depth; head length 3.17 (2.72–3.14) in SL; snout 4.05 (4.14–4.67) in head; front of upper lip of males not thickened and not pointed; diameter of orbit 3.08 (2.94–3.43) in head; interorbital space convex, the bony width 3.58 (3.58–3.93) in head; least depth of caudal peduncle 2.19 (2.22–2.67) in head.

Dentition similar to *A. v. hawaiiensis:* 14 large teeth along one side of upper jaw of holotype, and 15 on the other; more small teeth posterior to large ones on side of lower jaw than in *hawaiiensis*. Tongue, gill rakers, nostrils and head pores comparable to *hawaiiensis*.

Opercular spines and serrae of preopercle and subopercle as in *A. v. hawaiiensis;* holotype with 24 serrae on preopercle and 9 on subopercle. There are, however, usually more serrae on the average on the interopercle of *A. v. ventralis* (4 on holotype and 1 to 6 on paratypes).

Squamation similar to *A. v. hawaiiensis* except there are very few auxiliary scales on dorsal body scales, and small scales do not extend as far out on the median fins.

Origin of dorsal fin above upper end of gill opening; no dorsal spines prolonged; fifth to ninth dorsal spines the longest, 2.37 (2.13–2.52) in head; a small cirrus behind tip of each dorsal spine; twelfth dorsal soft ray, and to a lesser extent the eleventh and thirteenth, prolonged in adults, its length 3.7 (3.37–5.65) in SL; third anal spine 2.28 (2.17–2.47) in head; fourth anal soft ray, and to a lesser extent third and fifth rays, prolonged, 2.83 (2.45–4.65) in SL; caudal fin deeply emarginate, the caudal concavity 1.77 (1.53–2.12) in head; longest ray of pectoral fins (ninth) 3.09 (3.0–3.27) in SL; second pelvic ray, and to a lesser extent adjacent rays, greatly prolonged, reaching beyond spinous portion of anal fin and in some larger individuals posterior to rear base of anal fin, the ray length 2.54 (2.24–3.42) in SL.

Color in alcohol uniform pale with no dark markings. Color of holotype and other males when fresh: orange-yellow with small spots of lavender dorsally, shading to lavender on sides (zone of intergradation, especially anteriorly, with yellow streaks extending ventrally into lavender zone and vice versa), and to pale yellow ventrally. Snout, tip of chin, and postorbital part of head above level of center of eye bright yellow; lower part of head and all of thorax pale yellow; deep yellow streak mid-ventrally on head; broken line of lavender running from upper lip to eye; horizontal lavender band behind eye separating upper bright yellow and lower pale yellow of head; an arc of lavender beginning on opercle anterior to gill opening, rimming upper gill opening and joining posterior end of horizontal lavender line of postorbital head; broken lavender line on nape from upper edge of orbit to origin of dorsal fin. Dorsal fin yellow with a few small lavender spots basally; spines and adjacent membrane tips magenta; anterior margin of soft portion lavender; faint diagonal light blue line in fin running in part on eleventh to thirteenth soft rays; anal fin with a broad yellow-orange streak edged in lavender from origin of fin to tip of prolonged fourth ray; remainder of fin light yellow; caudal fin light yellow with lavender upper and lower margins basally, shifting to light blue distally; posterior edge of caudal fin in central part with faint light blue margin; faint wavy vertical dark-edged light blue band near middle of caudal fin; pectoral fins light yellowish with large semicircular yellow-orange spot edged in lavender at base; pelvic fins yellow, deeper yellow laterally, with lavender lateral margin. Iris yellow with two broad diagonal streaks of blue (dorso-anterior and ventro-posterior to pupil).

Color of a 33-mm female from the atoll of Temoe, Tuamotu Archipelago when fresh: body light magenta dorsally, shading to pale lavender ventrally and white on abdomen and thorax (lavender mid-ventrally), except for a zone of bright yellow above a line of demarcation from mid-base of dorsal fin to lower base of caudal fin (a deep orange streak separates the yellow and magenta from below base of fifth soft dorsal ray to anterior caudal peduncle). Tip of lower jaw and front of snout bright yellow; upper postorbital head light magenta; prominent V-shaped mark of deep yellow, edged with orange from apex at origin of dorsal fin to dorso-posterior edge of orbit of either side. Dorsal fin bright yellow; spines tipped with magenta; margin of anterior soft portion of fin lavender; anal fin similar but entire fin becoming lavender posteriorly; caudal fin light yellow, the upper and lower edges narrowly magenta; pectoral fins pale; pelvic fins pale with a broad deep yellow streak on first to third soft rays and associated membranes.

REMARKS: *A. v. ventralis* has been collected in the Pitcairn Group, Tuamotu Archipelago, and New Caledonia from 40 to 55 m. In addition, my associates and I obtained one specimen in 46 m from a cave in a vertical drop-off at the west end of Enewetak Atoll, Marshall Islands on July 5, 1975. This specimen is unusual in having five opercular spines on one side and four on the other, instead of the usual three, and mainly for this reason it is not regarded as a paratype. In other respects it is typical of the subspecies.

Populations of reef fishes in the Hawaiian Islands often are distinct from elsewhere in Oceania. The differences may be so slight as to not warrant nomenclatural recognition, or they may be of equal magnitude to those that separate many sympatric marine species. In the case of *A. ventralis*, recognition of the Hawaiian variant as a subspecies seems to be the best treatment. *A. v. hawaiiensis* differs in having slightly higher gill-raker counts, fewer interopercular serrae, a deeper body on the average (depth 2.37–2.94 compared to 2.85–3.13 for *A. v. ventralis*), larger size (largest 76.9 mm, compared to 54.3 mm for *A. v. ventralis;* since three of the four localities for *A. v. ventralis* are from higher latitudes than Oahu, one cannot explain the larger size as a cool-water effect), and color. The females in Hawaii do not have such a sharp demarcation of the yellow dorsoposteriorly on the body from lavender or magenta on the side, and the males in Hawaii have an orange-red wash over the middle and anterior part of the body (except ventrally) plus more orange and red in the fins. It is possible, however, that a larger male than any taken thus far outside Hawaii will have more red and orange color.

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THORACICAN CIRRIPEDIA OF THE LOWER PLIOCENE PANCHO RICO FORMATION, SALINAS VALLEY, MONTEREY COUNTY, CALIFORNIA

By Victor A. Zullo

Published by the NATURAL HISTORY MUSEUM OF LOS ANGELES COUNTY • 900 EXPOSITION BOULEVARD • LOS ANGELES, CALIFORNIA 90007

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Edward Ostermeyer
Editor

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CONTENTS

The *Science Bulletin* and *Contributions in Science* of the Natural History Museum of Los Angeles County were merged into a single imperial octavo serial, retaining the name *Contributions in Science* and beginning with Number 301.

This serial has been newly formatted for maximum use of typography and illustrations per page, and sized for maximum use of paper. All photography has been produced utilizing a 200-line screen for detail.

Since most institutions rebind *Contributions in Science* collectively into hardbound volumes, and many researchers using them desire to photocopy material, two new features have been incorporated into the new format. A suggested citation line provides the abbreviated serial title, year, number of publication, and total pagination, and appears in the lower left corner of each page; and pages of *Contributions in Science* have been printed off-center to provide a two-inch gutter between adjacent pages for easier accessibility in photocopying.

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Contributions in Science are articles in the earth and life sciences, presenting results of original research in Natural History. *Science Bulletin* (Numbers 1–30; 28 June 1965 to 10 April 1978) and *Contributions in Science* (Numbers 1–300; 23 January 1957 to 16 June 1978) were merged into a single imperial octavo serial beginning with Number 301.

THORACICAN CIRRIPEDIA OF THE LOWER PLIOCENE PANCHO RICO FORMATION, SALINAS VALLEY, MONTEREY COUNTY, CALIFORNIA[1]

By Victor A. Zullo[2]

ABSTRACT: Five thoracican barnacles, including *Balanus gregarius* (Conrad 1856), *B. proinus* Woodring 1950, and three new taxa, *B. proxinubilus*, *B. addicotti*, and *B. crenatus leipochoma*, were found in association with a nearshore warm temperate molluscan fauna. *Balanus proxinubilus*, which also occurs in the Upper Pliocene San Diego Formation, is related to the extant Pacific Coast species *B. nubilus* Darwin 1854. *Balanus addicotti* is allied to the extant pantropical species *B. trigonus* Darwin 1854, and *B. crenatus leipochoma* differs but slightly from extant *B. crenatus* Bruguière 1789. The Pancho Rico occurrence of *B. proinus* represents the oldest known record of this southern California Pliocene species.

The Pancho Rico Formation is of interest to students of fossil Cirripedia in that it is probably the type locality for *Balanus (Balanus) gregarius* (Conrad 1856). As first described by Conrad (1856, 1857a), this large and unusual barnacle was indicated as having been collected in Monterey County by A.S. Taylor, an early resident of Monterey. Except for its presence in the northernmost outcrops of the Upper Miocene Santa Margarita Formation near Vineyard Canyon, *B. gregarius* is known in Monterey County only from the Pancho Rico Formation (text figure 1). Its conspicuousness and abundance at several easily accessible localities in a part of the Salinas Valley that was populated during Taylor's lifetime strongly suggest that the original specimen came from the Pancho Rico, rather than the more southerly and limited exposures of the Santa Margarita. The type specimen, which presumably would have been deposited in the Academy of Natural Sciences of Philadelphia, has not been located and is probably lost.

The Lower Pliocene Pancho Rico Formation as redefined by Durham and Addicott (1964, 1965) is characterized by fine grained sandstone and lesser amounts of conglomerate and mudstone overlying Late Miocene or older rocks and underlying the Pliocene or Pleistocene Paso Robles Formation. According to Addicott (*in* Durham and Addicott 1965:A 18) the molluscan fauna of the Pancho Rico Formation suggests "that the local early Pliocene marine climate was generally warmer than modern climates at comparable latitudes off the central California coast" and that "living representatives or modern analogs [of the Pancho Rico molluscan fauna] are usually found in shallow nearshore areas of the northeastern Pacific Ocean."

The barnacles available from the Pancho Rico Formation suggest environmental conditions similar to those proposed for the molluscan assemblage. Besides *B. gregarius*, four additional taxa were present in collections examined. *Balanus proinus* Woodring 1950 is an extinct species commonly encountered in younger Pliocene deposits in the San Joaquin Valley, the Santa Maria district, and in San Diego County. A new species related to *B. trigonus* Darwin 1854 was found at two localities. *Balanus trigonus* is an extant tropical species with Pleistocene records in the Caribbean and on the Pacific side of Mexico, indicating its presence in the tropical American fauna prior to the late Miocene closure of Central American and northern South American seaways. A second new species is closely related to the extant northeastern Pacific *B. nubilus* Darwin 1854 that presently ranges from southeastern Alaska to northern Baja California, and has a fossil record extending back to at least the late Pliocene in northern California. The new subspecies is represented by seven specimens attached to a fragment of the test of a (?)schizasterid echinoid, and differs but slightly from extant *B. crenatus* Bruguière 1789, whose range on the Pacific Coast extends from the Bering Sea to Santa Barbara, California.

DESCRIPTION OF LOCALITIES

Natural History Museum of Los Angeles County, Invertebrate Paleontology Collection (LACMIP)

4660. North side of Wildhorse Canyon, NW 1/4 of SE 1/4 of Sec. 8, T. 20 S., R. 9 E., San Lucas Quadrangle. Collectors: J.A. Wolfe and V.A. Zullo, 1961 (= USGS locality M1341).

United States Geological Survey (USGS)

M903. Sandstone bluff on west side of State Highway 198, 425 feet south, 425 feet west of NE corner of Sec. 5, T. 21 S., R. 9 E., San Lucas quadrangle. Collectors: D.L. Durham, 1959; W.O. Addicott and D.L. Durham, 1964.

M913. North side of Wildhorse Canyon, 2650 feet north, 1075 feet east of SW corner of Sec. 8, T. 20 S., R. 9 E., San Lucas quadrangle. Collector: D.L. Durham, 1960.

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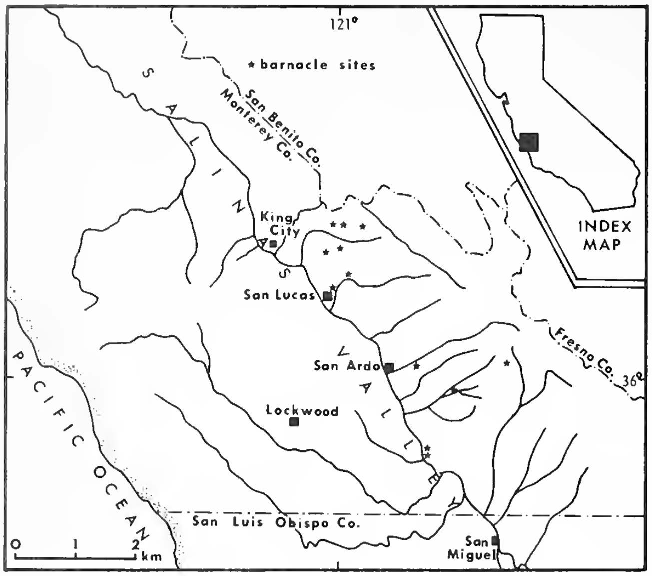


TEXT FIGURE 1. Generalized locality map of barnacle sites in the Pancho Rico Formation, Monterey County, California (adapted from Durham and Addicott 1965).

M977. Base of bluff on south side of Pancho Rico Creek, 1000 feet north, 3100 feet west of SE corner of Sec. 11, T. 22 S., R. 10 E., San Ardo 15 minute quadrangle. Collector: D.L. Durham, 1960.

M982. Roadcut on west side of U.S. Highway 101, 150 feet north, 2525 feet west of SE corner of Sec. 25, T. 23 S., R. 10 E., Wunpost quadrangle. Collectors: J.G. Vedder and C.A. Repenning, 1960.

M988. 3150 feet north, 325 feet east of SE corner of Sec. 28, T. 19 S., R. 9 E., San Lucas quadrangle. Collector: D.L. Durham, 1958–59.

M1935. North side of Walker Canyon, 900 feet north, 850 feet west of SE corner of Sec. 28, T. 22 S., R. 11 E., Wunpost quadrangle. Collectors: W.O. Addicott and D.L. Durham, 1963.

M1970. Railroad cut at mouth of small gully, 425 feet north, 175 feet west of SE corner of Sec. 25, T. 23 S., R. 10 E., Wunpost quadrangle. Collectors: W.O. Addicott and D.L. Durham, 1964.

M2275. Cut on north side of Bull Canyon Road, 100 feet south, 2400 feet east of NW corner of Sec. 26, T. 19 S., R. 9 E., Hernandez Valley quadrangle. Collector: W.O. Addicott, 1964.

M2279. Float collection near head of small gully on north side of Wildhorse Canyon, 2500 feet north, 300 feet west of SE corner of Sec. 8, T. 20 S., R. 9 E., King City 15 minute quadrangle. Collector: W.O. Addicott, 1964.

University of California Museum of Paleontology (UCMP)

A-3425. On ridge at head of Sargent Canyon, NW 1/4 corner of Sec. 9, T. 22 S., R. 12 E., Priest Valley 30 minute quadrangle.

A–4945. Same as USGS locality 1341, LACMIP locality 4660.

A–4947. Highest sandstone bed exposed on hill about 250 yards southeast of the center of the east half of Sec. 33, T. 20 S., R. 9 E., Priest Valley quadrangle (1915 edition).

A–7570. East branch of prominent south draining gully; from diatomite just below contact with sandy barnacle zone, about 15 feet above lowest outcrop in cliff. NE 1/4 Sec. 32, T. 19 S., R. 9 E., King City quadrangle (1941 edition). Collected September, 1951.

A–7571. Locality same as A–7570, but from higher bed in west branch of gully just below top of cliff.

A–8477. Eight-tenths of a mile east of the junction of U.S. Highway 101 and State Highway 198. First outcrop on north side of Highway 198 towards Priest Valley.

SYSTEMATIC DESCRIPTIONS

Suborder BALANOMORPHA Pilsbry 1916
Family BALANIDAE Leach 1817
Genus *BALANUS* Da Costa 1778
Subgenus *BALANUS* Da Costa 1778

Balanus gregarius (Conrad 1856)

Figures 1–9

Tamiosoma gregaria Conrad 1856:315; 1857a:72, pl. 4, fig. 18 [Monterey County, California]; Gabb 1869:61, pl. 18, figs. 22a–d; Dall 1902:5.

Balanus estrellanus Conrad 1857b:195, pl. 8, fig. 1 [Estrella, California]; 1877:156.

Radiolites gregaria Conrad 1864:214.

Balanus H. estrellanus Conrad 1876:273.

?*Balanus aquila* Pilsbry 1907:199, pl. 8, figs. 5–8; 1916:127, pl. 31, figs. 1–2, 4a, pl. 32, figs. 2–2c, text figs. 34a–b, 35a–c [Monterey Bay, California].

Balanus gregarius (Conrad). Pilsbry 1916:126, pl. 28, figs. 1–3, pl. 29; Zullo 1964:360; Durham and Addicott 1965: A11, A14, pl. 1, figs. 2, 3, 6, 8 [probably not pl. 2, figs. 4, 9, referred to *Balanus* sp. on legend, pl. 2]; Zullo 1969:6, figs. 3–7, 45.

Balanus (Tamiosoma) cf. *B. (T.) gregarius* (Conrad). Woodring, *in* Woodring, Stewart and Richards 1940:96, pl. 36, figs. 2–5, 8–9.

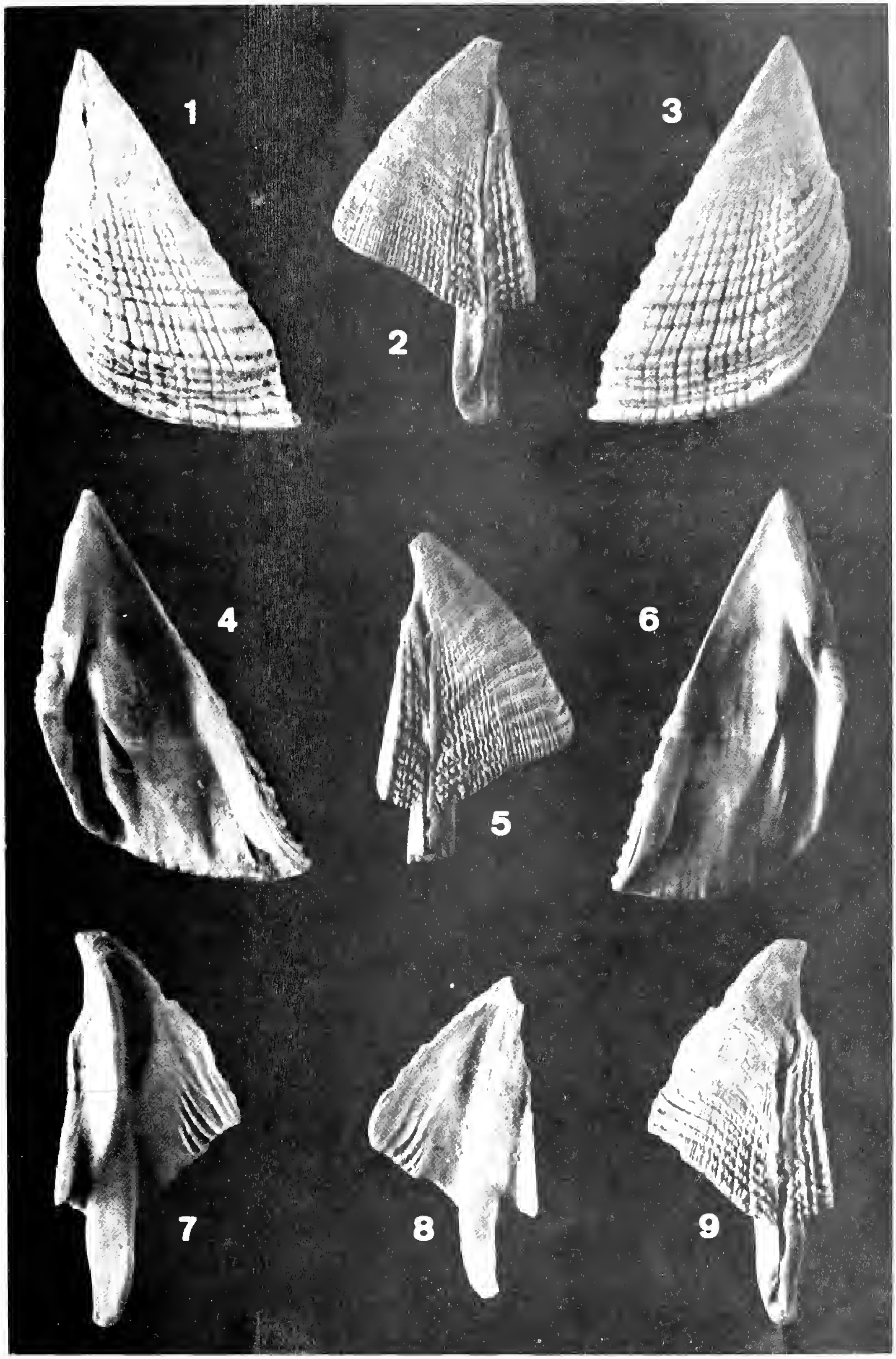
Balanus concavus concavus Bronn. Ross 1962:14, figs. 6–7.

OCCURRENCE: USGS locs. M903, M913, M977, M982, M1935, M1970; UCMP locs. A–3425, A–4945, A–7570, A–7571, A–8477; LACMIP loc. 4660.

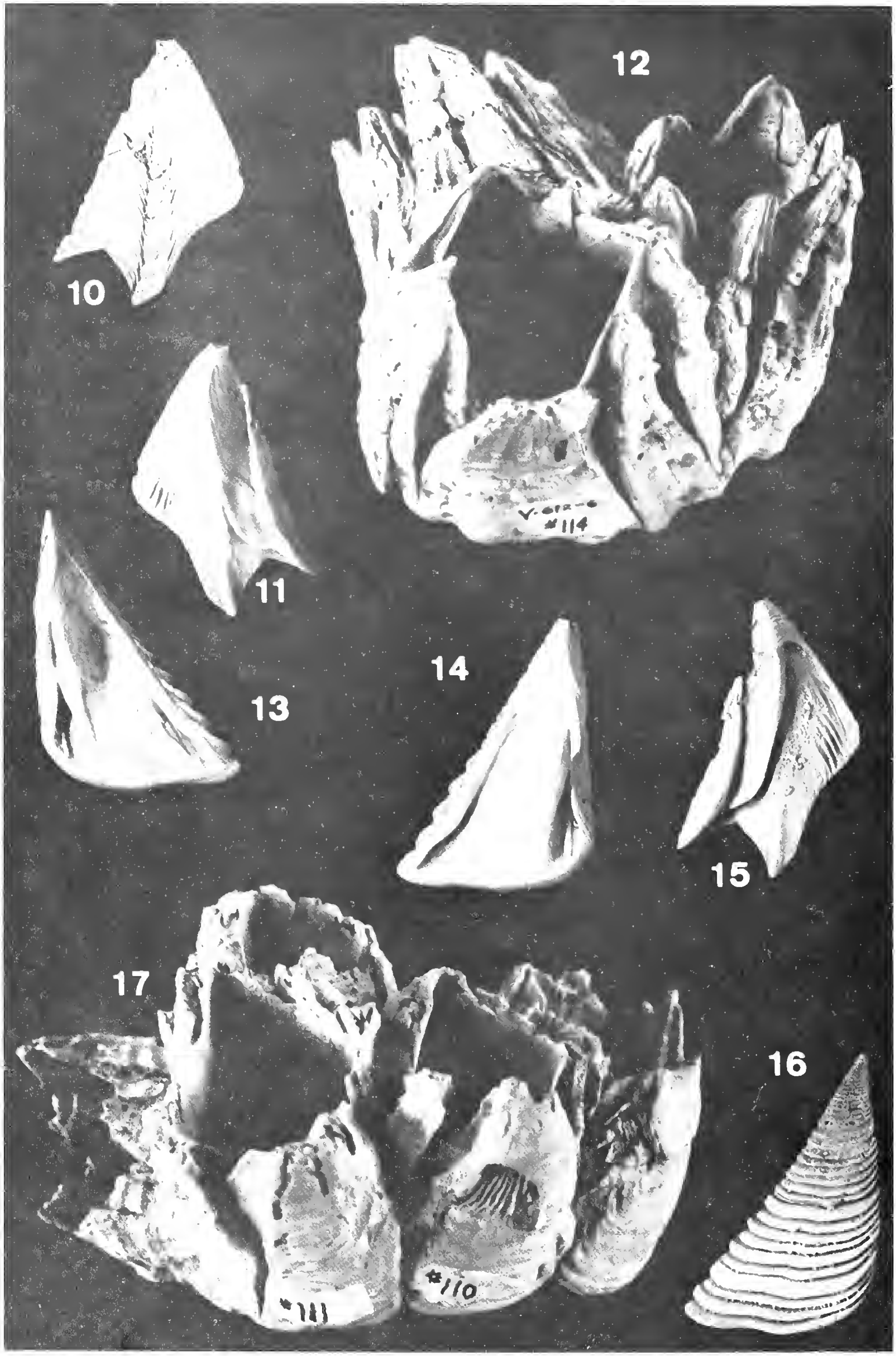
Distribution: Early Miocene—Late Pliocene, central and southern California, Baja California. (?)Pleistocene—Recent, central California to northern Baja California (as *B. aquila* Pilsbry 1907; see Zullo 1964).

REMARKS: *Balanus gregarius* is the most commonly encountered barnacle in the Pancho Rico Formation, and locally forms 'reefs' similar to those described by Woodring (*in* Woodring, Stewart and Richards 1940) in the Etchegoin Formation of the Kettleman Hills, Kings County, California. Preservation is excellent, and opercular valves retaining purple coloration on the beaks and in the medial part of the interior of the valve are often found either in life position or at the bottom of the sediment filled shell. About half of the Pancho Rico specimens collected lack an elongate, cellular basis. In those possessing such a basis, length (with respect to total height of shell) and density of cellular filling varied greatly. A few bases up to 35 cm in length were found, but most were in the range of from 8 to 15 cm.

Opercular valves obtained from shells with flat bases were not observed to differ from those found in shells with elongate bases. Similarly, Pancho Rico valves could not be differentiated from those previously illustrated from the Upper Pliocene San Diego Formation (Zullo 1969), or from those of Pleistocene or extant specimens of *B. aquila*. As suggested earlier (Zullo 1964), it is probable that *B. aquila* is a junior synonym of *B. gregarius*. The opercular valves of *B. gregarius* described and illustrated from the Kettleman Hills by Woodring (*in* Woodring, Stewart and Richards 1940) are also similar in form, but are not representative of the Etchegoin population. Bulk collections (which included over 200 opercular valves) made by the author from



FIGURES 1–9. Opercular valves of *Balanus (Balanus) gregarius* (Conrad). (1) exterior of scutum, hypotype LACMIP 4926; (2) exterior of tergum, hypotype LACMIP 4927; (3) exterior of scutum, hypotype LACMIP 4928; (4) interior of scutum, hypotype LACMIP 4929; (5) exterior of tergum, hypotype LACMIP 4930; (6) interior of scutum, hypotype LACMIP 4931; (7) interior of tergum, hypotype LACMIP 4932; (8) interior of tergum, hypotype LACMIP 4933; (9) exterior of tergum, hypotype LACMIP 4932 [Height of tergum, fig. 2, 21 mm; all valves to same scale.]



FIGURES 10–17. *Balanus (Balanus) proxinubilus*, new species. (10) exterior of tergum, holotype LACMIP 4934, height, 18 mm; (11) interior of same; (12) three shells of ribbed form, paratypes LACMIP 4937, 4938, 4940, carinorostral diameter of orifice, paratype LACMIP 4938 (center of photograph), 29 mm; (13) interior of scutum, holotype LACMIP 4934, height, 20 mm; (14) interior of scutum, holotype LACMIP 4934, height, 19 mm; (15) interior of tergum, holotype LACMIP 4934, height, 19 mm; (16) exterior of scutum shown in fig. 13; (17) shells of smooth form, including holotype LACMIP 4934 (second from right) and paratypes 4935, 4936, 4941, 4942, carinorostral diameter of orifice of paratype LACMIP 4935 (second from left), 27 mm.

Woodring's localities indicate that the Etchegoin population differs in two respects: 1) the tergal spur usually is flush with the basal margin, rather than being elevated above the basal margin by the closure of the spur furrow; and 2) the articular ridge of the scutum usually is joined to the adductor ridge, rather than being clearly separated. These differences are not constant, even in specimens from the same lot, but they suggest the possibility of the presence of a distinct race of *B. gregarius* in the San Joaquin embayment during Pliocene time.

The tergum figured by Durham and Addicott (1965, pl. 2, figs. 4, 9) from the Pancho Rico Formation was referred to *B. gregarius* in the text and to *Balanus* sp. in the plate legend. The specimen does not appear to represent a tergum of *B. gregarius*. The characteristic apical beak is missing, and the apex is neither broken nor significantly worn. There is no pit entering the apex on the carinal side of the articular ridge, the exterior surface of the valve lacks radial striae (especially prominent on the scutal side in *B. gregarius*), and the tergal spur is shorter and broader. In general form this tergum resembles those of either the *B. pacificus* Pilsbry 1916—*B. concavus* Bronn 1831 group, or of the subgenus *Megabalanus* Hoek 1913. An undescribed species, related to *B. pacificus* and with a similar tergum, occurs in association with *B. gregarius* in the Upper Miocene Santa Margarita Formation in San Luis Obispo County, California (UCMP collection). The megabalanid *B. wilsoni* Zullo 1969 and some questionable specimens of *B. pacificus* are found with *B. gregarius* in the Upper Pliocene San Diego Formation.

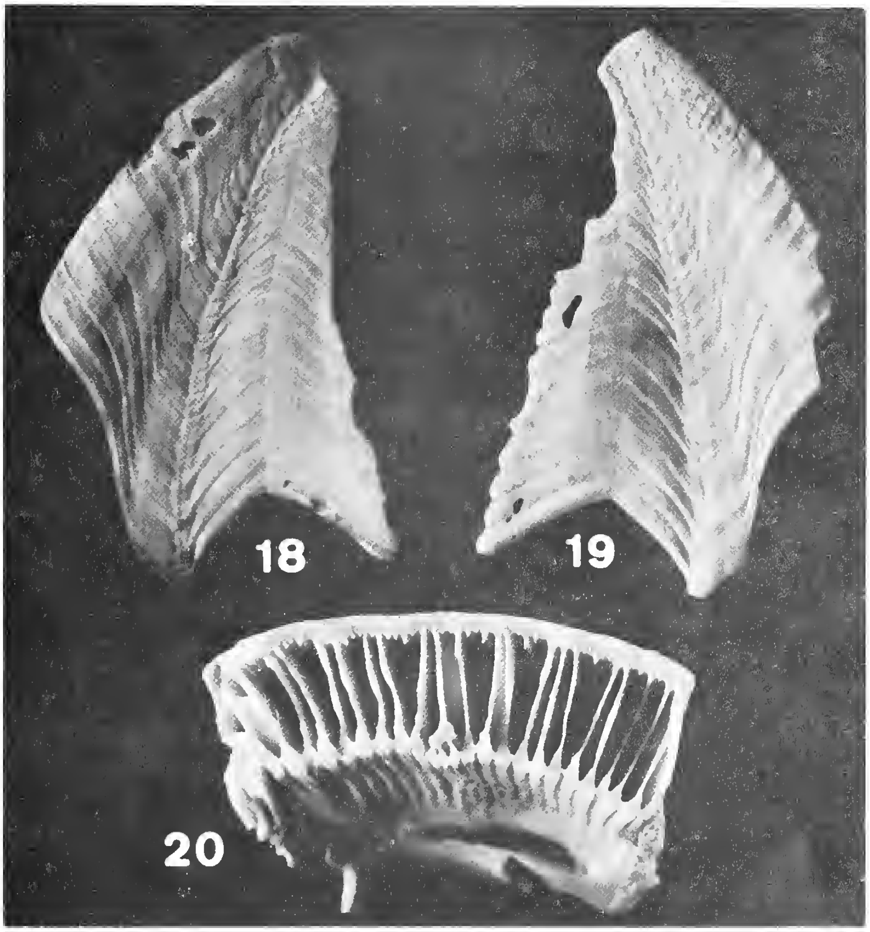
Balanus proxinubilus NEW SPECIES

Figures 10–20

Balanus n. sp.? Addicott, *in* Durham and Addicott 1965:14.
Balanus nubilus Darwin. Zullo 1969:8, figs. 8–10.

DIAGNOSIS: Large, high conic *Balanus* with open parietal tubes; scutum as in *B. nubilus* Darwin, but with smaller, circular adductor muscle pit placed higher on valve, and broader, lower adductor ridge; tergum as in *B. nubilus,* but with shorter, broader tergal spur placed farther from the basiscutal angle, and resulting marked prolongation of the scutal half of the basal margin, whose juncture with the spur is angular.

DESCRIPTION: Shell large, high conic; orifice toothed, subtriangular; exterior of parietes nearly smooth to rugose; radii moderately wide with oblique summits; sutural edges of radii with complex pattern of primary and secondary denticulae; alae broad, projecting slightly above radii; basis thick, porous, clinging firmly to compartmental plates; interior of parietes ribbed from sheath to basis; sheath one-half to two-thirds length of compartmental plates, with deep cavity under lower edge; parietal tubes large, numerous, open throughout length.



FIGURES 18–20. *Balanus (Balanus) proxinubilus*, new species. (18–19) exterior of terga, paratype LACMIP 4935, height, 20 mm; (20) basal view of paries, paratype LACMIP 4939, length (from left to right), 20 mm.

FIGURES 21–22. Exterior of terga of *Balanus (Balanus) nubilus* Darwin, illustrating lack of scutad prolongation of valve (after Pilsbry 1916, pl. 31, figs. 3,4).

Scutum sculptured externally by prominent, widely spaced growth lines; tergal margin not reflected; basitergal angle nearly 90 degrees; articular ridge moderately developed, reflected, slightly over half length of tergal margin; articular furrow broad, shallow; adductor ridge indistinct, low, merging with articular ridge above to form low swelling between articular ridge and adductor muscle pit; adductor muscle pit small, well defined, circular, placed high on valve; depressor muscle pit large, triangular, with distinct longitudinal ridge bisecting pit; occludent margin bearing prominent teeth formed by alternate growth increments; tergal margin one-third again as long as basal margin; scutum slightly concave between basal margin and apex.

Tergum broad, triangular; articular ridge blunt, not reflexed, long; articular furrow broad, shallow; scutal margin prominently reflexed; crests for lateral depressor muscles well developed, thin, long, about six in number; length of basal margin equal to height of tergum excluding spur; width of tergal spur equals three-eights length of basal margin; spur V-shaped, forming angle slightly greater than 90 degrees with basal margin on scutal side, less angulate on carinal side; spur placed centrally on basal margin (about its own width from basiscutal angle), giving an elongate appearance to scutal half of tergum; spur fasciole delimited by grooves on either side.

DIMENSIONS:	*Height*	*Carinorostral diameter of orifice*
Holotype LACMIP 4934:	37 mm	22 mm
Paratype LACMIP 4935:	50 mm	27 mm
Paratype LACMIP 4938:	54 mm	29 mm

DISPOSITION OF TYPES: Holotype and paratypes are deposited in the Invertebrate Paleontology collection, Natural History Museum of Los Angeles County.

OCCURRENCE: Lower Pliocene, Pancho Rico Formation, LACMIP locality 4660 (type locality, = UCMP loc. A–4945, USGS loc. M1341), and USGS loc. M913; Upper Pliocene, San Diego Formation, LACMIP loc. 305.

ETYMOLOGY: A compound word from the Latin, meaning nearest *nubilus*.

REMARKS: *Balanus proxinubilus* is quite similar in appearance to the extant Pacific Coast species *B. nubilus*. The shells of the two species are virtually identical in form. The scuta of *B. proxinubilus* differ somewhat in having a lower, broader adductor ridge and a smaller adductor muscle pit. The tergum of *B. proxinubilus*, however, can be distinguished readily from that of *B. nubilus*. The marked prolongation of the basiscutal part of the tergum, the short, broad tergal spur, and the angularity of the juncture between the spur and the basal margin on the scutal side give to the tergum a distinctive appearance that is not found in extant and fossil examples of *B. nubilus*.

The fragmentary terga from the Upper Pliocene San Diego Formation referred to *B. nubilus* in an earlier paper (Zullo 1969) are similar in form to the Pancho Rico terga, and also appear to represent *B. proxinubilus*. *Balanus nubilus* is known from deposits of Late Pliocene age on the Pacific Coast, but unlike *B. proxinubilus*, the species is associated with a cool water fauna in northern California. By Pleistocene time, *B. nubilus* was widely distributed, as evidenced by the numerous examples available from rocks of this age from Oregon south to Baja California. *Balanus proxinubilus* thus appears to have been a southern, warm water Pliocene species that may well have succumbed to the southern advance of *B. nubilus* during the Pleistocene.

Balanus addicotti NEW SPECIES

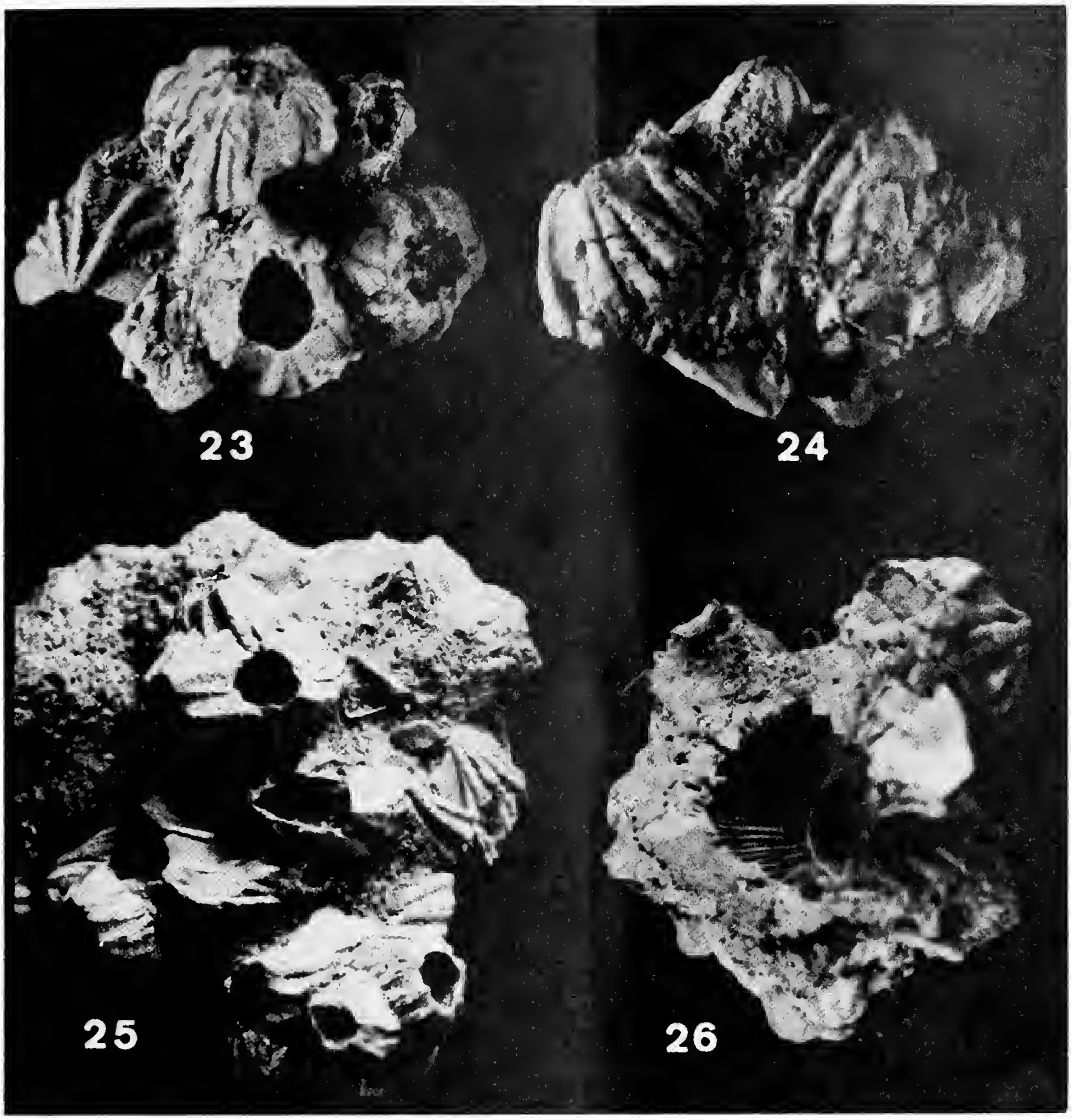
Figures 23–32

DIAGNOSIS: Small, high conic, ribbed *Balanus* with broad radii; external growth ridges of scutum cut by deep radial striae, giving marked cancellate appearance to exterior of valve; scutal adductor ridge short, stout and high; tergum with short, broad, basally truncate spur and open spur furrow.

DESCRIPTION: Shell small, high conic; orifice untoothed, subtrigonal to diamond shaped; parietes regularly ribbed; parietal tubes small, rounded, numerous, without transverse septa, but filled in upper half; radii broad, solid, thick, with horizontal summits; sutural edges of radii coarsely denticulate; alae thinner, with oblique summits; sheath about one-half height of shell, lower edge dependent; interior of parietes sharply ribbed from basis to lower edge of sheath; basis moderately thick, with small, radiating non-septate tubes.

Scutum thick, narrow; exterior ornamented by closely spaced growth ridges crossed by deeply incised radial striae that cut growth ridges into a series of high nodes; tergal border reflexed 90 degrees; adductor ridge high, short and stout, situated in center of valve, and with a small pit between it and the tergal margin; adductor muscle pit oval, shallow, situated close to occludent margin; depressor muscle pit large, deep; articular ridge two-thirds to three-fourths length of tergal margin, broadly arched, and reflexed over deep, narrow, articular furrow.

Tergum thin, broad; tergal spur short, broad, situated close to basiscutal angle, and truncate basally; spur width from one-half to two-thirds width of basal margin; juncture of spur with basal margin angular on both sides; spur furrow broad, open; articular



FIGURES 23–26. *Balanus (Balanus) addicotti,* new species, USGS loc. M1935. (23) Holotype USNM 248194 (center, bottom) and paratypes USNM 248194/a–d, carinorostral diameter of orifice of holotype, 4.5 mm; (24) group of shells, paratype lot USNM 248195, length of cluster, 21 mm; (25) group of shells, USNM 248196, maximum height of photographed portion of cluster, 35 mm; (26) interior of shell from paratype lot USNM 248195 (fig. 24) showing basal tubes, parietal ribbing, and sheath.

ridge low, short; articular furrow broad, shallow; depressor muscle crests numerous, short, dependent below basal margin.

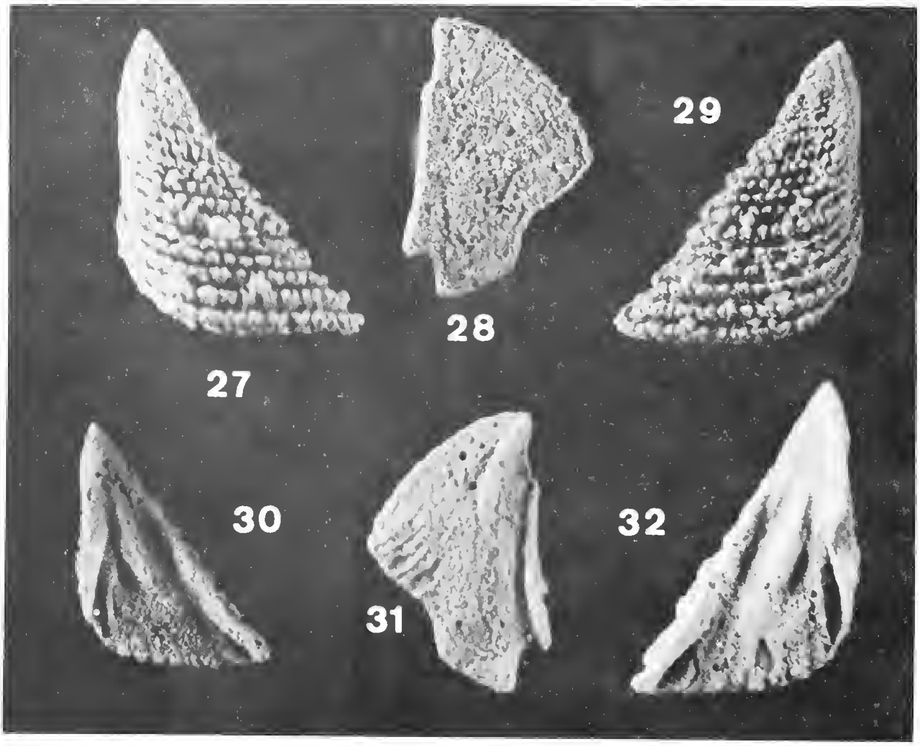
DIMENSIONS:	*Height*	*Greatest Diameter*
Holotype USNM	11 mm	9 mm
Paratype USNM 1	8 mm	12 mm
Paratype USNM 2	6.5 mm	10 mm

DISPOSITION OF TYPES: Holotype and described paratypes deposited in the United States National Museum; other paratypes deposited in the University of California Museum of Paleontology.

OCCURRENCE: Lower Pliocene, Pancho Rico Formation, USGS locs. M1935 (type locality) and M2275; UCMP loc. A–7570.

ETYMOLOGY: This species is named for Warren O. Addicott.

REMARKS: *Balanus addicotti* bears marked resemblance to the extant tropicopolitan species *B. trigonus* Darwin. It differs from this species in the less distinctly trigonal shell orifice, in the cancellate rather than pitted sculpture of the scutum, and in the stouter and more pronounced scutal adductor ridge. The cancellate ornamentation of the scutum is like that of *B. spongicola* Brown 1827, but this species differs in lacking a distinct scutal adductor ridge, and in having a much narrower tergal spur and a smooth shell wall. The opercular valves of the tropical American species *B. calidus* Pilsbry, 1916 are similar to those of *B. addicotti,* but the radial striae of the scutum of *B. calidus* are not deeply incised and thus do not impart a cancellate appearance to the surface of the valve. Also, the radii of *B. calidus* are much narrower, and the shell wall is plicate rather than regularly ribbed. *Balanus addicotti* is also similar to *B. kanakoffi* Zullo



FIGURES 27–32. Opercular valves of *Balanus (Balanus) addicotti,* new species, holotype USNM 248194, USGS loc. M1935. (27) exterior of scutum, height, 3.8 mm; (28) exterior of tergum, height, 3.5 mm; (29) exterior of scutum, height, 3.8 mm; (30) interior of scutum of fig. 29; (31) interior of tergum of fig. 28; (32) interior of scutum of fig. 27.

1969, which is known only from the Upper Pliocene San Diego Formation of southern California. However, *B. kanakoffi* has a plicate shell with narrow radii (the suture between the carina and carinolaterals being linear or obscured), and a beaked, narrow tergum. In addition the scutum of *B. kanakoffi* lacks a distinct adductor ridge.

The extant and fossil distribution of *B. trigonus* in tropical American waters indicates that this species ranged at least as far back as the Late Miocene in the eastern Pacific, and was thus probably present along the southern and central California coast during the time of deposition of the Pancho Rico Formation. *Balanus addicotti* may have been a geographically and temporally localized derivative of *B. trigonus* that became extinct upon withdrawal of the sea from the Pliocene Salinas Valley embayment. *Balanus addicotti* may yet be discovered in rocks of Jacalitos age on the eastern side of the San Andreas fault, but it does not appear to have been present in younger Pliocene warm water faunas of the San Diego Formation (Zullo 1969) and of the Etchegoin and San Joaquin Formation of the Kettleman Hills (unpublished data).

Balanus crenatus leipochoma

NEW SUBSPECIES

Figures 33–37

DIAGNOSIS: Small, low conic shell with non-septate parietal tubes and narrow, oblique radii; interior of parietes ribbed; basis thin, nonporous; space behind dependent basal margin of sheath bearing cellular secondary deposits; scutum broader than tall, externally concave, with prominent articular ridge and indistinct adductor ridge; tergum broad, with broad, short, subtruncate spur.

DESCRIPTION: Shell small, low conic; orifice of moderate to large size, diamond shaped; parietes thin, smooth, or plicate in basal third; parietal tubes square, without transverse septa; radii narrow, oblique; alae wider than radii and projecting above summits of radii; sheath one-half to two-thirds length of compartment; space under lower edge of sheath crudely septate or secondarily filled; interior of parietes ribbed; basis thin, solid.

External surface of scutum concave, ornamented solely by growth increments; basal margin slightly longer than tergal margin; articular ridge prominent, nearly erect, occupying slightly more than half of the tergal margin, articular furrow deep, broad; adductor ridge indistinct, basically a calloused region between adductor muscle pit and articular ridge; adductor muscle pit prominent, deep, lenticular in shape; depressor muscle pit shallow, triangular.

Tergum broad, thin; tergal spur broad, short, near basiscutal angle, and rounded basally; spur width about one-half that of width of basal margin; juncture of spur with basal margin gently curved on both sides; spur furrow broad, open; articular ridge prominent, not reflexed, restricted to upper half of valve, articular furrow broad, deep; five short, well developed depressor muscle crests depend slightly below basal margin.

DIMENSIONS:	*Height*	*Greatest Diameter*
Holotype UCMP 10929	4 mm	8.5 mm

DISPOSITION OF TYPES: Holotype and six paratypes deposited in the University of California Museum of Paleontology collection.

OCCURRENCE: Lower Pliocene, Pancho Rico Formation, UCMP loc. A–4946, on fragment of (?)schizasteroid echinoid test.

ETYMOLOGY: Subspecific epithet a compound word from the Greek *leipo*, 'without' and *choma*, 'bulwark'.

REMARKS: It is perhaps inappropriate to characterize these fossil specimens as distinct from typical *B. crenatus*. The opercular valves are unremarkable and the shell, in all features but one, is that of *B. crenatus*. However, examination of the parietal tubes of several fragmental shells associated with the type lot, and of the holotype itself revealed no trace of transverse septa; a feature characteristic of typical *B. crenatus* and its known subspecies.

The opercular valves and external shell form are easily confused with those of *B. proinus*. However, none of the over two hundred shells of *B. proinus* examined exhibited any trace of parietal tubes or of secondary cellular deposits below the dependent margin of the sheath.

Subgenus *SOLIDOBALANUS* Hoek 1913

Balanus proinus Woodring 1950

Figures 38–41

Balanus hesperius Pilsbry, var. Woodring, *in* Woodring, Stewart and Richards 1940:30, 97.
Balanus hesperius proinus Woodring, *in* Woodring and Bramlette 1950: 92, pl. 14, figs. 11, 15, pl. 16, figs. 1–3, 8–12.
Balanus proinus Woodring. Zullo 1969:16, figs. 26–32.

OCCURRENCE: UCMP locs. A–4947, A–7570.

DISTRIBUTION: Pliocene, southern California: Lower Pliocene, Pancho Rico Formation, Salinas Valley; 'Middle' Pliocene, Foxen Mudstone, Santa Maria district; Upper Pliocene, San Joaquin Formation, Kettleman Hills, Careaga Sandstone, Santa Maria district (type locality), San Diego Formation, San Diego County.

REMARKS: The specimens of *B. proinus* from the Pancho Rico Formation represents the oldest recognized occurrence of the species. It is apparently as common in Pliocene deposits of southern California as is *B. gregarius* but, because of its diminutive size, is not as well known. Shells are often found attached to pectens and occasionally to clypeasteroid echinoids and gastropods, but they have not been observed in association with other barnacles.

Balanus proinus is the youngest known member of a Tertiary tropical to warm temperate eastern Pacific group that goes back to the Late Eocene (Zullo 1966). There are no known warm water survivors, but the extant boreal Pacific species *B. hesperius* Pilsbry 1916 appears to be a derivative of this lineage.

ACKNOWLEDGMENTS

I wish to thank Warren O. Addicott and Jack A. Wolfe of the U.S. Geological Survey, Menlo Park, California for their help in obtaining the specimens used in this study.

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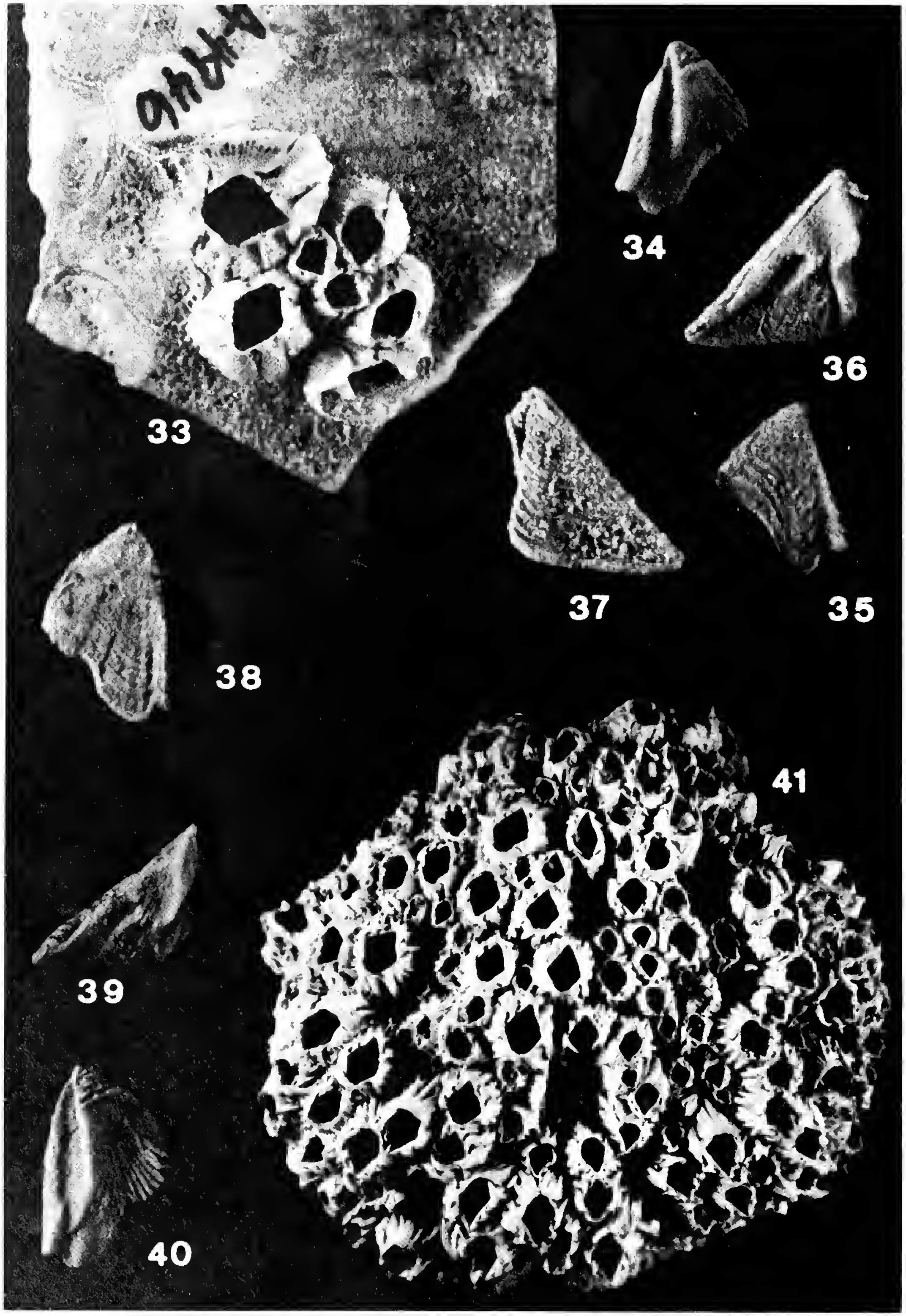

FIGURES 33–37. *Balanus (Balanus) crenatus leipochoma,* new subspecies, UCMP loc. A–4946. (33) Shells of type lot (holotype UCMP 10929 and paratypes UCMP 10930a–f), lateral paries of holotype ground to show non-septate tubes; (34–35) tergum of holotype UCMP 10929, height, 2.1 mm; (36–37) scutum of holotype UCMP 10929, height, 2.2 mm. FIGURES 38–41. *Balanus (Solidobalanus) proinus* Woodring, UCMP loc. A–4947. (38) exterior of tergum, hypotype UCMP 10931, height, 2.5 mm; (39) interior of scutum, hypotype UCMP 10931, height, 1.6 mm; (40) interior of tergum of fig. 38; (41) group of shells on *Lyropecten estrellanus* (Conrad), hypotype lot UCMP 10932, height, 51 mm.

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A HOLLOW SPINED *ANAPACHYDISCUS PENINSULARIS* WITH POSSIBLE MOSASAUR BITE IMPRESSIONS

By LouElla R. Saul

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The *Science Bulletin* and *Contributions in Science* of the Natural History Museum of Los Angeles County were merged into a single imperial octavo serial, retaining the name *Contributions in Science* and beginning with Number 301.

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A HOLLOW SPINED *ANAPACHYDISCUS PENINSULARIS* WITH POSSIBLE MOSASAUR BITE IMPRESSIONS[1]

By LouElla R. Saul[2]

ABSTRACT: A specimen of Early Maestrichtian age *Anapachydiscus peninsularis* (Anderson and Hanna) from Arroyo Santa Catarina, Baja California, Mexico, has nearly round holes punched in the shell so arranged that they suggest mosasaur bite marks. The early whorls are ornamented with hollow lateral spines which could have served as vertical stabilizers.

A concretion of roughly 20 cm diameter protruding from the near vertical side of a gully cut into Rosario Formation siltstone was overlooked by local entrepreneurs who, in 1968, collected for use in the manufacture of lamp bases, etc., all exposed or near surface ammonites from the well-known locality in Arroyo Santa Catarina, Baja California, Mexico. A blow or two with sledge and chisel split the concretion and freed from the rock a well-preserved ammonite, *Anapachydiscus peninsularis* (Anderson and Hanna). Matrix plugs remained in the umbilicus, and a lump of siltstone adhered to and filled what remained of the broken body chamber. Four curiously round holes, two on each side marred the specimen. Their shape, spacing and alignment are reminiscent of those in the mosasaur-bitten ammonite described by Kauffman and Kesling (1960). The siltstone matrix at the apertural end was sawed away and most of the plug in the umbilicus on the right side was removed so that the specimen might be used to display evidence of interaction between animals. Removal of the matrix in the umbilicus exposed one more roundish hole in the shell and, bordering the umbilicus, hollow spines which have not been previously noted in descriptions of this species (Anderson and Hanna 1935, p. 20, pl. 4, fig. 1; pl. 5, fig. 1–2; pl. 6, fig. 3–4; pl. 7, fig. 5; text–fig. 1; Anderson, 1958, p. 225; Matsumoto, 1959, p. 38).

THE ROUND HOLES

The holes are not truly round, but give the impression of having been punched by round objects intersecting the curved, ribbed surface of the ammonite shell. In addition to the five roundish holes — two on one side, three on the other — the specimen has a small angular hole (Fig. 6) on the abapertural side of the umbilicus that could have been made by the tip of a tooth. The shell is not depressed around the holes as in the specimen described by Kauffman and Kesling (1960), but each hole has cracks radiating from it. The holes are in the chambered portion of the conch, and the edge of the shell along which most of the body chamber broke off resembles a tear along perforations. If the rounded embayments of this edge are considered to represent half-tooth marks, there are ten tooth marks. Figures 1 and 2 diagram two possible bites. The plump rounded whorls of *A. peninsularis* are not as advantageously shaped for displaying the bite of a mosasaur as is the discoidal shape of the *Placenticeras* of Kauffman and Kesling (1960), and other sortings of the holes into bites can be argued for. Camp (1942) discussed two genera of mosasaurs from the Maestrichtian of California, *Plotosaurus* and *Pleisiotylosaurus*, but the limited record of these "bites" (Figs. 1–3, 5–6) does not indict either. This probable mosasaur may have regularly dined on ammonite as it seems to have been more efficient about acquiring the benefits of its chase than did the one inferred by Kauffman and Kesling. The Baja California mosasaur apparently required only two bites to break off the body chamber and thus free the edible soft parts rather than the 16 bites shown on the *Placenticeras*. An even more adept mosasaur might bite just at the rear of the body chamber and leave as a record of its predation only the torn-on-perforations shell edge.

THE HOLLOW SPINES

The spines on the specimen, UCLA cat. no. 38765, are formed by a thin outer layer of the shell (3rd abapertural spine of figure 5 has wall .3mm thick) and are readily removed along with the matrix leaving as their bases of attachment, bordering the umbilicus, the flat-topped tubercles of previous descriptions (Anderson and Hanna 1935, p. 20; Anderson 1958, p. 225). The maximum diameter of this specimen is 11.8 cm; the last flat-topped tubercles occur at a diameter of about 7.3 cm. The spines and spine bases have been best exposed on the last whorl of their occurrence; here they are not evenly spaced; they occur on every second to fourth rib. They appear to be more regularly spaced on earlier whorls. The tallest spine (incomplete) is 8 mm high; it is the next to the last adapertural one preserved (figure 5) and is filled with crystalline calcite. The last spine is 6.5 mm high, has the tip closed, and is probably nearly complete. The outermost end of all the earlier formed ones were damaged in preparation,

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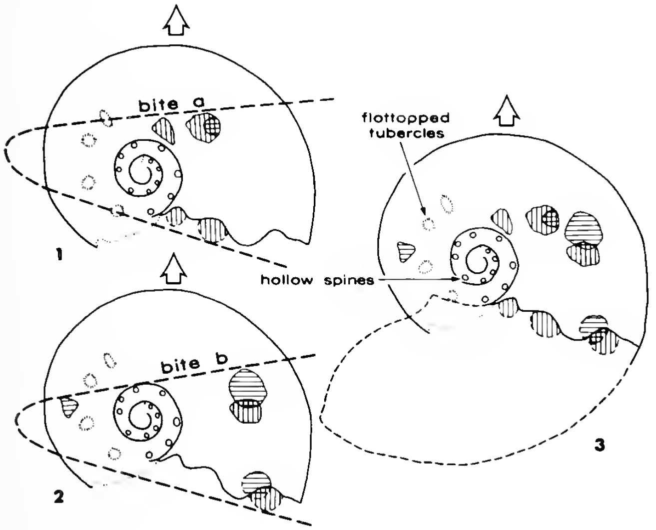
TABLE 1
Measurements (in mm.) of *Anapachydiscus peninsularis* (Anderson and Hanna.)

cat. no.	maximum D	maximum W	last flat-topped tubercle W	D	W/D	
CAS 4250	41.5	27.5	too poorly preserved		.66	paratype, poorly preserved
CAS 4253	92	55	36	(60)	.6	paratype
UCLA 28717	107	58	29.5	(54)	.54	hypotype
UCLA 38765	118	67.5	51	(89)	.57	hypotype, with spines and holes
CAS 4249	120	64	42	(79)	.53	paratype, one spine showing?
CAS 4257	123	72	50	(85)	.58	paratype
CAS 4248	355	144	too poorly preserved		.41	holotype

D = diameter; (D) = diameter calculated from width of whorl; W = width of whorl; CAS = California Academy of Sciences; UCLA = University of California, Los Angeles. The average diameter at which *A. peninsularis* apparently ceased to generate spines was 73 mm.; however, two specimens, 4253 and 28717, ceased notably sooner at an average diameter of 57 mm. than the other three measurable specimens which ceased at an average of 84 mm. The gap in estimated size at which they ceased to grow spines may result from measuring too few specimens or it may be an indication of sexual dimorphism. The ratio W/D shows a loss of inflation with increase in size.

some because these structures were unexpected and the others because they are so frail that they adhered to the matrix being removed. All except the two abapertural spines are filled with siltstone and thus were broken prior to entombment. Earlier formed spines appear to have been longer relative to the size of the ammonite shell than the later ones. The thin-walled, hollow spines were sealed off at their bases by the formation of the next inner shell layer. The umbilical wall of the enveloping whorl does not touch the spines; there is now a thin layer of siltstone between spine and umbilical wall, and the spines apparently stood free.



FIGURES 1–3. *Anapachydiscus peninsularis* (Anderson and Hanna) with aligned rounded holes. Holes of near side vertically lined, of far side horizontally lined. Ammonite in presumed living position, arrows point up. Because of the size of the ammonite and its inflation, too few "tooth marks" are present to determine direction of bite, but two bites seem to be required by the positions of the holes. Figures 1 and 2 diagram two of several possible positions for the bites. Figure 1. Bite *a* caught the ammonite and began to break off the body chamber. Figure 2. Bite *b* broke off the body chamber. Figure 3. All holes indicated and body chamber restored. Inferred body chamber length from Raup (1967, text-fig. 16) is minimum length and results in most horizontal bite. A longer body chamber rotates the diagrammed ammonite counter-clockwise and suggests attack from above.

The original type lot of *Parapachydiscus peninsularis* Anderson and Hanna comprises five specimens. Of these, three are not well enough preserved to show spines or flat-topped tubercles. The smallest specimen, California Academy of Sciences cat. no. 4250, has strong ribs with obvious tubercles bordering the umbilicus; but if the tubercles had rimmed flat-tops, weathering has obliterated this detail. The specimen is, however, because of the strength of the ribs, listed in Table 1 as having been spiny throughout. With spines of equivalent length to those on UCLA cat. no. 38765, it would have had a ventral profile like that in figure 4. One of the paratypes, CAS cat. no. 4249, has a circlet of shell that is probably a spine showing through the matrix in the umbilicus. As can be seen from Table 1, the size at which *A. peninsularis* ceased to grow spines was not consistent. UCLA cat. no. 28717 (Popenoe 1954, fig. 3 (9)) had a width of only 29.5 mm when its last spine formed; but UCLA cat. no. 38765 has its last flat-topped tubercle at a width of 51 mm. The difference between the two specimens of least diameter and the three of larger diameter may reflect sexual dimorphism, but the sample is too small to be significant.

An *Anapachydiscus* was collected by John Alderson from the NW¼ of section 6, T24S, R16E, Cholame 7½ min. quad., Monterey Co., California (UCLA loc. 6337), or approximately 1 mile westward along strike from LSJU (Stanford University) loc. 3354, from which Matsumoto (1959, p. 38; 1960, p. 127) identified *Anapachydiscus* cf. *A. arrialoorensis* (Stoliczka). Alderson's specimen (UCLA cat. no. 57245) is plumper and has closer spaced stronger ribs than specimens of *A. peninsularis* from Baja California, and thus resembles Stoliczka's (1865, p. 126, pl. 63, fig. 2–4; pl. 64, fig. 1) figures of *Ammonites arrialoorensis*. It differs from these figures in having more elliptical spine bases.

The outer whorl(s?) of Alderson's Cholame specimen was broken and eroded and discarded in the field leaving a specimen, septate throughout, with diameter 90.5 mm and width 53 mm. Most of one volution is present, the inner whorls being broken. A flange of shell that formed the umbilical flank of the next outer volution remains on the right side of the specimen. The thickness of this umbilical flank shell is about .6 mm. Broken hollow spines are present at a diameter of 68 mm, width approximately 33 mm. The spine wall is almost one-third the thickness of the flank wall. Spines appear to have been formed at a diameter of 87 mm, width 49 mm, but preservation and breakage are such that I cannot be sure of their presence or absence. Also the spines are less obvious than on UCLA cat. no. 38765 because in the Cholame specimen the enveloping umbilical wall nearly engulfs them. Considering the size to which some *Anapachydiscus* grew, they seem to have had remarkably thin shells. Their shell walls were about one-half as thick as those of *Nautilus pompilius* and only a third thicker than that of an argonaut of similar diameter.

The spines were apparently secreted at the apertural edge as part of the outermost layer of the conch. There is no evidence that the leading side of the spine was open as is commonly the case with spines arming the aperture of a gastropod. Compared to spines on *Murex* spp., the spines on *Anapachydiscus* have a wall that is one-half to one-third as thick and is of equal thickness all around. The diameter of the hollow center is approximately 3 times the thickness of the spine wall. Spines on *Murex* spp. have adaperturally placed holes whose diameters are one-third or less the thickness of the spine wall. The sealing off of the bases of the *Anapachydiscus* spines probably took place soon after their formation as the next inner strengthening layer of the conch was deposited. Since the spines were apparently not open along their leading edge and were probably soon sealed off at their base, it seems unlikely that they functioned as supports for soft parts at the aperture edge or as channels for current flow.

Teichert (1967, p. 204) included spines on ammonites in his tabulation of adaptive devices to regulate buoyancy. Kennedy and Cobban (1976, p. 28) suggested that spines might serve as balancing aids when the shell rested on the bottom or as horizontal stabilizers to prevent yawing. Westermann (1971, p. 7) has listed as functions of ornament on ammonites: strengthening the relatively thin shell against implosion, protection against impact, protection against smaller predators, decrease of drag under conditions of turbulent flow, and camouflage. Arkell, Kummel, and Wright (*in* Moore 1957, p. L122) suggested that spines could have served as balancers or stabilizers or as a protection against enemies. It is this latter function that Westermann inferred lateral and ventrolateral spines to have served. Cephalopods of all kinds are noted for their varied camouflage techniques (Lane 1960, p. 93–104; Cowen et al. 1973; Young and Roper 1976), and Cowen et al. (1973) suggest that the primary function of ammonite ornament was camouflage for a nektobenthonic organism.

Ornament to decrease drag is more likely to be ribbing or noding than long spines (Chamberlain and Westermann 1976, p. 329). Such long frail spines were probably not secreted to strengthen the shell. They could have offered some protection against impact, absorbing some of the impact energy or perhaps more importantly putting distance between the primary impact

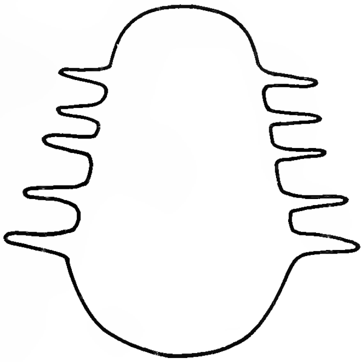
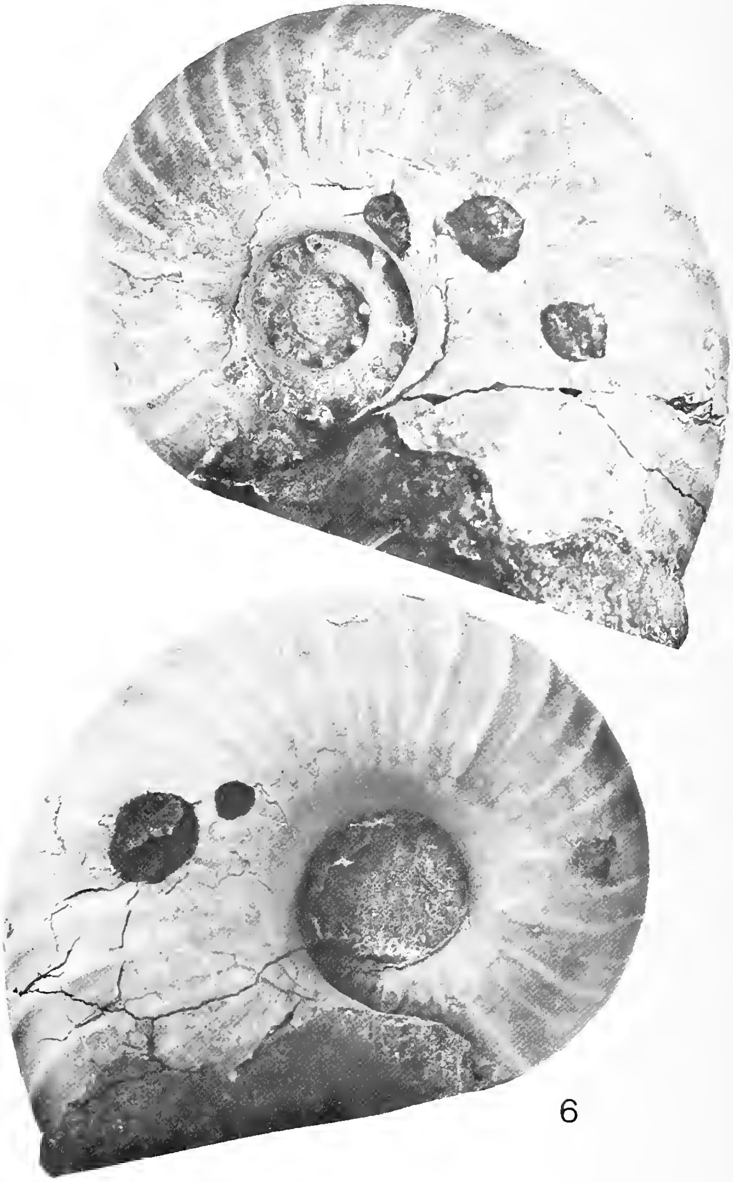


FIGURE 4. Reconstruction of ventral view of young *A. peninsularis*. Ammonite outline based on CAS 4250 and spines similar in length to those on UCLA 38765 added. Spines produce an obviously unstreamlined outline and effectively increase width of ammonite with respect to height.



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FIGURES 5–6. *Anapachydiscus peninsularis* (Anderson and Hanna). UCLA hypotype cat. no. 38765, x 3/4. (5) lateral view with three rounded holes and "torn-on-perforation" edge to broken body chamber. Twelve hollow spines show in umbilicus and are followed adaperaturally by four flat-topped, rimmed tubercles. (6) opposite side of figure 5 with two rounded holes and on opposite side of umbilicus one triangular hole interpreted as being made by tip of tooth. Six flat-topped, rimmed tubercles bordering the umbilicus considered to be bases of hollow spines.

and the conch, but if this were their main function a more useful placement would seem to be nearer the unprotected venter, especially if the ammonite was nekto-benthonic. Nor do they seem well placed as defensive armaments. Gastropods arm their aperture and anterior siphon; the bivalve *Hysteroconcha* has spines on its corcelet which thus surround the siphons; but the spines on young *Anapachydiscus* neither surround soft parts nor are they on the outer perimeter of the animal to discourage attack. They are thinner walled and even though liquid filled were apparently frailer structures than the probably defensive spines of the gastropods and bivalves. They would have increased the apparent size of the young ammonite and so might have discouraged some smaller predator. The need for camouflage (Cowen et al. 1973, p. 211) was in part inferred from the paucity of ammonite specimens showing pigmentation, but some few specimens have been found (e.g., Arkell *in* Moore 1957, p. L92; Reyment 1958) and some indicate the presence of *Nautilus*-like counter shading.

Surrogate ammonites were formed of sculpturing and investing waxes. The investing wax was heavier, the sculpturing wax lighter than water. As it has been suggested that ammonite and shell were of near neutral buoyancy (Trueman 1941; Raup and Chamberlain 1967), waxes were melted together empirically until disks of approximately neutral buoyancy were obtained. These disks were of similar diameter and width to the small paratype CAS cat. no. 4250. Being homogeneous, they lacked the orienting separated centers of gravity and buoyancy of actual ammonites (Trueman 1941, figs. 14 and 15). Such a wax disk, lighter than water, comes to rest floating with either lateral side up and the venter directed horizontally. Disks of near neutral buoyancy also usually settled toward a similar position, and a heavier disk sank and usually lay flat on the bottom. The addition of lateral spines gave the disks vertical stability, and they floated or sank with the venter directed vertically. For the light disk the spines had to be quite long to change its orientation in the water, at least twice as long as those on *A. peninsularis*. Spines of similar length to those on *A. peninsularis* gave the neutrally buoyant and heavier disks vertical stability and greatly slowed the descent of the heavier disk. Vertical stability could also be achieved by carving out rough umbilici and adding the wax to the ventrolateral margin to produce a shape similar to young *Tropites subbullatus* (Hauer). The greater breadth of young *A. peninsularis* relative to adult (Table 1) may have also tended to increase vertical stability in the young although the breadth of young *A. peninsularis* is not great enough to produce vertical stability in the absence of spines. Spines are not considered to have provided all vertical stabilization. Well separated centers of buoyancy and gravity would also lend vertical stability in addition to apertural stability, but the somewhat depressed form and probably longer body chamber (Raup 1967, fig. 16) of young *A. peninsularis* would have caused the centers of buoyancy and gravity to be closer together (Trueman 1941, p. 371). The spines would have provided added stability. They were of appropriate length to provide a neutrally buoyant ammonite similar to the small paratype with vertical stability.

A pelagic youth has generally been assumed for ammonoids (Arkell, Kummel, and Wright, *in* Moore 1957, p. L100; Kennedy and Cobban 1976, p. 34). Cowen et al. (1973, p. 211) suggest that the sculpture of ribbed ammonites indicates that they were necto-benthonic inhabitants of the photic zone, their sculpture serving to hide them from the predator above, and their close association with the bottom insuring that there was seldom a predator below. That ammonites lived in the photic zone is also suggested by the discovery that unlike the nocturnal *Nautilus* and some deep water octopods, at least some ammonites had an ink-sack (Lehmann 1971a, p. 1262). As the spines on young *A. peninsularis* and *A.* cf. *A. arrialoorensis* would not have improved the streamlining of a shell which was already poorly streamlined (Kummel and Lloyd 1955; Chamberlain 1976), swimming must have been at a rather deliberate pace, the entrapment of food effected without much darting about. The holotype of *A. peninsularis* is over 35 cm in diameter and much less strongly ornamented on its outer whorls and similarly less ornamented than specimens of less than 9 cm diameter. This reduction in relief of ribbing can be considered to accord with findings of Chamberlain and Westermann (1976, p. 328) that ribbing can serve to reduce drag and conserve propulsive power on smaller ammonites, but that large ones should be smooth. Young *A. peninsularis*, however, additionally had spines, and it does not merely become smoother as it approaches 10 cm in diameter; it also becomes higher relative to width and reduces the relative size of its umbilicus, thus improving streamlining slightly.

This complex of morphologic changes suggests that spiny young *Anapachydiscus peninsularis* may have been virtually planktonic and feeding on plankton. Ammonites have usually been considered to share the macrophagous diet of other living cephalopods, but a microphagous plankton-feeding mode of life has been suggested for some (Morton and Yonge *in* Wilbur and Yonge 1964, p. 49; Busnardo 1965, p. 110; Kennedy and Cobban 1976, p. 35), and Lehmann (1971b, p. 339) reports the preserved crops of ammonites containing the remains of prey too

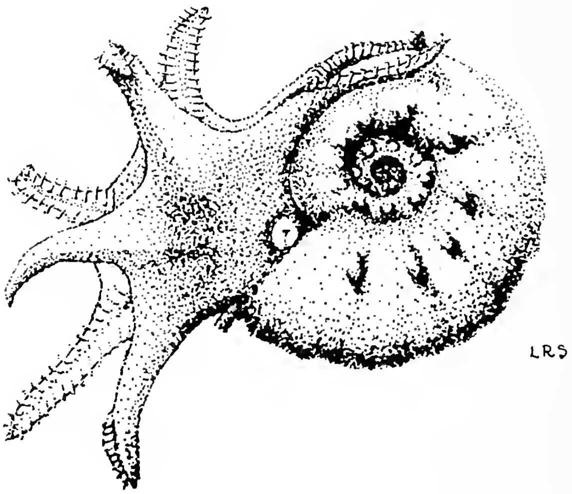

FIGURE 7. Hypothetical ammonite with eight webbed cirrated arms. Webbed arms suggested by distribution of epizoans of Seilacher (1960) and Meischner (1968). In both cases the epizoans were able to settle on the living ammonite shell posterior to the aperture and on the body chamber especially on the venter. They did not settle on the conch above the aperture. If the ammonite had tentacles as does *Nautilus* this selective infestation would not be expected, and long arms as in *Argonauta* would be able to sweep the whole conch clean. But webbed arms should be able to remove any larvae from the conch above the aperture while being restrained from reaching the lower and rearward portions of the conch. Webbed arms could be used to trap food or also for propulsion as in octopods (Lane 1960, p. 69).

small for the application of jaws. Studies of the jaws themselves (Kaiser and Lehmann 1971) indicate that the jaws of ammonites were not capable of actual biting. Reconstruction of the living ammonite is often based on analogy with *Nautilus* (e.g., Arkell *in* Moore 1957, p. L82, fig. 124); but *Nautilus* may be a poor model for ammonites (Mutvei and Reyment 1973; Kennedy and Cobban 1976, p. 2). Lehmann (1971a and b) has shown that the radula of ammonites is more like that of octopods and Vampyromorpha; and Flower (1955, p. 866) has argued for fewer arms, than the 60+ tentacles possessed by *Nautilus*, in groups considered ancestral to ammonites (Sweet and Moore *in* Moore 1964, p. K101, fig. 70). Mutvei and Reyment (1973, p. 632) propose a long bodied ammonite without funnel. But their proposed long ctenidia in narrow mantle cavity would require maintenance of a current of water to ward off asphixiation, and as the funnel is primarily a means of ejecting from the mantle cavity water which has passed over the ctenidia, the funnel is here retained to aid respiration. Figure 7 equips young *A. peninsularis* with eight webbed cirri-bearing arms. The position of the arms back over the upper part of the shell was suggested by the distribution of epibionts described by Seilacher (1960) and Meischner (1968). Webbed arms with cirri (as suggested by Kaiser and Lehmann 1971, p. 31) could have been used by young planktonic *A. peninsularis* to gather in a planktonic feast as its outrigger spines steadied it in the water.

The abandonment of spines, reduction of sculpture, increase of height and decrease of umbilical size may mark the change to greater swimming ability and more actively pelagic life. The thinness of the shell suggests that this did not lead to the exploration of great depths.

ACKNOWLEDGEMENTS

The other members of our safari, W.P. Popenoe, R.B. Saul, and W.C. Cornell, made the collecting trip possible. Robert Springfels donated sculpturing and investment waxes. Peter U. Rodda granted permission to study the type specimens of *Parapachydiscus peninsularis* Anderson and Hanna at the California Academy of Sciences. John Alderson became interested in the spines and loaned a specimen of *Anapachydiscus* cf. *A. arrialoorensis* (Stoliczka) for comparison. The manuscript has been improved by the suggestion and needed criticism of R.B. Saul, W.P. Popenoe, G.B. Cleveland, M.A. Murphy, and R. Cowen. Final drafting of figures 1–4 was by Victoria Doyle Jones. To all of the above I am grateful.

RESUMEN

Un espécimen de la temprana época Maestrichtian *Anapachydiscus peninsularis* (Anderson y Hanna) de Arroyo Santa Catarina, Baja California, México, tiene cavidades casi redondas taladradas en la concha arregladas de tal manera que sugieren muestras de las mordeduras del mosasaur. Las tempranas espirales están adornadas con huecas espinas laterales, las cuales podrían haber servido de estabilizadores verticales.

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CHELODESMID STUDIES. VIII. A NEW MILLIPED OF THE GENUS TRICHOMORPHA FROM COCOS ISLAND, WITH NOTES ON RELATED SPECIES AND THE PROPOSAL OF THE NEW TRIBE TRICHOMORPHINI (POLYDESMIDA: CHELODESMIDAE)

By Richard L. Hoffman

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The *Science Bulletin* and *Contributions in Science* of the Natural History Museum of Los Angeles County were merged into a single imperial octavo serial, retaining the name *Contributions in Science* and beginning with Number 301.

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Contributions in Science are articles in the earth and life sciences, presenting results of original research in Natural History. *Science Bulletin* (Numbers 1–30; 28 June 1965 to 10 April 1978) and *Contributions in Science* Numbers 1–300; 23 January 1957 to 16 June 1978) were merged into a single imperial octavo serial beginning with Number 301.

CHELODESMID STUDIES. VIII.
A NEW MILLIPED OF THE GENUS TRICHOMORPHA FROM COCOS ISLAND, WITH NOTES ON RELATED SPECIES AND THE PROPOSAL OF THE NEW TRIBE TRICHOMORPHINI (POLYDESMIDA: CHELODESMIDAE)[1]

By Richard L. Hoffman[2]

ABSTRACT: A new species of chelodesmid milliped, *Trichomorpha hyla,* is described from Cocos Island, Costa Rica. It differs from *T. folium* (Brolemann), from the same island in reduced tergal setation, absence of lateral paranotal dentation, lack of middorsal pink spots, and in a less complex gonopod structure. The new tribe Trichomorphini is proposed to accommodate the genera *Trichomorpha, Phylactophallus, Ancholeptodesmus, Belonodesmus, Allarithmus, Talamancia,* and the new genus *Loomisiola,* based on *Trichomorpha crinitapes* Loomis, 1972, from Costa Rica. The new name *Trichomorpha crucicola* is proposed to replace *T. gracilis* Loomis, 1974, preoccupied by *T. gracilis* Carl, 1914.

Dr. C. L. Hogue, Senior Curator in Entomology in the Natural History Museum of Los Angeles County, recently placed in my hands a small collection of diplopods picked up by him on Cocos Island. Most of the specimens are female pyrgodesmoids and not definitely identifiable to genus or species, but there is one adult male of an undescribed species in the chelodesmoid genus *Trichomorpha,* which is being described here in order to make the name available for use in Dr. Hogue's studies. The occasion is taken to append some additional information on the nomenclature and taxonomy of the genus and related forms.

Trichomorpha, endemic to the region between Ecuador and Costa Rica, is apparently now in the expanding phase of its phylogeny, as the known species are very numerous and yet basically similar in terms of general gonopod structure; specific differentiation is most pronounced in various external non-sexual characteristics. Sympatry and apparent syntopy seem to be common. In most features *Trichomorpha* appears to be a rather specialized genus of chelodesmoids, apparently related to members of the tribe Batodesmini, which has a very similar geographic distribution. Along with several other genera of the northern Andean-Panamanian region, *Trichomorpha* can be segregated into another distinct tribe which is proposed later in this paper.

I wish to express here my thanks to Dr. Hogue for providing the occasion for preparation of the following information about this group of interesting Neotropical myriapods.

FAMILY CHELODESMIDAE
GENUS TRICHOMORPHA SILVESTRI

Trichomorpha Silvestri 1898, Boll. Mus. Torino, vol. 12, no. 305, p. 11. Type species: *T. elegans* Silvestri 1898 (Ecuador), by monotypy.

Ethophallus Chamberlin 1933, Pan-Pacif. Entom., vol. 9, p. 20. Type species, *E. cervantes* Chamberlin 1933 (Costa Rica), by original designation.

Typophallus Chamberlin 1940, Bull. Univ. Utah (biol. ser.), vol. 5, no. 6, p. 10. Type species, *T. evidens* Chamberlin 1940 (Panama) by original designation.

Desmachrides Chamberlin 1940, op. cit., p. 11. Type species, *D. dichrus* Chamberlin 1940 (Panama), by original designation.

DIAGNOSIS: A trichomorphine genus in which the gonopod prefemur is short to moderate in length and the femur greatly reduced or absent, the solenomerite appearing to originate at the end of the prefemur; postfemoral elements simple to complex in form, but usually partially enclosing solenomerite. Coxa with prominent dorsal apophysis. Anterior legs of males with large distal tibial pad, subtending the tarsus; in some species the coxa and femur of the 7th pair of legs are lobed or otherwise modified. Anterior sterna with or without paramedian processes or lobes. Prefemora of some or all legs usually with apical spine in both sexes. Antennae long and slender, extending back at least to paranota of 3rd segment.

NOTES: About 40 specific names have been based upon specimens referable to this genus, as well as a number of unjustifiable generic names. Loomis (1964, 1972) has shown some of these names to be synonyms and so reduced the total somewhat, but a number of undescribed species at hand, and the small fraction of the generic range that has been sampled thus far, suggest that eventually as many as 200 species of *Trichomorpha* may be discovered.

In 1972 Loomis merged the name *Ethophallus* with *Trichomorpha,* but in a later paper (1974) kept the two separate on the

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basis of a supposed difference in proportions of several podomeres. Having the opportunity to study type material in the collection of the late R. V. Chamberlin, I can verify that *Ethophallus cervantes* is in fact only a species of *Trichomorpha* and the 'difference' in lengths of the tibia and tarsus entirely illusory. At the same time I can confirm Loomis's disposal of the two names *Typophallus* and *Desmachrides* as strict junior synonyms of *Trichomorpha*.

The name *Trichomorpha gracilis*, proposed by Loomis in 1974 for a Costa Rican species, is preoccupied by *Trichomorpha gracilis* Carl 1914, from Colombia. On learning of my intention to describe the Cocos Island species, Mr. Loomis asked me to use the occasion to provide a new name for his *gracilis*. I herewith propose the new name ***Trichomorpha crucicola***, in reference to the type locality (Finca las Cruces, near San Vito, Costa Rica).

Trichomorpha hyla NEW SPECIES

Figures 1–8

Holotype. — Adult male (LACM) collected at Wafer Bay, Cocos Island, Costa Rica, 18 April 1975, by Charles L. Hogue.

DIAGNOSIS: A moderate-sized member of the genus characterized by the smooth metaterga, each with only two setae; presence of tibial pads on legs 2–6 of males; denticulate posterior edge of most paranota; occurrence of paramedian processes on the sterna between legs of the 2nd, 3rd, and 5th pairs, and of a prominent basal lobe on the femora of the 7th pair; and by the relative simplicity of gonopod structure, the acropodite set off by a distinct suture and virtually without any lobes or processes.

DESCRIPTION: Body ca. 17.0 mm in length, 2.1 mm wide over most body segments, W/L ratio about 12.4%. Body generally light brown. Metaterga pale testaceous brown, fading to nearly colorless on the paranota, dorsal surface of prozona darker brown, imparting a somewhat annulate appearance with low magnification. Labrum and clypeus nearly colorless, basal antennomere very pale brown, 2nd–6th antennomeres fuscous, 7th nearly white. Podosterna and midventrum of prozona whitish, basal four podomeres also nearly white, tibia light brown, tarsus dark brown except for apical fourth which is white.

Head of normal appearance for the genus, front with sparse, prominent, setiferous punctures; epicranial suture fine but distinct down to level of antennae; genae convex, lateral margin narrow but well-defined, with five or six marginal setae. Ventral edge of labrum marginate except proximad to median teeth; 8–8 labral setae. Interantennal space broad, wider than length of 1st antennomere. Antennae long and slender, articles 5 and 6 with well-defined, oval, white, sensory field on outer distal surface. Sensory cones small, indistinctly grouped into two diads.

Collum about as wide as head, surface convex, smooth and polished; lateral ends acute, forming about a 70° angle, lateral edges set off up to level of mandibular articulation. 8 setae along anterior margin, and 4 in a transverse row approximately at midlength.

Body segments not deeply telescoped, paranota thus well-separated, subsegments not strongly separated, stricture shallow, its anterior edge sharply defined. Paranota well developed, set high on body and nearly horizontal, middorsum somewhat convex, surface of metaterga smooth and polished, with two paramedian setae; transverse sulcus evident on segments 5–17, dorsal surface of paranota slightly convex basally. Posterior corners of all paranota acute, becoming increasingly prolonged and subspiniform back to about segment 17, posterior edge of most paranota distinctly denticulate, lateral edge with prominent offset at midlength on segments 2–7, thereafter nearly smooth and straight (Figs. 1, 2); ozopores opening dorsolaterad, peritremata moderately developed, elongate, not set off from remainder of paranotal edge; anterior corners of paranota with a prominent denticulation. Paranota of segment 19 small, curved mesad.

Epiproct of normal shape, but lateral and apical dorsal tubercules a little more prominent than usual (Fig. 3). Paraprocts and hypoproct without peculiarities.

Sterna of midbody segments broad (about equal to combined length of coxa and prefemur), slightly elevated above prozona, smooth and glabrous, with indistinct transverse groove, no subcoxal spines or lobes. Stigmata minute, without raised edges. Side of metazona smooth. Pleurosternal carinae visible only on first two or three segments. Prefemora with prominent apical spine from 2nd to 18th pair of legs. Tibial pads present on legs of 2nd–6th pairs, much the largest anteriorly where about 2/3rds length of tarsus. Tarsal claw small and straight.

Gonopores opening flush with surface of coxae of 2nd pair of legs. Sternum between 3rd pair of legs with two small paramedian lappets, that between 4th pair of legs with very large, compressed, divergent, apically truncated processes (Fig. 4), that between 6th pair of legs with two small contiguous acutely conical projections (Fig. 5). Coxae of 6th and 7th legs produced ventrad, the projection especially prominent on 7th legs, the femora of which are provided with a large proximal lobe or process on the ventral side (Fig. 5).

Gonopod aperture transverse, lateral and posterior edges produced ventrad, anterior edge unmodified; gonopods projecting forward over sternum of 6th segment, of the form shown in figures 6–8. Coxae without median sternal remnant (Fig. 6), the dorsal apophysis robust, with two setae; telopodite attached at a right angle to coxa, nearly straight, setose prefemoral region about one-third total length of telopodite, femoral region strongly reduced and indicated only by the point of origin of the solenomerite; latter slender, nearly straight, its entire length visible in mesal aspect (Fig. 8); postfemoral region a simple, spatulate, apically concave process with a small thin lamella on the dorsal side. Lateral side with a prominent postfemoral cingulum (Fig. 7, C).

NOTES: Dr. Hogue supplied the following information on the habitat of this species (in litt., 19 September 1975): "All of this material definitely came from bromeliads, although the collecting occurred fairly close to ground level, approximately 4–6 feet. The specimens were taken from very large plants growing on downed logs and branches of *Hibiscus tiliaceus*, a mangrove species. The ground beneath the site from which the millipeds came was flooded by high tide twice daily."

The relationships of this species are not easy to establish. There are now about 35 presumably valid species of *Trichomorpha*, 22 of them described from Colombia, 5 from Panama, and 6 from Costa Ricas. Attems (1938) gave a key to 20 South American species, but was unable to include most of the forms named by Chamberlin because of inadequate descriptions. An additional member of this genus (*T. folium* Brolemann 1903) was misplaced by Attems in *Camptomorpha*, where it has no affinities whatever.

T. hyla will not trace through Attems' 1938 key at all, being excluded by both of the choices in the first couplet (metaterga with numerous irregular setae as opposed to setae in two or three transverse rows). In this species each metatergum has only a single row composed of two setae, placed paramedially behind the transverse sulcus (increasing to four on the last few segments). On the basis of "best fit" we select the second choice, *T. venusta* Carl 1914, from Colombia, but *hyla* differs from this form in a number of ways including a different gonopod structure.

Of the four Panamanian species keyed by Loomis (1964), *hyla* runs out to *T. nidicola* Chamberlin, but differs in lacking a pale middorsal line and lateral paranotal dentations (four to six prominent teeth in *nidicola*).

Six Costa Rican species are keyed by Loomis (1972), of them *hyla* comes closest to *T. folium,* coincidentally the *Trichomorpha* already known from Cocos Island.

In light of present knowledge of the genus, it seems impossible to confidently relate *T. hyla* to any mainland species, and for the present it may be justifiable to consider it a valid species endemic to Cocos Island. In this respect then, comparison needs be made primarily with *T. folium* (Brolemann).

This species was supported by a detailed description and good drawings, and the following points of difference may be noted: *folium* is slightly longer and more robust than *hyla,* its W/L ratio 14% as opposed to 12%; the metaterga in *folium* are reddish-brown with a series of middorsal red spots and the legs are uniformly yellowish; although Brolemann did not allude to tergal setation generally, he stated that the collum has three transverse series of hairs and generally the arrangement of the collum persists on the metaterga as well. In *folium* the paranota are laterally dentate (nearly smooth in *hyla*); the femur of the 7th pair of legs lacks the prominent basal lobe found in *hyla;* and the gonopod telopodite is provided on its dorsolateral surface with three triangular projections not present in *hyla.* There is no doubt whatever that they are quite different, despite some points of similarity such as lobation of the anterior sterna and general gonopod pattern.

Loomis (1972:192) suggested that perhaps *T. evidens* (Chamberlin) from the Canal Zone is a junior synonym of *folium.* I have been able to study the type material of *evidens* and find it to be quite different from *folium;* among other things *evidens* completely lacks processes on the anterior sterna and it is moreover the least setose of known *Trichomorpha* species. I was unable to locate either setae or setal sockets on any of the terga.

The present opportunity is taken to implement a long-standing intention, to formally recognize a suprageneric taxon to include *Trichomorpha* and related genera within the subfamily Chelodesminae:

Trichomorphini NEW TRIBE

DIAGNOSIS: Small (9–24 mm) chelodesmoids in which the gonosternum is reduced or lost; gonopod aperture transversely narrow with flared edges; gonopod coxae with prominent dorsal apophyses; femoral region of gonopod very short and merged with end of prefemur, solenomerite appearing to originate from prefemur; without prefemoral process; solonomerite long and slender, usually partly or entirely enveloped within the postfemoral region, latter straight or strongly curved dorsad.

Body parallel-sided, none of anterior segments broadened or narrowed, relatively slender; segments not deeply telescoped into each other. Antennae long and slender, with sensory fields on outer side of articles 5–7. Mandibles relatively large. Collum hemispherical and convex. Paranota of moderate size and usually set high on sides; at least some metaterga with transverse sulcus (usually segments 5–17), and most species with at least two or three transverse rows of setae; pore formula normal, pores opening dorsolaterad in elongated peritremata, latter continuous with edge of paranota. Epiproct usually with enlarged lateral and subterminal tubercules. Sterna relatively broad and flat, at most produced into low subcoxal cones. Anterior legs of males usually with tibial pads subtending tarsi, often coxae and prefemora variously lobed or otherwise modified.

COMPONENTS: *Trichomorpha* Silvestri 1897; *Ancholeptodesmus* Brolemann 1919; *Belonodesmus* Chamberlin 1918; *Allarithmus* Attems 1933; *Phylactophallus* Pocock 1909; *Talamancia* Loomis 1974; *Loomisiola* new genus.

DISTRIBUTION: Northern Cordilleran region, from Ecuador to Costa Rica, east as far as Trinidad.

REMARKS: All of the generic names listed above are subject to major change when sufficient material is at hand for a revision of the group. Some may prove to be junior synonyms and *Trichomorpha* itself may be divided into two or more smaller genera. Loomis (1964, 1972) reduced the Chamberlinian names *Typophallus, Desmachrides,* and *Ethophallus* to the synonymy of *Trichomorpha,* and it seems quite possible, on the basis of published information, that *Ancholeptodesmus* and *Allarithmus* may suffer a similar fate.

I know the genus *Phylactophallus* only from Pocock's original description, but it seems to be based on a trichomorphine species, and to be a distinct genus. I think it is very likely that *Isidrona forficula* Attems (1933) is a generic and probably also a specific synonym of *P. stenomerus* Pocock. In the "Checklist" of Central America millipeds, Loomis (1968:15)—on the basis of a suggestion made by me *in litt.* many years ago—combined the names *Phylactophallus* and *Allarithmus.* I now suspect that my opinion was based upon a confusion of two names *(Allarithmus* instead of *Isidrona),* in any case it was egregiously incorrect.

Most of the species referred to *Trichomorpha* and its satellite genera have the gonopods formed on a basically similar pattern. One Costa Rican species, however, is so divergent that some kind of recognition in a separate status seems desirable.

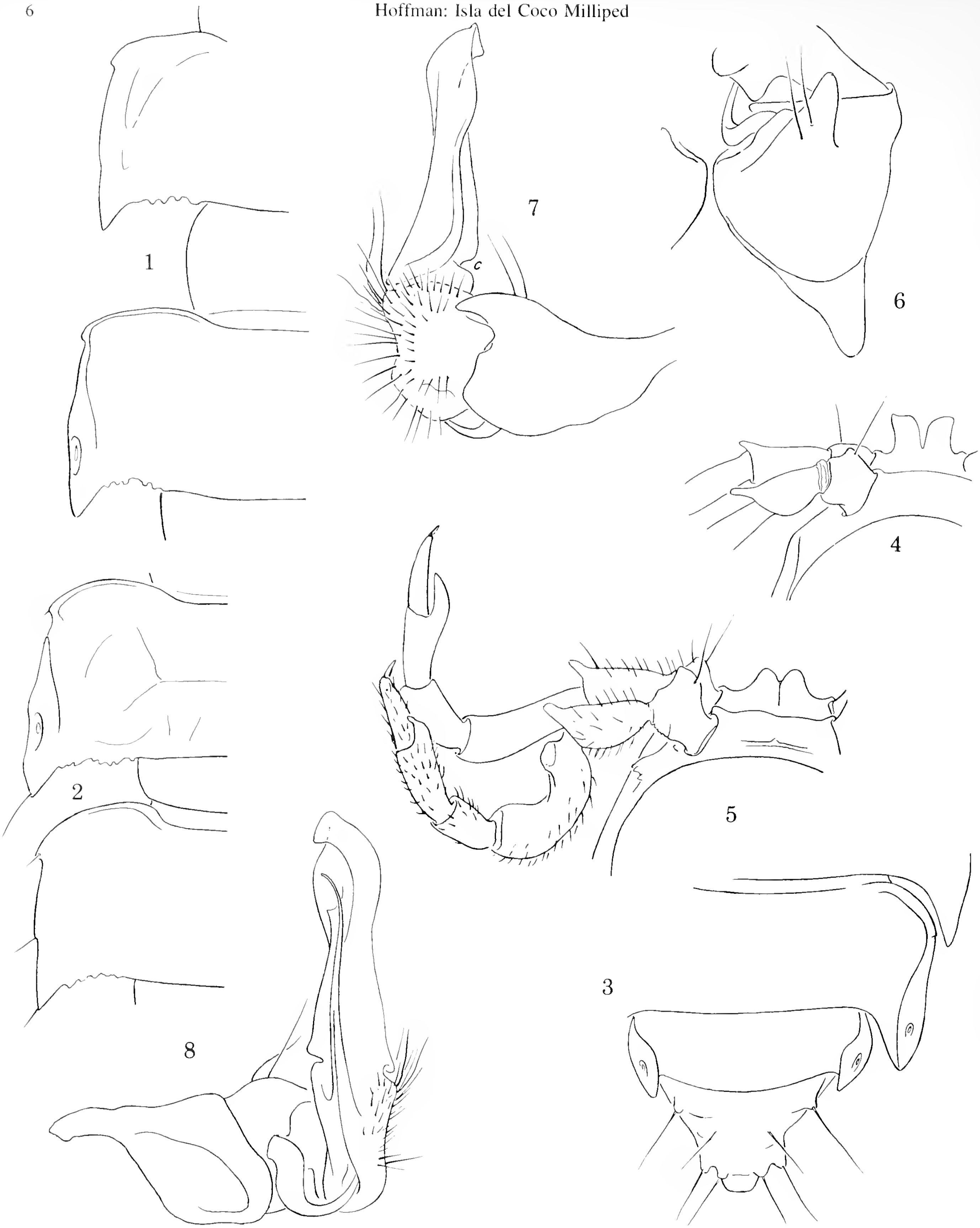
Loomisiola NEW GENUS

Type species.—*Trichomorpha crinitapes* Loomis 1972.

DIAGNOSIS: A trichomorphine genus differing peripherally from *Trichomorpha* in having shorter and stouter antennae, and paranota with less prominently produced posterior corners. The gonopod prefemur is unusually long, distally broadened, and provided apically on the lateral side with an oblique lobe set with numerous long slender setae; postfemoral elements of gonopod strongly reduced.

DISTRIBUTION: *Loomisiola crinitapes* is known so far only from the original type material, taken at Cairo, Province Limon, Costa Rica.

ETYMOLOGY: It is appropriate that this taxon commemorate the name of H. F. Loomis, who has contributed most to our knowledge of Central American and Antillean Diplopoda, in numerous papers spanning four decades.



FIGURES 1–8. *Trichomorpha hyla,* structural details, from holotype. Figure 1, left paranota of segments 8 and 9, dorsal aspect. Figure 2, left paranota of segments 13 and 14, dorsal aspect. Figure 3, posterior end of body, dorsal aspect. Figure 4, sternum and bases of right legs of segment 5, aboral aspect. Figure 5, sternum and right legs of segment 6, aboral aspect (setation omitted from anterior leg). Figure 6, coxa and base of telopodite of right gonopod, dorsal aspect. Figure 7, left gonopod, lateral aspect (*c,* cingulum). Figure 8, left gonopod mesal aspect. Figures 1–5 drawn X45, 6–8 X 90.

RESUMEN

Se describe una especie de la familia Chelodesmidae, *Trichomorpha hyla,* que se encuentra en la Isla del Coco de Costa Rica. Se diferencia de *T. folium* (Brolemann 1903) de esa misma isla en la setación dorsal reducida, en la ausencia de dentación de los paranota, y en una estructura gonopoda menos compleja. Le nueva tribu Trichomorphini se propone para acomodar los géneros *Trichomorpha, Phylactophallus, Ancholeptodesmus, Belonodesmus, Allarithmus, Talamancia,* y el nuevo género *Loomisiola,* basado en *Trichomorpha crinitapes* Loomis 1972, de Costa Rica.

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SYSTEMATICS OF THE SPECIES OF *CRYPTORHOPALUM* (COLEOPTERA: DERMESTIDAE) OCCURRING IN CALIFORNIA

By R.S. Beal, Jr.

Published by the NATURAL HISTORY MUSEUM OF LOS ANGELES COUNTY • 900 EXPOSITION BOULEVARD • LOS ANGELES, CALIFORNIA 90007

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Edward Ostermeyer
Editor

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CONTENTS

The *Science Bulletin* and *Contributions in Science* of the Natural History Museum of Los Angeles County were merged into a single imperial octavo serial, retaining the name *Contributions in Science* and beginning with Number 301.

This serial has been newly formatted for maximum use of typography and illustrations per page, and sized for maximum use of paper. All photography has been produced utilizing a 200-line screen for detail.

Since most institutions rebind *Contributions in Science* collectively into hardbound volumes, and many researchers using them desire to photocopy material, two new features have been incorporated into the new format. A suggested citation line provides the abbreviated serial title, year, number of publication, and total pagination, and appears in the lower left corner of each page; and pages of *Contributions in Science* have been printed off-center to provide a two-inch gutter between adjacent pages for easier accessibility in photocopying.

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Contributions in Science are articles in the earth and life sciences, presenting results of original research in Natural History. *Science Bulletin* (Numbers 1–30; 28 June 1965 to 10 April 1978) and *Contributions in Science* Numbers 1–300; 23 January 1957 to 16 June 1978) were merged into a single imperial octavo serial beginning with Number 301.

SYSTEMATICS OF THE SPECIES OF *CRYPTORHOPALUM* (COLEOPTERA: DERMESTIDAE) OCCURRING IN CALIFORNIA[1]

By R.S. Beal, Jr.[2]

ABSTRACT: The following described species are recognized as occurring in California: *C. triste* LeConte (= *C. modestum* Casey, *C. fusciclave* Casey, NEW SYNONYMS), *C. uteanum* Casey (= *C. nephianum* Casey, *C. aridum* Casey, *C. bakeri* Casey, NEW SYNONYMS), *C. apicale* (Mannerheim) (= *C. coloradense* Casey, *C. tuckeri* Casey, *C. fontinale* Casey, *C. grisescens* Casey, NEW SYNONYMS), *C. fusculum* LeConte (= *C. anthrax* Casey, *C. granum* Casey, *C. pumilum* Casey, *C. piceum* Casey, NEW SYNONYMS, and *C. affine* Casey, REVISED SYNONYMY), *C. filitarse* Casey, and *C. balteatum* LeConte. Two new species are described: *C. rubidum*, for which Yuma, Arizona, is the type locality, and *C. haplotes*, known only from Jacumba, California. The species can best be distinguished by characters found associated with the aedeagus and lateral lobes and with the eighth morphological abdominal sternum of the males. Redescriptions of existing species are provided together with lectotype designations wherever necessary. A key to the species is provided for forms of adults occurring in California. Flower hosts, geographic distribution, and synonymies are given for each species insofar as known. In addition to the species above, synonymies are given and lectotypes designated for two species closely related to *C. balteatum* but occurring outside California: *C. reversum* Casey (= *C. festivum* Casey, *C. balteatum* Casey [non *balteatum* LeConte], *C. pallens* Casey, NEW SYNONYMS), and *C. pruddeni* Casey (= *C. insigne* Casey, *C. anthrenoides* Casey, NEW SYNONYMS).

Adults of the genus *Cryptorhopalum* are small, ovate beetles, almost always taken on flowers, and readily recognized as dermestids by the presence of a median ocellus and a hind coxa grooved for the reception of the femur. The two-segmented antennal club, which fits closely into a fossa on the underside of the prothorax, and the covering of hairs rather than of scales easily separates them from all other Nearctic dermestids.

Relatively large numbers of specimens of the genus are found in the collections of most insect museums. Nevertheless, no revision of the genus has been undertaken since that of Thomas L. Casey in 1900. Because Casey worked from very small numbers of specimens and described his species from a typological rather than a population concept, his "species" in many instances are simple variants of previously described species or of another of his species. Consequently his key to the species is of little value. There is a clear need to investigate the species from a population concept, to develop a workable key for distinguishing them, and to provide accurate descriptions for them. This paper is an effort to accomplish these goals for those species presently known to occur in California.

Other than records of flowers on which the adults are found, very little is known of the biology of species of *Cryptorhopalum*. Larvae of some unidentified species have been intercepted at border inspection stations on cheese and other food products from Mexico. Nevertheless, no Nearctic species has ever been known to occur as a pest of stored food products. Larvae of a very rare Arizona species, *C. poorei*, have been found associated with spider nests under the bark of dead ponderosa pine trees (Beal 1975), yet an association with spider nests does not seem to be a likely natural habitat for larvae of most of the species, judging from their numbers and the situations in which adults are often found. Hopefully, the present study will stimulate further investigations into the biologies of the species.

SYSTEMATICS

SPECIES CHARACTERS

Adults of some species are readily distinguished by patterns formed on the elytra by light and dark colored setae or by the shapes of the antennal club. The form of the anterior tibia is diagnostic for a few species, as is the density of punctation on the pronotum. Some species, however, are virtually indistinguishable from each other on the basis of external characters. Nevertheless, apparently reliable characters for the recognition of all California species and for many other Nearctic species are found in struc-

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tures associated with the male genital apparatus.

The male genital tube is formed by the terga and the sterna of the 8th and 9th morphological abdominal segments, the weakly sclerotized tegmen (or basal piece) that lies beneath the base of the aedeagus, and the lateral lobes and aedeagus. Except in copulation, these parts are telescoped together within the abdomen. Discriminating characters are found in the shape of the aedeagus, in the shape of the lateral lobes and the "bridge" that connects the two lobes, and most particularly in the shape of the apical margin of the sternum of abdominal segment 8 and the form of the setae that are inserted on it.

SPECIES IDENTIFICATION

Any effort to identify species on the basis of external characters alone is complicated by two problems. One is the relative paucity of such characters. The other is the relatively large degree of geographic variation that occurs over the range of some of the species. It is usually fairly easy to separate members of any two species occurring within a limited geographic area. Yet convergence of external characters may make quite difficult separation of specimens of one species from those of another from a distance of only a few hundred miles. In the key that follows, an effort is made to distinguish only those forms of each species that are found in California. However, the formal description for each is given for all variations within its entire range, as far as known.

SPECIES GROUPS

Based on the total number of known adult characters, the Nearctic species fall into three rather distinct groups. The California representatives of these groups are the following.

TRISTE group
  C. triste LeConte
  C. rubidum, new species
  C. uteanum Casey
  C. apicale (Mannerheim)
  C. fusculum LeConte
QUADRIPUNCTATUM group
  C. filitarse Casey
  C. balteatum LeConte
HAPLOTES group
  C. haplotes, new species

The *quadripunctatum* group is characterized by the presence of an appendage-like structure on each lateral posterior angle of the 8th (morphological) abdominal sternum of the male (Figs. 14, 15). Externally it is characterized by the presence of three bands of light-colored pubescence on the elytron, a feature not found in members of either the *triste* or *haplotes* groups. As far as the California species are concerned, the *quadripunctatum* group is further separable by the ovate outline of the male antennal club. In distinction to this, members of the *haplotes* and *triste* groups have a subcylindrical antennal club in the males.

In members of the *triste* group the 8th (morphological) abdominal sternum of the male lacks lateral appendage-like structures or sublateral marginal papillae but has a posterior median process at the apex of which are various specialized setae. The one exception is *C. rubidum,* which has a median cluster of setae but no process. The dorsal setae in members of this group are commonly unicolorous, but if bicolorous they do not form three more or less distinct bands on the elytron. (*C. apicale* usually has bicolorous setae and these often form an oblique subbasal band and a subapical spot, but there is no submedian band.)

The *haplotes* group, for which there is but a single Nearctic representative, is distinguished from both of the preceding groups by its more elongate form (Fig. 1). The 8th (morphological) sternum of the male lacks a median apical process and lateral appendage-like structures, but possesses sublateral papillae on which are inserted several moderately long setae (Fig. 12). The margin of the sternum has a cluster of setae inserted at the midline. The dorsal setae are unicolorous, at least in this and the one Mexican species I have studied.

C. rubidum is the least specialized of all the species considered, at least as far as the male genital structures are concerned. Conceivably it could be placed in a separate group or attached to any of the three groups as its most primitive member. However, here it is placed in the *triste* group because of its very close similarity in external characters to *C. uteanum.*

ABBREVIATIONS

In the discussion of species below, museums frequently referred to are abbreviated as follows: CAS — California Academy of Sciences, San Francisco; MCZ — Museum of Comparative Zoology, Cambridge, Massachusetts; LACM — Natural History Museum of Los Angeles County, California; NMNH — United States National Museum of Natural History, Washington, D.C.

GENERIC NOMENCLATURE AND DESCRIPTION

Cryptorhopalum Guérin-Méneville

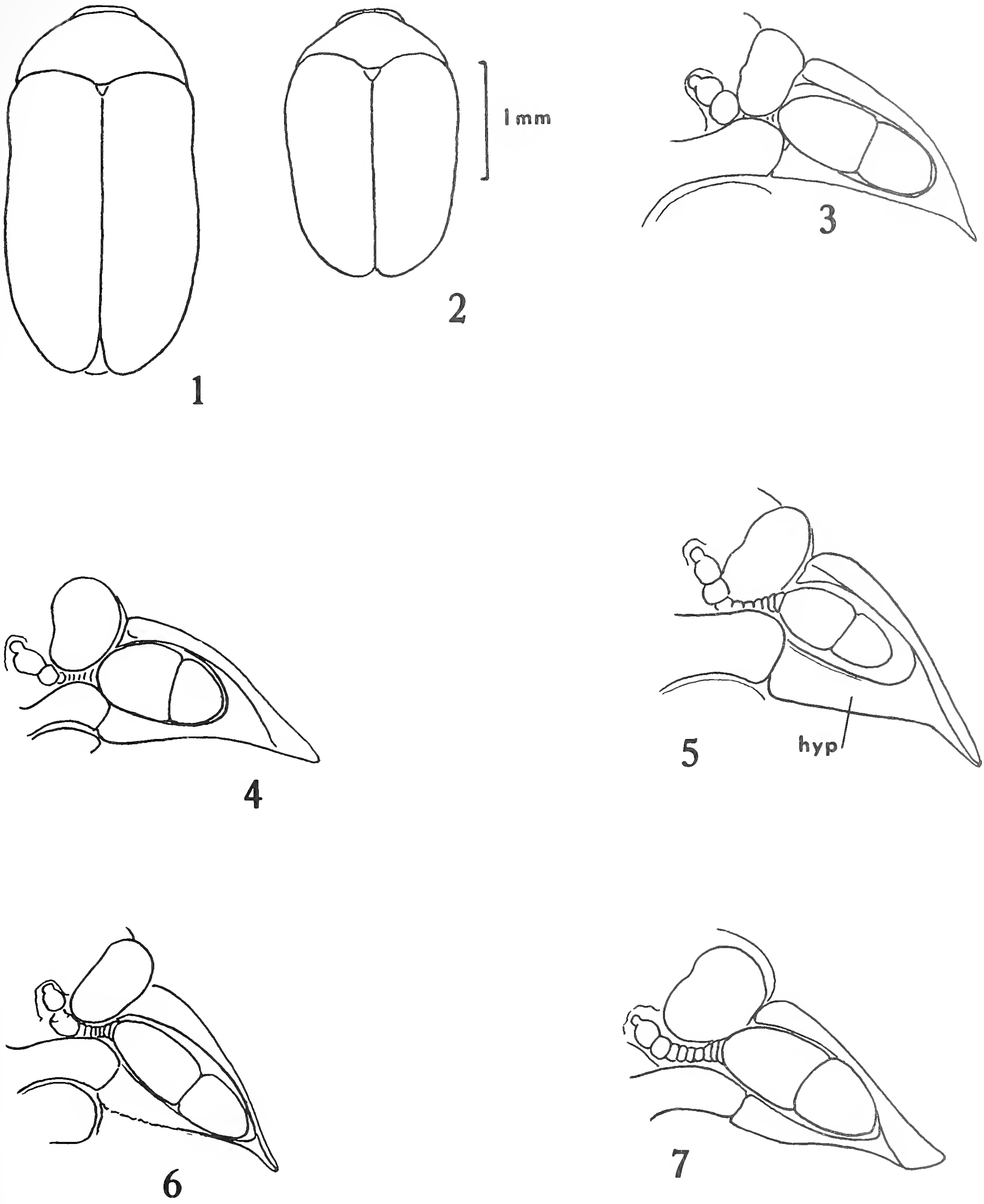
Cryptorhopalum Guérin-Méneville 1834 (1838), p. 67. LeConte 1854, pp. 106–107. Reitter 1880 (1881), p. 43. Jayne 1882, p. 364. Casey 1900, pp. 145, 155. Sharp 1902, p. 652. Rees 1943, p. 11. Beal 1959, p. 101 (in key to genera). Beal 1975, pp. 228–233 (larval description).

Cryptorrhopalum Arrow 1915, pp. 437, 442.

Type of the genus: *Cryptorhopalum quadripunctatum* Guérin-Méneville 1838.

DESCRIPTIONS

ADULT MALES: Body ovate, moderately convex, covered on dorsal surfaces with moderately short, subrecumbent hairs; scales absent although some setae may be slightly ensiform. Head slightly inflexed with front inclined 10 to 30 degrees from the vertical; median ocellus present. Antenna 11-segmented; club 2-segmented, ovate or subcylindrical; segment 10 subequal in length to segment 11 or longer than segment 11. Pronotum carinate on lateral margins but without sublateral carinae or impunctate areas; basal lobe not raised (on same plane as posterior margins), projecting posteriad moderately to strongly. Scutellum visible. Elytra across humeri slightly wider than width of pronotum at base; epipleuron inflexed with surface in approximately same plane as metepisternum. Prosternum with anterior margin very weakly or not at all deflexed, arcuately rounding to sides with area in front of lateral margin of procoxa somewhat longer than area in front of middle of procoxa; process moderately broad, received in mesosternal sulcus, and attaining mesosternum. Hypomeron with fossa closely conforming to size and shape of antennal club; fossa occupying most of hypomeron and margined behind by thread-like carina; posterior margin of



FIGURES 1–7. Figure 1: Dorsal aspect of *C. haplotes*. Figure 2: Dorsal aspect of *C. apicale*. Figure 3: Underside of prothorax showing antennal club in place within antennal fossa of male of *C. haplotes*. Figure 4: Same of male of *C. balteatum*. Figure 5: Same of female of *C. haplotes* (hyp = hypomeron). Figure 6: Same of male of *C. rubidum*. Figure 7: Same of male of *C. fusculum*.

KEY TO ADULTS FROM CALIFORNIA

1. Subbasal, subapical, and apical bands and sometimes basal band of light-colored pubescence present on elytron; basal and subbasal bands sometimes coalesce. Basal half of 1st visible abdominal sternum with 2 oblique striae extending from beneath each trochanter (leg may need to be relaxed and moved to observe character). Male antennal club ovate (Fig. 4). Female with 2 circular foveae on disc of 5th visible abdominal sternum (Fig. 33) 2

— Elytral pubescence unicolorous, or with subapical spot of light-colored pubescence with or without subbasal band of light-colored pubescence, or covered with light-colored pubescence with few to many intermingled dark hairs, particularly at apical third. Basal half of 1st visible abdominal sternum with 1 oblique stria extending from beneath each trochanter. Male antennal club more or less elongate, subcylindrical (Figs. 3, 5–7). Female without 2 circular foveae on disc of 5th visible abdominal sternum 3

2. Light-colored pubescence of elytron a deep gold color (orichalceous). Integument of pronotum generally appreciably darker in color than elytron at base. Sternum of 8th (morphological) abdominal segment without cluster of setae at middle of apical margin; lateral process with stout, curved seta at apex (Fig. 15) .... *balteatum*

— Light-colored pubescence of elytron white with slight golden cast. Integument of pronotum and base of elytron usually identically colored. Sternum of 8th (morphological) abdominal segment with cluster of setae at middle of apical margin; lateral process with slender seta at apex (Fig. 14) .... *filitarse*

3. Form elongate: ratio of width (across humeri) to length (of pronotum and elytra) 1:1.85 or longer (Fig. 1) .... *haplotes*

— Form more ovate: ratio of width to length 1:1.80 or shorter (Fig. 2) 4

4. Pubescence of elytron consisting of piceous to black hairs with subapical patch of light golden or whitish pubescence (rarely limited to as few as 3 or 4 light-colored hairs) with or without subbasal band of golden or whitish pubescence, or (form limited to southern deserts) elytron completely covered with whitish pubescence except for few scattered blackish hairs, mostly at apical ⅓. Both segments of antennal club identically colored (ochreous to reddish) .... *apicale*

— Pubescence of elytron uniformly light golden or piceous but not whitish and without subbasal band or subapical patch of light-colored hairs. Segments of antennal club variously colored 5

5. Protibia expanded at apex (Fig. 29). Pronotum with punctures of disc about 1⅓ times diameter of facet of eye and separated by ½ to 2 times diameter of single puncture. Male antennal club dark reddish brown to black. .... *triste*

— Protibia gradually narrowing from middle to apex (as in Fig. 30). Pronotum with punctures of disc no wider than diameter of facet of eye and separated by 3 or more times diameter of single puncture, or, if not separated by more than twice diameter of puncture, then proximal segment of male antennal club light yellowish brown to ochreous. Male antennal club light or dark 6

6. Male with hypomeron continued behind antennal fossa; hypomeron about as wide at narrowest point behind fossa as width of segment 3 of antenna. Male and female antennal clubs with segment 10 light yellowish brown or light ochreous and segment 11 usually somewhat darker, particularly on anterior side and at apex. Pronotum and elytra usually dark mahogany brown to black with pronotum same color as elytra (lighter colored specimens probably teneral) .... *fusculum*

— Male with hypomeron behind lateral ⅓ of antennal fossa obliterated or narrowed to no more than half width of segment 3 of antenna (not including width of carina bounding fossa). Segments of antennal club in males and females concolorous or segment 11 darker than segment 10, but when segment 11 darker, then segment 10 rufous rather than light yellowish brown or ochreous. Head and pronotum usually black to dark mahogany with elytra rufous; elytra frequently dark mahogany at base and along basal half of median suture and rufous apically and along sides 7

7. (Species indistinguishable by external morphological characters.) 8th (morphological) sternum more or less evenly rounded apically with cluster of simple setae at middle and without extended median process bearing two recurved setae (Fig. 9); aedeagus without proximally directed hook at genital pore (Fig. 22). Western California deserts from Inyo Mts. to Yuma .... *rubidum*

— 8th (morphological) sternum with distal process bearing tight cluster of acutely pointed setae and two, long, recurved setae at apex (Fig. 13, 17); aedeagus with proximally directed hook at opening of genital pore (Fig. 24). Western Texas to SW Wyoming across Utah and Nevada to California; in California in coastal range and along coast .... *uteanum* hypomeron sharply angled with or without feeble, thread-like carina. Mesosternal disc completely divided by deep and broad sulcus for reception of prosternal process. Metasternal episternum less than ¼ as wide as metasternum. Metasternal epimeron broadly joined to lateral margin of metasternal coxa. Legs with tibia spinose on dorsal margin but without teeth; tarsus of hind leg with first segment subequal in length to or slightly longer than second segment.

ADULT FEMALES: As males except antennal club about half size of male club; antennal fossa correspondingly smaller.

DISCUSSION: Members of the genus are characteristically dermestid-like, having a distinct median ocellus, the hind coxa grooved for the reception of the femur, and the head hypognathous and partially recessed within the pronotum. They somewhat resemble members of the genus *Anthrenus* in size and shape, but are covered with hairs rather than scales. The most distinctive character is the 2-segmented antennal club, in which the segments are subequal or segment 10 is longer than segment 11. Members of *Orphinus* Motschulsky, which in the United States occur only in Florida and Hawaii, have a 2-segmented club, but segment 11 is greatly enlarged and nearly round with segment 10 at most only a third as long.

The genus most nearly related to *Cryptorhopalum* seems to be *Hemirhopalum* Sharp, a Neotropical genus. According to Sharp (1902) members of *Hemirhopalum* lack a median ocellus, have "a large, but ordinary, laxly-jointed" male antennal club, and have "the sides of the thorax beneath" with "a large impression which is shallow behind instead of a depression that exactly fits the club of the antennae: this impression in front is broadly open." I have not seen any specimens with the particular characters that Sharp seems to have described. I have seen unidentified Neotropical species that belong to the same species group as *C. haplotes*. I suspect that some of the species now placed in *Hemirhopalum* properly belong in the *haplotes* group within *Cryptorhopalum*. Obviously there is a definite need for a revisionary study of the Neotropical members of both genera.

Aside from *Hemirhopalum*, species of *Cryptorhopalum* appear to have the closest affinities with *Orphinus* and *Thaumaglossa* Redtenbacher. This judgment is based on larval as well as adult characters. Significantly, the larvae of all 3 genera have a cluster of hastisetae inserted on the membrane behind each side of the tergum of abdominal segment 7, but not behind any other segment. The endemic Hawaiian genus *Labrocerus* also has larvae that are quite similar to those of *Cryptorhopalum* (Beal 1975), although the elongated form and the many-segmented antennal club of the adults make them appear more closely related to *Megatoma* or *Trogoderma*. *Cryptorhopalum*, *Orphinus*, *Thaumaglossa*, and *Labrocerus* most likely share a more recent common ancestry than any one of these genera does with any other genus of Dermestidae for which larval characters are known.

GEOGRAPHIC DISTRIBUTION: The genus is primarily Neotropical with 120 species currently recognized from South and Central America. Probably a total of 18 species occur within the United States, including 3 as yet undescribed from states other than California. The genus is found across the entire country with the exception of the northern New England States. The greatest proliferation of Nearctic species is in the southwest.

DESCRIPTIONS AND DISCUSSION OF CALIFORNIA SPECIES

Cryptorhopalum triste LeConte

Cryptorhopalum triste LeConte, 1854, p. 111. Reitter, 1880 (1881), p. 44. Jayne 1882, p. 367. Casey, 1900, p. 158. Blatchley, 1910, p. 594. Casey, 1916, p. 191. Hatch, 1962, p. 290.
Cryptorhopalum nigricorne LeConte, 1861, p. 344.
Cryptorhopalum picicorne LeConte, 1854, p. 111. Casey, 1900, p. 159. Dillon and Dillon, 1961, pp. 375, 376. Kirk, 1969, p. 57.
Cryptorhopalum modestum Casey, 1900, p. 158 NEW SYNONYMY.
Cryptorhopalum fusciclave Casey, 1900, p. 158 NEW SYNONYMY.

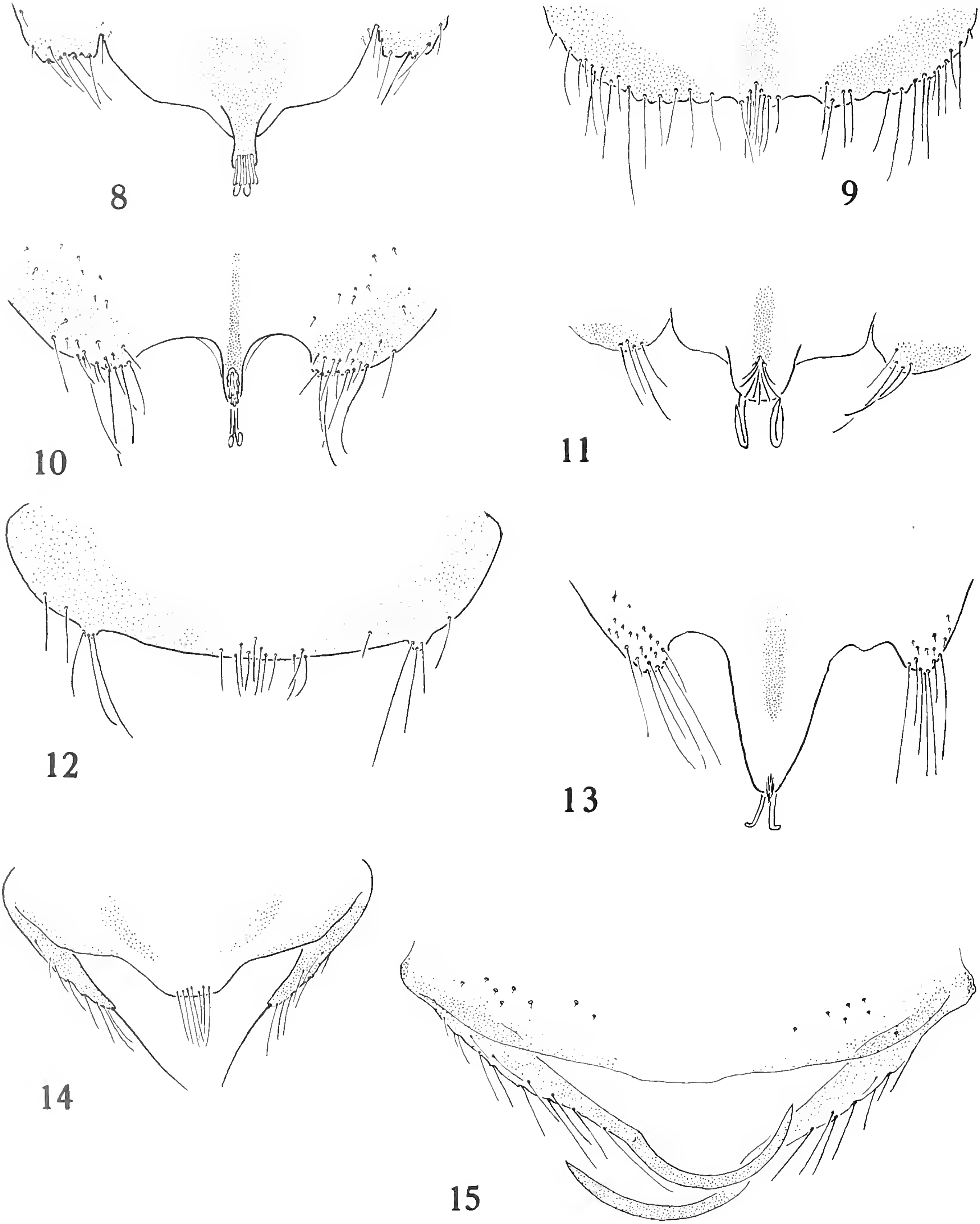
DESCRIPTIONS

ADULT MALES: Dorsal pubescence uniformly piceous to light golden brown. Dorsal integument immaculate, black to yellowish brown. Antennal club subcylindrical.

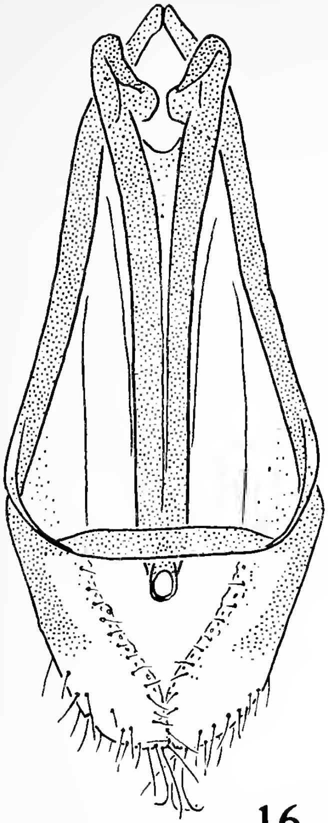
Pronotum with punctures of disc about 1⅓ times diameter of facet of eye and separated by ½ to 2 times diameter of single puncture. Antennal club light brown to black; ratio of width to length of segment 10 varying from 1:1.2 to 1:1.7; ratio of length of segment 11 to length of segment 10 varying from 1:1.1 to 1:1.8. Carina on lateroposterior margin of antennal fossa attaining margin of hypomeron so that hypomeron not continuous behind fossa or carina not quite attaining margin of hypomeron so that plane of hypomeron continued very narrowly behind carina with hypomeron at narrowest point no wider than twice width of carina bounding fossa. Prosternal process without median carina. Metasternum with long or short diagonal stria originating at margin behind mesocoxa and directed toward lateroposterior angle of metasternum. First abdominal sternum with single oblique stria extending on each side from anterior margin of segment beneath trochanter for about ¾ length of segment. Tibia of front leg slightly expanded and widest at apex (Fig. 29). Eighth (morphological) sternum with apical margin as illustrated (Fig. 10); two dorsal setae of median process inserted close together, their sockets separated by less than width of single socket and positioned distad to insertions of setae of ventral brush; setae of ventral brush erect, compact; each seta with obtuse apex (Fig. 20). Aedeagus and lateral lobes as illustrated (Fig. 19); base of aedeagus furcate with hinges widely separated. Ratio of width (across humeri) to length (of pronotum and elytra) varying from 1:1.55 to 1:1.73. Length ranging from 1.92 mm to 2.45 mm.

ADULT FEMALES: As males except antennal fossa occupying about half area of hypomeron. 5th visible abdominal sternum without foveae. Length ranging from 2.06 mm to 2.83 mm.

LECTOTYPE DESIGNATIONS: The lectotype of *C. triste* is herewith designated as the second of the two specimens standing under the name in the LeConte collection in the MCZ. From the original description, in which LeConte indicated a range of size for the species, it is obvious that he had more than one specimen before him when he wrote the description. The first specimen in the series, one which bears a "type" label (probably placed on it by Nathan Banks), is not *C. triste* as the species was interpreted by Jayne, Casey, and Hatch, but is *C. apicale* Mannerheim. This first specimen happens to bear a label with the species name on it in LeConte's handwriting, but judging from the pin holes in the label, it has been removed at least four times and there is no



FIGURES 8–15. Apical margin of morphological abdominal sternum 8 of males of species of *Cryptorhopalum*. Figure 8: *fusculum*. Figure 9: *rubidum*. Figure 10: *triste*. Figure 11: *apicale*. Figure 12: *haplotes*. Figure 13: *uteanum*. Figure 14: *filitarse*. Figure 15: *balteatum*.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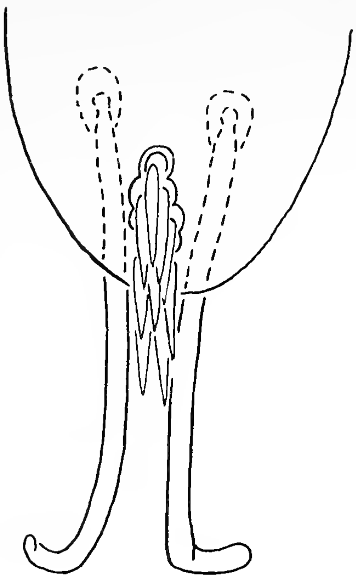
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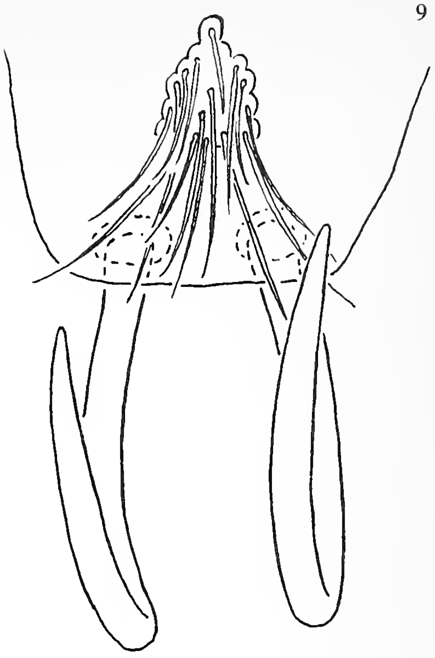
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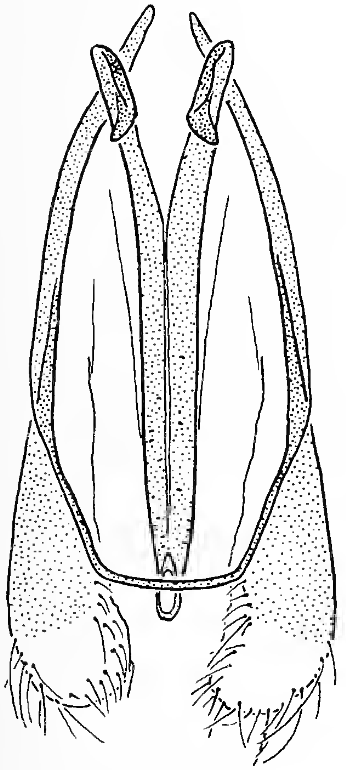
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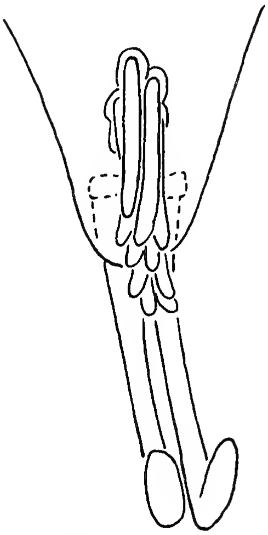
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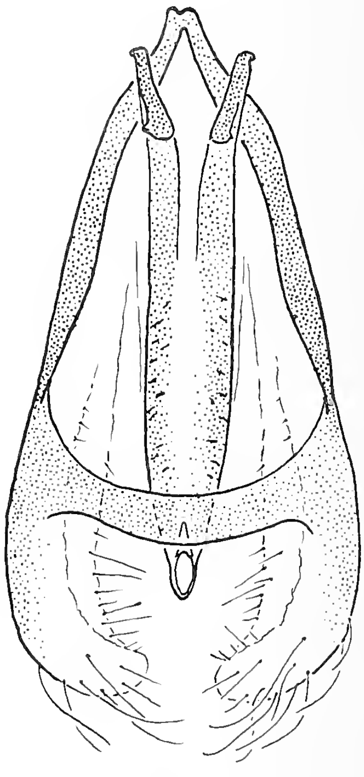
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FIGURES 16–21. Figure 16: Ventral aspect of aedeagus and lateral lobes of *C. haplotes*. Figure 17: Detail of apical process of abdominal sternum 8 of *C. uteanum*. Figure 18: Same of *C. apicale*. Figure 19: ventral aspect of aedeagus and lateral lobes of *C. triste*. Figure 20: Detail of apical process of abdominal sternum 8 of *C. triste*. Figure 21: Ventral aspect of aedeagus and lateral lobes of *C. balteatum*.

certainty that it is now on the specimen on which it was originally placed by LeConte. Nomenclatural stability can best be assured by designating the second specimen as the lectotype. The type locality is San Jose, California.

The lectotype of *C. nigricorne* LeConte is herewith designated as the specimen in the LeConte collection in the MCZ bearing the type label No. 6879. The type-locality is California.

The lectotype of *C. picicorne* LeConte is herewith designated as the specimen in the LeConte collection in the MCZ bearing the type label No. 6878. The pink label on the specimen is LeConte's symbol for "Middle States."

The lectotype of *C. modestum* Casey is herewith designated as the specimen in the Casey collection in the NMNH bearing the type label No. 37572. The type-locality is Brownsville, Texas.

The holotype of *C. fusciclave* in the Casey collection in the NMNH bears the type label No. 37573. The type-locality is Texas.

GEOGRAPHIC DISTRIBUTION: The species is found from northern New York State (and doubtlessly into Canada) to Florida and west to Kansas, Oklahoma, and Texas. No specimens have been found in the Rocky Mountain states, but it is common in the Pacific Coast states (Fig. 36). Whether the two populations are continuous through Canada or (less likely) through Mexico is not known at present. It is possible that the California population, which appears quite homogeneous, is an introduction by early emigrants. Collections of the species have been made in the Mexican states of Nuevo León, Tamaulipas, Veracruz, and Puebla, but, to the author's knowledge, not on the western side of the Sierra Madre Occidental.

DISCUSSION: This species can be recognized with moderate ease, being distinguished by the slightly expanded apex of the front tibia and the relatively dense punctation of the pronotum. Some specimens of *C. apicale* have pronotal punctation almost as dense as that found in *C. triste*. However, wherever these two species are known to occur sympatrically, that form of *C. apicale* is found in which most of the elytron is covered with dark pubescence with an area of light colored pubescence present near the apex of each elytron. The dorsal pubescence of *C. triste* is always unicolorous. The two species are also distinguished in California by the light ochreous to rufous color of the antennal club in *C. apicale* and the dark reddish brown to black color of the antennal club in *C. triste*. The longer, narrower shape of the male antennal club and the much narrower rim of the hypomeron behind the antennal fossa in the male of *C. triste* will further serve to distinguish the species. *C. triste* is more difficult to distinguish from dark forms of *C. uteanum* and from *C. fusculum*, but the denser pronotal punctation and the expanded apex of the front tibia should make its separation positive.

INFRASPECIFIC VARIATIONS: Specimens from New Jersey and Maryland are generally narrower than specimens from California, but the ranges of ratios of width to length slightly overlap. On the other hand, specimens from Kansas, Oklahoma, and Arkansas have a range of ratios of width to length broadly overlapping both those of the East Coast and the West Coast. The light reddish brown color of the dorsal pubescence and the piceous to black color of the antennal club characterize specimens from both the East Coast, the West Coast and the Middle Plains states. Specimens from Florida and along the Rio Grande River in Texas have a somewhat lighter dorsal pubescence and a light brown to reddish brown antennal club. Not enough specimens have been available from Mexico to warrant conclusions about variations in populations there. However, a series of ten specimens from the State of Puebla in Central Mexico is scarcely distinguishable from specimens from the Central Atlantic United States.

ECOLOGY: Adults are collected on a wide variety of flowers. The most extensive records of their occurrences on flowers have been made by A.R. Moldenke (P.H. Raven, *in litt.*) for collections from San Mateo County, California. Why they come to some flowers and not to others is not apparent, but it will be noticed from the following list that their most frequent occurrences are on members of the lily family and on flowers clustered into inflorescences. In the following list, flower species on which three or more collections of *C. triste* have been made are followed by an asterisk. Liliaceae: *Brodiaea hyacinthina* (Lindl.) Baker*, *B. peduncularis* (Lindl.) Wats., *Calochortus venustus* Dougl.*, *C. luteus* Dougl., *Muilla maritima* (Torr.) Wats.; Iridaceae: *Sisyrinchium bellum* Wats.; Ranunculaceae: *Ranunculus californicus* Benth.; Cruciferae: "mustard"; Rosaceae: *Amelanchier* sp., *Adenostoma fasciculatum* H. & A.*, *Prunus ilicifolia* Walp., *Rosa* sp., *Potentilla* sp.; Leguminosae: *Melilotus* sp.; Polygalaceae: *Polygala alba* Nutt.; Rhamnaceae: *Ceanothus sorediatus* H. & A., *Ceanothus* sp.; Cactaceae: *Opuntia* sp.; Umbelliferae: *Lomatium utriculatum* (T. & G.) C. & R., *Daucus carota* L., *Heracleum lanatum* Michx.; Cornaceae: *Cornus* sp.; Asclepiadaceae: *Asclepias* sp.; Hydrophyllaceae: *Phacelia* sp., *Eriodictyon californicum* (H. & A.) Greene*; Scrophulariaceae: *Penstemon* sp.; Compositae: *Achillea borealis* Bong.*, *Baeria* sp., *Bidens* sp.*, *Cirsium* sp., *Coreopsis* sp., *Erigeron* sp., *Eriophyllum confertiflorum* Gray*, *Lasthenia chrysostoma* (F. & M.) Greene*, *Rudbeckia hirta* L., *Solidago* sp., *Wyethia angustifolia* Nutt., *W. glabra* Gray. Blatchley (1910) recorded the species in Indiana on yellow puccoon (*Lithospermum* sp., Boraginaceae), red haw (*Crataegus coccinea* L., Rosaceae), and goldenrod (*Solidago* sp., Compositae).

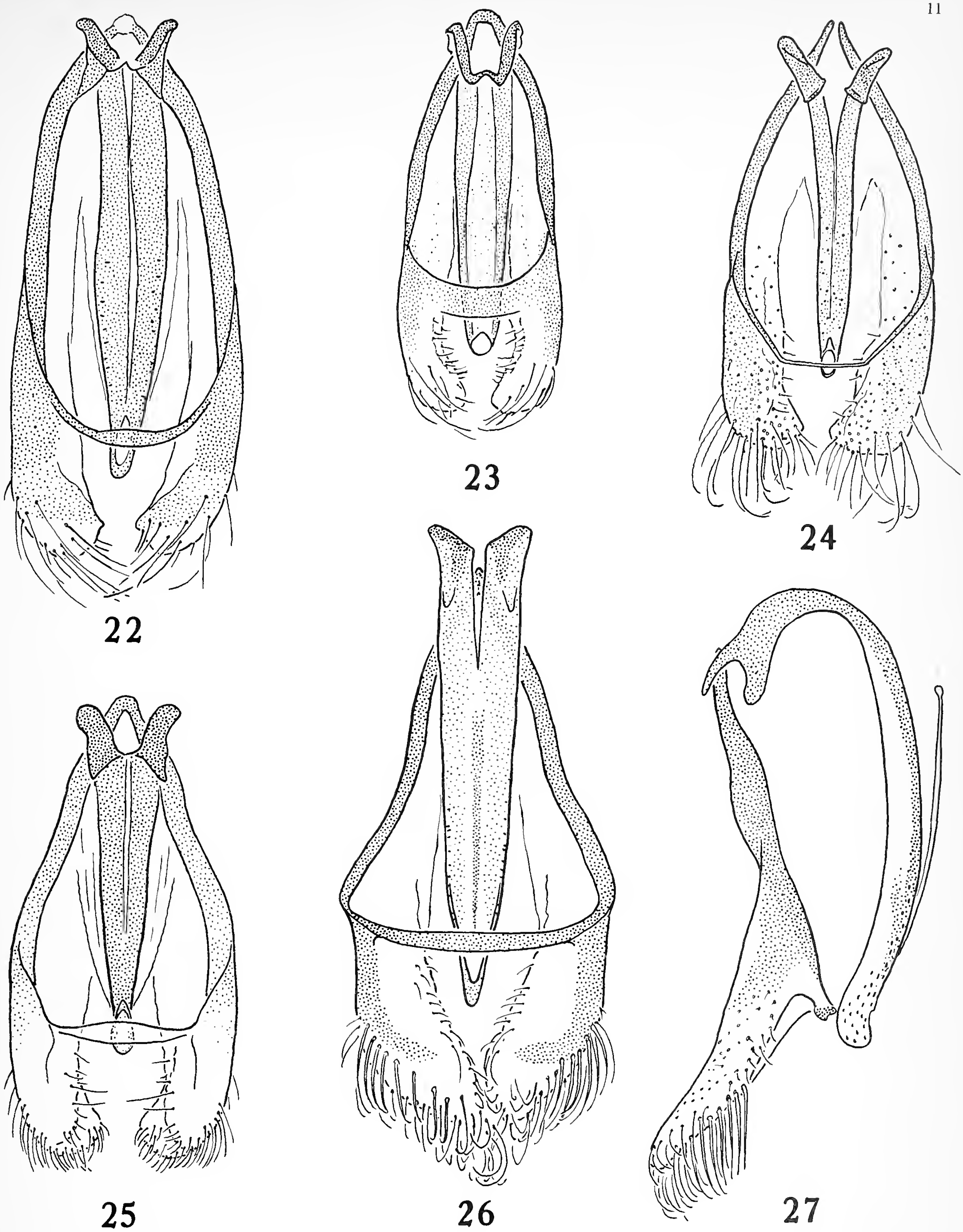
Cryptorhopalum rubidum NEW SPECIES

DIAGNOSIS: 8th (morphological) abdominal sternum of male without lateral processes, sublateral marginal papillae, or median posterior process but with cluster of simple setae at midline near apical margin; apex of aedeagus without proximally directed hook.

DESCRIPTIONS

ADULT MALE: Dorsal pubescence uniformly golden brown. Integument of dorsal surfaces with head, pronotum, and base of elytra piceous; elytra becoming ochreous red on sides and on apical half. Antennal club subcylindrical.

Pronotum with punctures of disc about ¾ diameter of facet of compound eye and separated by 4 to 5 times diameter of single puncture. Antennal club with both segments fuscous; segment 10 with ratio of width to length 1:1.45; length of segment 11 to segment 10 with ratio of 1:1.15. Carina on lateroposterior margin of antennal fossa attaining margin of hypomeron so that plane of hypomeron not continuous behind fossa (Fig. 6). Prosternal process with slight transverse convexity and without median carina. Metasternum with very short, almost transverse stria originating at posterior margin of socket of mesocoxa. First abdominal sternum with single oblique stria on each side extending about ½ length of segment from anterior margin of segment beneath trochanter. Tibia of front leg widest at middle and taper-



FIGURES 22–27. Figure 22: Ventral aspect of aedeagus and lateral lobes of *C. rubidum*. Figure 23: Same of *C. filitarse*. Figure 24: Same of *C. uteanum*. Figure 25: Same of *C. apicale*. Figure 26: Same of *C. fusculum*. Figure 27: aedeagus and lateral lobes of *C. fusculum* in lateral aspect; for clarity, apex of aedeagus is figured ventrad of bridge whereas it is normally positioned dorsad (inside) of bridge.

ing very slightly toward apex. Eighth (morphological) abdominal sternum with apical margin as illustrated (Fig. 9); no apical median process present but dense brush of setae present at middle of margin. Aedeagus and lateral lobes as illustrated (Fig. 22). Ratio of width (across humeri) to length (of pronotum and elytra): 1:1.67. Length: 1.92 mm.

ADULT FEMALE: Elytra entirely ochreous red. Ratio of width to length of segment 10 of antenna 1:1.42; ratio of length of segment 11 to length of segment 10, 1:1.11. Antennal fossa occupying about half of area of hypomeron. 5th visible abdominal sternum without foveae. Ratio of width (across humeri) to length (of pronotum and elytra) 1:1.72. Length 2.57 mm.

RANGE OF OBSERVED VARIATIONS: Elytra entirely ochreous red, or dark brown or black at basal 1/5 gradually becoming reddish brown on apical half. Antennal club of male with ratio of width to length of segment 10 varying from 1:1.4 to 1:1.9; ratio of length of segment 11 to length of segment 10 varying from 1:1.2 to 1:1.7. Plane of hypomeron continued behind antennal fossa or not; if continued behind fossa, then no wider at narrowest point than ⅓ times width of segment 3 of antenna. Ratio of width (across humeri) to length (of pronotum and elytra) varying from 1:1.61 to 1:1.76. Length of males ranging from 1.90 mm to 2.26 mm; of females ranging from 2.09 mm to 2.95 mm.

TYPE OF MATERIAL: *Holotype* male, allotype female, 17 paratypes: Yuma, Arizona, April 13, 1955, Butler and Tuttle. Additional paratypes as follows: Palm Canyon [Kofa Mts., Yuma Co.] Ariz., May 29, 1955 (G. Butler and D. Tuttle), 3 spm.; Roll, Arizona, April 14, 1955 (Butler and Werner), 1 spm.; Inyo Mountains, California, 7000 to 9000 feet elevation, July 7–11 (Wickham), 16 spms.; Potholes [near Laguna Dam], Imperial County, California, April 9, 1923 (E.P. VanDuzee), 3 spms. Holotype and allotype deposited in the CAS collection. Paratypes distributed to collections of the CAS, LACM, MCZ, NMNH, the University of Arizona, and the University of Wisconsin.

ETYMOLOGY: The specific epithet is a Latin adjective meaning "reddish" or "brownish" in reference to the color of the elytra.

DISCUSSION: The reddish orange (rarely reddish brown) color of the apical ½ and often of the entire elytra contrasting with the black head and pronotum superficially distinguish this species from any California *Cryptorhopalum* except *C. uteanum*. Occasional specimens of *C. apicale* may have elytra that are dark at the base and rufous apically. These may be distinguished from specimens of *C. rubidum* in that the elytral pubescence of *C. apicale* is mostly dark with a distinct subapical spot of white pubescence, or the elytral pubescence is whitish, rather than golden brown. Specimens of *C. uteanum* usually have a darker reddish brown elytral integument than specimens of *C. rubidum*, but this is not invariably true. The author knows of no consistent external character by which these 2 species may be distinguished. However, the males are easily separated by the very distinctive differences in the structure of the 8th (morphological) sternum.

ECOLOGY: The specimens from Yuma were collected on mesquite (*Prosopis* sp.), and the 3 females from Palm Canyon, Arizona, were taken on the mint *Hyptis emoryi* Torr. *in* Ives.

Cryptorhopalum uteanum Casey

Cryptorhopalum uteanum Casey 1916, p. 195.
Cryptorhopalum nephianum Casey 1916, p. 196 NEW SYNONYMY.
Cryptorhopalum aridum Casey 1916, p. 196 NEW SYNONYMY.
Cryptorhopalum bakeri Casey 1916, p. 197 NEW SYNONYMY.

DESCRIPTIONS

ADULT MALES: Dorsal pubescence uniformly whitish to light golden brown. Integument of head and pronotum black, integument of elytra entirely black or reddish with suffused black area at base and along suture at basal third, or entirely reddish.

Pronotum with punctures of disc equal in diameter to diameter of facet of compound eye and separated by 3 to 4 times diameter of puncture. Antennal club black except for suffused dark reddish area at base of segment 10, or segment 11 reddish black with segment 10 ochraceous; ratio of width to length of segment 10 varying from 1:1.28 to 1:1.92; ratio of length of segment 11 to length of segment 10 varying from 1:1.15 to 1:1.51. Antennal fossa at lateroposterior margin reaching posterior margin of hypomeron so that plane of hypomeron not continuous behind fossa, or plane of hypomeron continued very narrowly behind fossa with plane at narrowest point behind fossa no wider than twice width of carina bounding fossa. Prosternal process transversely convex without median carina. Metasternum with short diagonal stria originating at margin behind mesocoxa and directed toward middle of lateral margin of metasternum. First (visible) abdominal sternum with single oblique stria on each side extending from anterior margin of segment beneath trochanter for about ¾ length of segment. Tibia of front leg widest at basal third and tapering very slightly to apex, or sides parallel from basal third to apex. Morphological abdominal sternum 8 with apical margin as illustrated (Fig. 13); two recurved dorsal setae of median process inserted proximally to ventral brush of setae with bases separated about twice width of one socket; setae of ventral brush erect, compact, with acute apices (Fig. 17). Aedeagus and lateral lobes as illustrated (Fig. 24); base of aedeagus furcate with hinges widely separated. Ratio of width (across humeri) to length (of pronotum and elytra) varying from 1:1.60 to 1:1.74. Length varying from 1.94 mm to 2.52 mm.

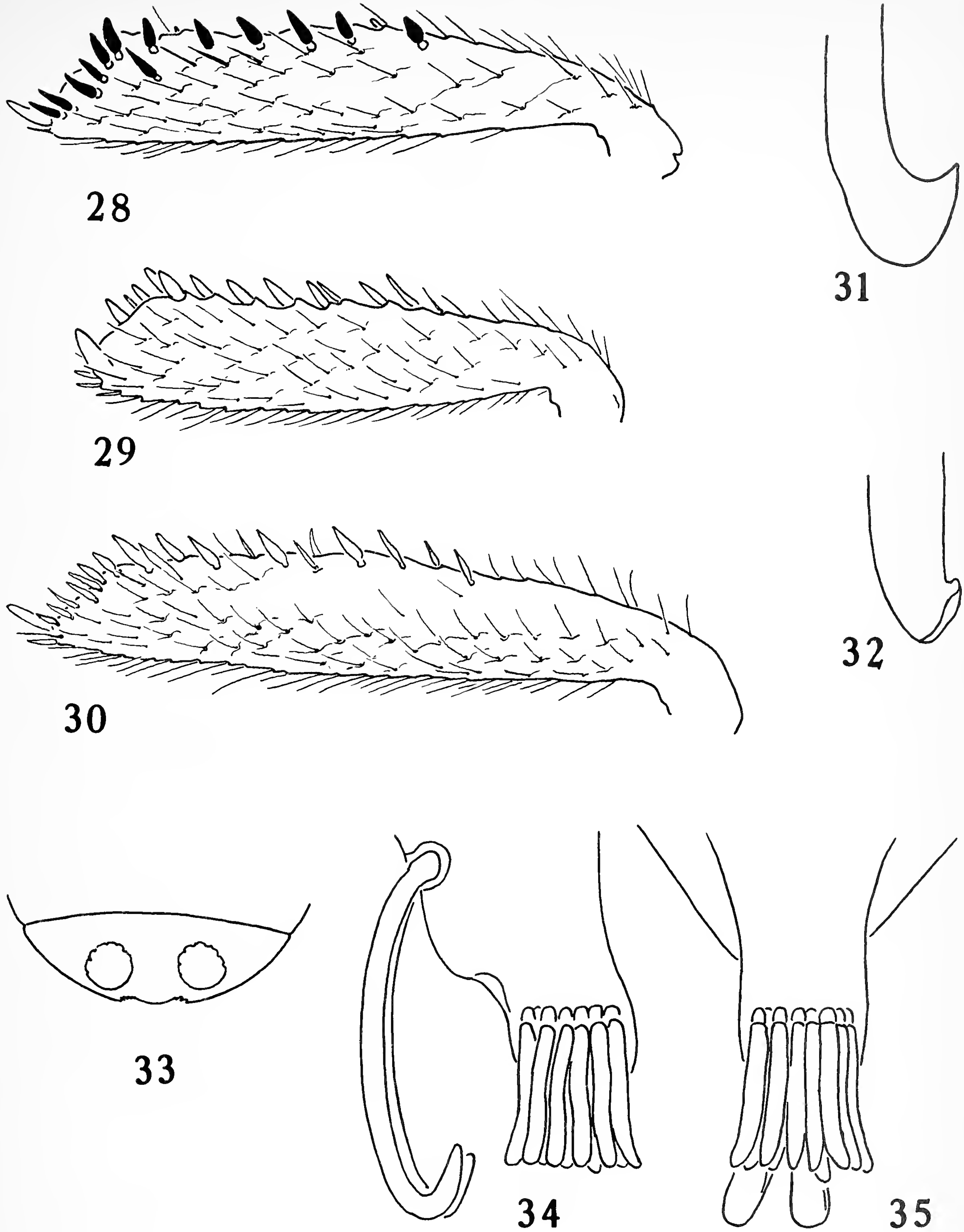
ADULT FEMALES: As males except that antennal fossa occupying about ½ area of hypomeron and antennal club correspondingly smaller. 5th visible abdominal sternum without foveae. Ratio of width (across humeri) to length (of pronotum and elytra) varying from 1:1.62 to 1:1.80. Length varying from 2.06 mm to 2.83 mm.

LECTOTYPE DESIGNATIONS AND NOMENCLATURE: A male from Provo, Utah, bearing NMNH type No. 37562 is herewith designated as the lectotype of *C. uteanum*. A male from the same series was dissected and the genitalia found to be similar to the structures figured for this species.

A female from Nephi, Utah, bearing NMNH type No. 73561 is herewith designated as the lectotype of *C. nephianum*. This specimen and the 2 females next to it in the Casey collection definitely appear to be synonyms of *C. uteanum* although confirming male genitalic characters are not available.

A male from 8,000 ft. elevation in the Inyo Mts. of California bearing NMNH type label No. 37568 is herewith designated as the lectotype of *C. aridum*. Another specimen from the same series was dissected and found to have genitalic characters identical to those of *C. uteanum*.

The unique female from "Mts. near Claremont, Calif." for which Casey erected the species *C. bakeri* (NMNH type No. 37563) has here been placed in synonymy with *C. uteanum*, since it seems to match this species better than any other. The identification carries a certain degree of uncertainty.



FIGURES 28–35. Figure 28: Posterior view of left front tibia of *C. haplotes*. Figure 29: Same of *C. triste*. Figure 30: Same of *C. apicale*. Figure 31: Lateral view of apex of aedeagus of *C. triste*. Figure 32: Same of *C. filitarse*. Figure 33: Fifth visible abdominal sternum of female of *C. filitarse*. Figure 34: Detail of apex of median process of abdominal sternum 8 of *C. fusculum* in lateral view. Figure 35: Same in ventral view.

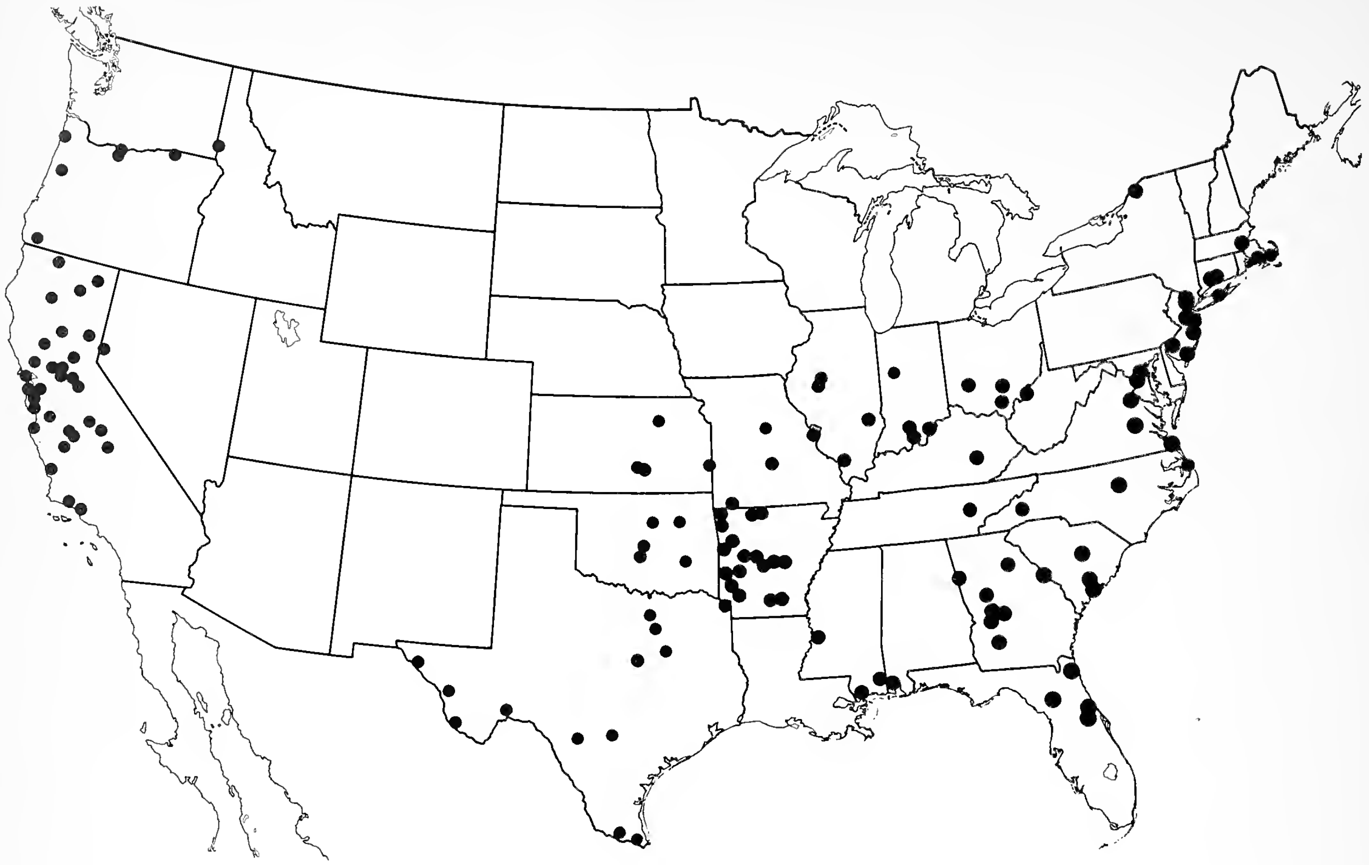


FIGURE 36. Nearctic distribution of *C. triste*.

DISCUSSION: This species and *C. rubidum* cannot be distinguished by any consistent external character. Males of *C. uteanum* and *C. rubidum* are easily distinguished, however, by those genitalic characters described for each. Males of *C. uteanum* can be distinguished from males of *C. fusculum* and *C. apicale* in that *C. uteanum* males have a very narrow or obliterated extension of the hypomeron behind the antennal fossa. In males of both *C. fusculum* and *C. apicale* the hypomeron behind the fossa is at least ⅔ as wide as segment 3 of the antenna. Color characters can usually be used to separate both males and females of *C. uteanum* from those of *C. apicale* and *C. fusculum*. Specimens of *C. apicale* usually have a subapical spot of white pubescence on the elytron or are covered with mostly whitish hair with some intermingled dark hairs, whereas the dorsal pubescence of *C. uteanum* is always a uniform light golden white to golden brown. *C. fusculum* is ordinarily piceous or black in color. The integument of California specimens of *C. uteanum* always includes a certain amount of rufous coloration on the elytron.

INFRASPECIFIC VARIATIONS: Moderate series of the species have been taken from San Diego County, California, southern Utah and northern Arizona, and the southeastern corner of Arizona. Specimens from San Diego County tend to have darker, mahogany red elytra in contrast to the lighter ochreous red of specimens from southern Utah and northern Arizona. Specimens from the Chiricahua Mts. in southwestern Arizona and from the Davis Mts. in western Texas are entirely black.

DISTRIBUTION (See Fig. 37) ARIZONA: Cochise Co.: Chiricahua Mts., July 9, 1959 (D.J. and J.N. Knull); same locality, July 26, 1952 (D.J. and J.N. Knull). Coconino County: Cameron, June 6, 1967 (C.D. Johnson); Cameron, Little Colorado River, June, 1967 (C.D. Johnson); Soap Creek at Cliff Dwellers, 7 mi. southwest of Marble Canyon, June 5, 1953 (G.D. Butler). CALIFORNIA: Contra Costa Co.: Berkeley, July 19, 1958 (J.A. Litsinger). Inyo Co.: Silver Canyon, White Mts., May 10, 1926 (J.O. Martin). Los Angeles Co.: Downey, May, 1945. San Diego Co.: 1 mi. south Del Mar, May 23, 1971 (M. and A. Gilbert); Idyllwild, June 20, 1958 (P.S. Bartholomew); Julian, June 12, 1963 (C.D. Johnson); 2 miles west Mt. Springs (E.P. Van Duzee); San Diego, May 10, June 8, 9, 12, 1920 (E. Schiffel). NEVADA: Elko Co.: Wendover, June 12, 1933 (J.T. Howell). Nye Co.: Tonopah, June 1, 1914. NEW MEXICO: San Miguel Co.: Las Vegas H.S., July 2, 4, 6, 9 (Barber and Schwarz). TEXAS: El Paso Co.: El Paso, June 27, 1921 (C.D. Duncan); Ft. Bliss, May 1, 1915 (J.I. Carlson). Jeff Davis Co.: Davis Mts., July 6, 1936 and July 15, 1955 (D.J. and J.N. Knull). WYOMING: Sweetwater Co.: Green River, July 2, 1920.

Four specimens in the CAS are labeled as taken at Seabrook, Texas (Galveston Co.). One specimen in the collection of V.M. Kirk is labeled as being from Yankton, S.D. I believe both of these localities should be reconfirmed, since they are outside the apparent range of the species.

ECOLOGY: Adults have been collected on the crucifer *Stanleya* sp., on the garden stock, *Matthiola incana* (L.) R. Br., and on carrot blossoms.

Cryptorhopalum apicale (Mannerheim)

Anthrenus apicale Mannerheim 1843, p. 258.
Cryptorhopalum apicale: Jayne 1882, p. 366. Reitter 1880 (1881), p. 44. Casey, 1900, p. 157. Hatch 1962, p. 290.
Cryptorhopalum haemorrhoidale Horn 1894 (pars), p. 321.
Cryptorhopalum coloradense Casey 1916, pp. 192–193 NEW SYNONYMY.
Cryptorhopalum tuckeri Casey 1916, p. 192 NEW SYNONYMY.
Cryptorhopalum fontinale Casey 1916, p. 194 NEW SYNONYMY.
Cryptorhopalum grisescens Casey 1916, p. 195 NEW SYNONYMY.

DESCRIPTIONS

ADULT MALES. Dorsal pubescence entirely whitish, or entirely light golden brown, or a mixture of varying amounts of whitish with golden brown or blackish hairs, or almost entirely blackish with a very few golden brown hairs; light colored hairs of elytra often forming subbasal band and distinct subapical spot with other hairs of elytra mostly black. Dorsal integument black, immaculate, or black with subapical rufous spot on each elytron, or with head and pronotum brownish black and elytra ochreous except for brownish area at base and along median suture. Antennal club subcylindrical.

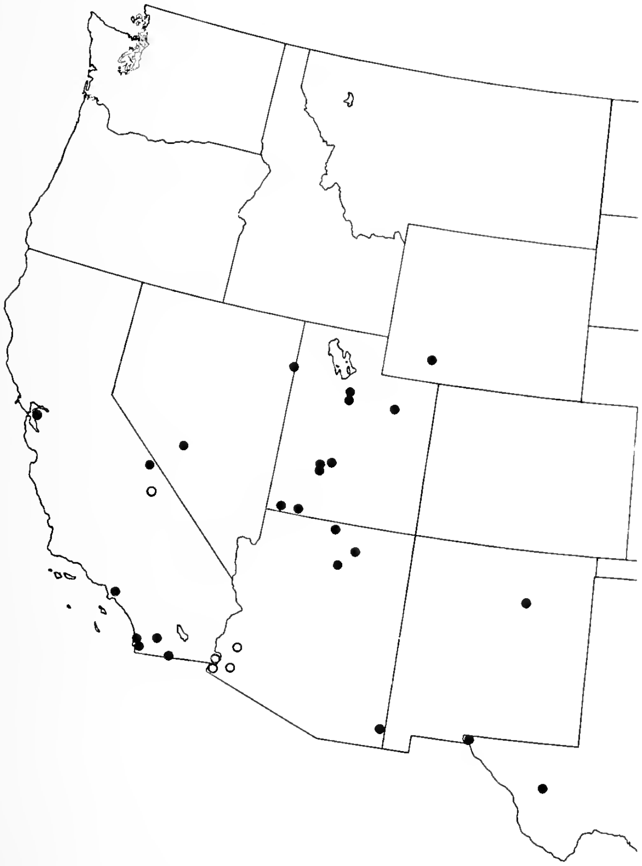


FIGURE 37. Dots, distribution of *C. uteanum*. Circles, distribution of *C. rubidum*.

Pronotum with punctures of disc about as wide as diameter of facet of eye and separated by 1 to 3 times diameter of single puncture. Antennal club ochreous to dark reddish brown; ratio of length of segment 11 to segment 10 varying from 1:1.1 to 1:1.5; ratio of length of segment 11 to segment 10 varying from 1:1.2 to 1:1.7. Antennal fossa at lateroposterior margin not attaining posterior margin of hypomeron; plane of hypomeron continued narrowly behind fossa with plane at narrowest point as wide as ⅔ to 2 times width of antennal segment 3. Pronotal process without median carina or with very narrow impunctate area suggesting median carina. Metasternum with diagonal stria originating at margin behind mesocoxa and extending ¼ to ½ distance toward lateroposterior angle of metasternum. First visible abdominal sternum with single oblique stria extending on each side from anterior margin of segment beneath trochanter to posterior margin. Tibia of front leg widest near middle and tapering gradually toward apex. Eighth (morphological) abdominal sternum with apical median process as illustrated (Fig. 11); two median dorsal setae at apex of process recurved almost 270°, inserted distad to ventral brush of setae with bases separated by distance about equal to width of single socket (Fig. 18). Aedeagus and lateral lobes as illustrated (Fig. 25); base of aedeagus not furcate; apex of aedeagus with short, proximally directed hook; lateral lobes rounding at apices. Ratio of width (across humeri) to length (of pronotum and elytra) varying from 1:1.46 to 1:1.72. Length ranging from 1.87 mm to 2.64 mm (Fig. 2).

ADULT FEMALES: As males except that antennal fossa occupying about half of hypomeron with antennal club correspondingly smaller. 5th visible abdominal sternum without foveae. Ratio of width (across humeri) to length (of pronotum and elytra) varying from 1:1.50 to 1:1.72. Length ranging from 2.12 mm to 2.69 mm.

LECTOTYPE DESIGNATIONS AND NOMENCLATURE: Each of the species synonymized here with *C. apicale* is clearly assignable to it on the basis of dorsal setal characters. The specimen in the NMNH from Tucson, Arizona, bearing type No. 37566 is hereby designated as the lectotype of *C. grisescens* Casey. A male from the same series was dissected and found to have genitalic structures typical of *C. apicale*.

The lectotype of *C. fontinale* Casey is herewith designated as NMNH type No. 37560. It is one of a series of 7 specimens from Jemez Springs, New Mexico. The genitalic structures of one of the specimens are well exposed and serve to verify the identification of the form with *C. apicale*.

The unique specimen of *C. tuckeri* Casey from Tucson, Arizona (NMNH type No. 37555) has not been dissected, but is clearly *C. apicale*.

The unique female type of *C. coloradense* Casey (NMNH type No. 37556) from Golden, Colorado, lacks a distinct subapical spot of light-colored pubescence on the elytron but does have a pronounced subbasal band of light-colored hairs. It falls within the range of variation of the form of *C. apicale* found along the eastern slope of the Colorado Rocky Mts.

GEOGRAPHIC DISTRIBUTION: See the distribution map, Fig. 29. Specimens have also been collected at widely scatterned localities in Mexico as far south as Cuernavaca.

DISCUSSION: For most California specimens the presence of a subapical spot of pale pubescence on the elytron is diagnostic. Usually there is also a subapical rufous area in the integument corresponding with the spot of light-colored pubescence. Specimens from the San Francisco Bay area (Santa Cruz and Santa

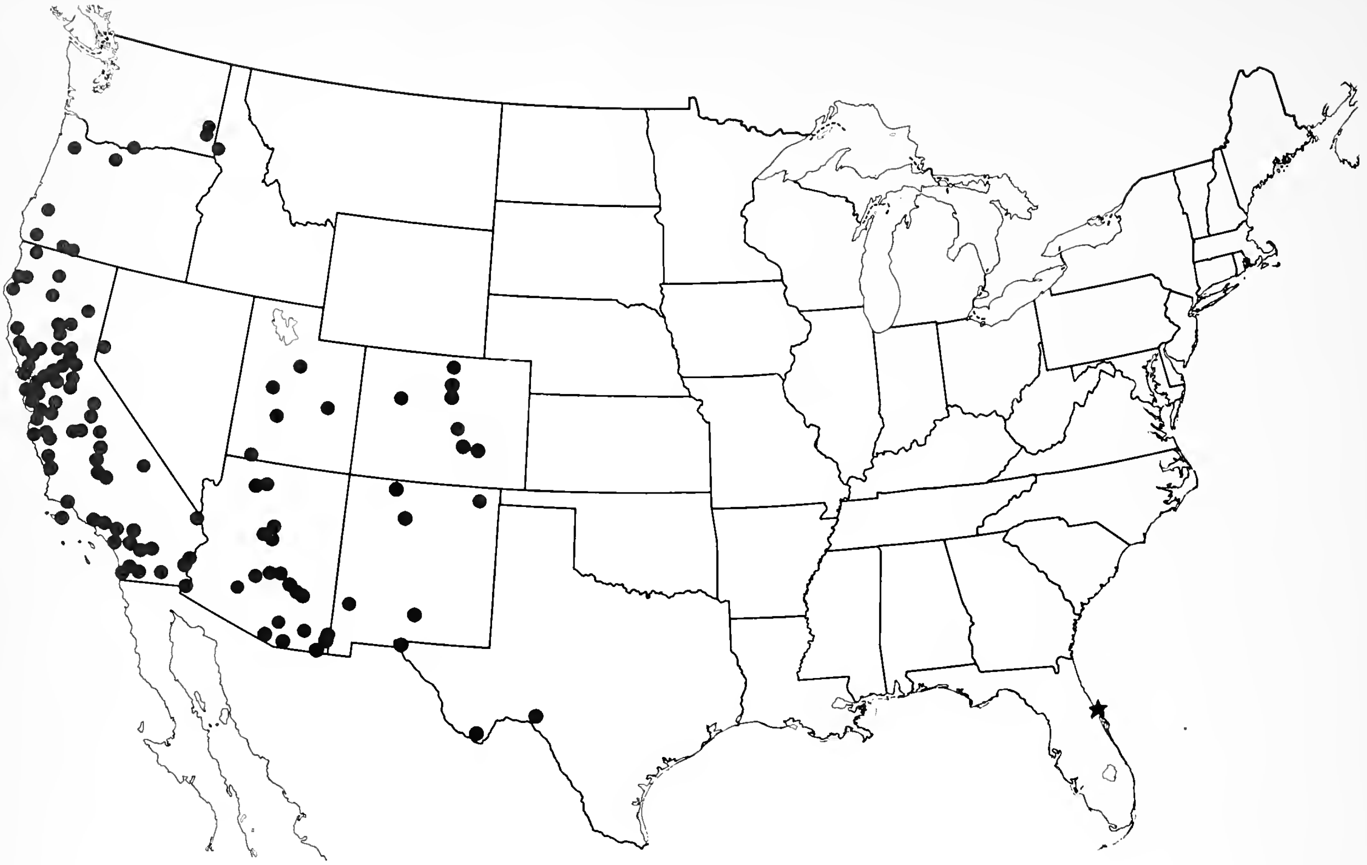


FIGURE 38. Dots, Nearctic distribution of *C. apicale*. Star, Florida locality of closely related unnamed species or form conspecific with *C. apicale*.

Clara Counties north to Marin, Napa, and Solano Counties) often have the apical spot reduced to a very few hairs and very rarely are found lacking the apical spot. Males without a subapical spot can be distinguished from other California species by the slightly broader extension of the hypomeron behind the antennal fossa. Both males and females can usually be recognized by the color of the antennal club, which is a light yellowish brown to a medium reddish brown, but never a dark brownish black. Furthermore, both segments of the club are the same color. The base of segment 10 may be lighter in color than the apex of segment 11, but there is no change of color between the apex of segment 10 and the base of segment 11. Desert forms of *C. apicale* may be covered almost entirely with whitish pubescence, but forms from the California deserts, in contrast to those from Southern Arizona deserts, seem always to have a few intermingled dark hairs, particularly at the apical ⅓ of the elytra. In the case of a few specimens collected near Yuma, Arizona, the "darker" hairs are a light golden brown and are not quickly distinguishable from the whitish hairs.

SUBSPECIFIC VARIATIONS: Because this is a highly polytypic species, it is not surprising that Casey should have described 5 of its different forms as separate species. Each form, however, intergrades more or less completely with neighboring forms. In the north of California and extending south along the Sierra Nevada to the San Gabriel Mountains, specimens are found with the integument black except for a large rufous area on the apical declivity of the elytron. The setae are brownish black except for a few light golden hairs along the lateral and posterior margins of the pronotum, a small lateral patch at the basal ¼ of the elytron, and a prominent subapical patch. In the San Francisco Bay area the apical rufous area is much reduced or absent and the number of light golden hairs is reduced considerably. In the coastal ranges and valleys of Southern California, specimens tend to have a large subapical elytral patch of light golden hairs with a somewhat pronounced subbasal band of light golden hairs. The most abrupt transition occurs between the montane and the desert areas, where the light colored hairs become whitish rather than golden and the areas of light-colored hairs expand to cover the pronotum and most of the elytra.

ECOLOGY: Adults have been recorded from flowers of 14 families of plants. In comparison with the number of collections that have been made of the species, plant records are too sparse to draw any firm conclusions with respect to the factors that may make one plant more attractive than another. In the following list, any plant species on which *C. apicale* has been collected 3 or more times is followed by an asterisk. Liliaceae: *Brodiaea hyacinthina* (Lindl.), *Calochortus venustus* Dougl.*; Salicaceae: *Salix* spp.*; Fagaceae: *Quercus* sp.; Cruciferae: *Brassica* sp.; Capparidaceae: *Cleome* sp.; Rosaceae: *Rubus* sp., *Adenostoma fasciculatum* H. & A.*, *Holodiscus discolor* (Pursh) Maxim., *Physocarpus* sp., *Prunus ilicifolia* Walp.*; Leguminosae: *Melilotus alba* Desr.*, *Astragalus* sp.; Rhamnaceae: *Ceanothus sore-*

diatus H. & A.*, *C. integerrimus* H. & A.*, *C. cuneatus* (Hook) Nutt., *Ceanothus* sp.*, *Rhamnus crocea* Nutt.; Malvaceae: cotton; Tamaricaceae: *Tamarix gallica* L.*; Umbelliferae: *Heracleum lanatum* Michx., *Ligusticum apiodorum* (Gray) C. & R., *Angelica tomentosa* Wats.*, "wild parsnip"; Asclepiadaceae: *Asclepias* sp.; Boraginaceae: *Cryptantha* sp.; Rubiaceae: *Galium boreale* L.; Caprifoliaceae: *Sambucus mexicana* Presl.; Compositae: *Baccharis glutinosa* Pers.* *Baccharis* sp., *Senecio salignus* DC.

In San Mateo County, California, where *C. apicale* occurs sympatrically with *C. triste,* both species occur with moderate frequency on *Calochortus venustus* and *Adenostoma fasciculatum* (P.H. Raven, *in litt.*). *C. apicale* occurs with great frequency on species of *Ceanothus,* on which *C. triste* is taken only occasionally. On the other hand, although *C. apicale* occurs on various Compositae elsewhere in its range, it has not been taken on any composites in San Mateo County. Yet *C. triste* occurs frequently in San Mateo County on a number of composites, particularly *Achillea borealis, Eriophyllum confertiflorum,* and *Lasthenia chrysostoma.*

At Granite Reef Dam, Maricopa County, Arizona, a moderate series was taken on March 18, 1974, on catkins of *Salix* sp. and one specimen on *Tamarix gallica.* However, no specimens could be collected on other adjacent flowers, including *Baccharis* sp., *Nicotiana glauca* Graham, or *Pluchea sericea* (Nutt.) Coville.

Records of occurrence of adults have not been kept for any one locality through a long enough period of time to discover any correlations between dates of their appearance and environmental factors. Across the entire range for the species, adults have been taken between December 30 and October 23. In California west of the Sierra Nevada, the greatest number of collections were made in the two week period from April 22 through May 5. In the deserts of California and Arizona, the greatest number of collections were made in the two week period of July 29 through August 11, no doubt correlations with blooming periods.

Cryptorhopalum fusculum LeConte

Cryptorhopalum fusculum LeConte 1854, p. 111. Reitter 1880 (1881), p. 44. Casey 1900, p. 158.
Cryptorhopalum triste var. *fusculum:* Jayne 1882, p. 367.
Cryptorhopalum anthrax Casey 1900, p. 157 NEW SYNONYMY.
Cryptorhopalum granum Casey 1900, p. 157 NEW SYNONYMY.
Cryptorhopalum affine Casey 1900, p. 157 (non *affine* Reitter 1880 (1881)). Sharp 1902, p. 657 REVISED SYNONYMY.
Cryptorhopalum pumilum Casey 1900, p. 158 NEW SYNONYMY.
Cryptorhopalum caseyi Dalla Torre 1911, p. 73 (nov. nom. pro *C. affine* Casey 1900).
Cryptorhopalum piceum Casey 1916, p. 198 NEW SYNONYMY.

DESCRIPTIONS

ADULT MALES: Dorsal pubescence uniformly light golden to dark golden brown; integument of dorsal surfaces immaculate, mahogany brown to black. Antennal club subcylindrical.

Pronotum with punctures of disc minute, ⅔ times as wide as to equal in width to diameter of single facet of eye; punctures separated by distance equal to 3 to 5 times diameter of single puncture. Antennal club with segment 10 entirely light yellowish brown or light yellowish brown at base becoming fuscous apically; segment 11 usually entirely fuscous but occasionally light yellowish brown at base; ratio of width to length of segment 10 varying from 1:1.2 to 1:1.7 (Fig. 7). Plane of hypomeron continued behind antennal fossa with hypomeron at narrowest point behind lateroposterior margin of fossa equal to or not less than 4/5 as wide as segment 3 of antenna (Fig. 7). Prosternal process transversely flat to slightly concave without median carina or rarely with low, thread-like carina on apical half. Metasternum with short, oblique stria originating at medial margin of mesocoxal socket and extending not more than ½ distance toward middle of lateral margin of metasternum. First visible abdominal sternum with single oblique stria on each side extending from anterior margin of segment beneath trochanter ½ to ⅞ length of segment. Tibia of front leg widest at middle and tapering slightly toward apex. Eighth (morphological) abdominal sternum with apical margin as illustrated (Fig. 8); two recurved setae inserted dorsally on median process; setae of ventral brush inserted apically on process, compactly arranged, with rounding apices (Figs. 34, 35). Aedeagus strongly curved dorsoventrally; apex without proximally directed hook (Fig. 27). Lateral lobes with long, somewhat coarse setae at apices (Fig. 26). Ratio of width (across humeri) to length (of pronotum and elytra) varying from 1:1.51 to 1:1.70. Length ranging from 1.63 mm to 2.50 mm.

ADULT FEMALES: As males except that antennal fossa occupying about ½ of hypomeron and antennal club correspondingly smaller. Fifth visible abdominal sternum without foveae. Length ranging from 2.06 mm to 2.66 mm.

NOMENCLATURE: The female holotype of *C. fusculum* (MCZ type No. 6880) from "Colorado River, California," seems quite certainly to be identical with the species described here. The dark color of the dorsal integument practically excludes its identity with *C. rubidum.* The only California species with which it might be confused is *C. uteanum,* but this does not occur where LeConte probably collected his specimen.

The female holotype of *C. affine* Casey (NMNH type No. 37565) from Benicia, Solano Co., California, is identical with this species. On my advice, Mroczkowski (1968) synonymized *C. affine* Casey with *C. triste* LeConte. A reexamination of the specimen shows that I was in error. The apex of the front tibia is definitely not expanded, as is true of specimens of *C. triste.*

Also identical with this species are the unique types of *C. anthrax* Casey (NMNH type No. 37570), a female from Arizona, *C. piceum* Casey (NMNH type No. 37564), a female from Claremont, California, and *C. pumilum* Casey (NMNH type No. 37571), a female from Arizona. Although confirming genitalic characters are unavailable, these all have setal characters typical of *C. fusculum.* The male type of *C. granum* Casey (NMNH type No. 37569) from Arizona was dissected and found definitely to be this species.

GEOGRAPHIC DISTRIBUTION: See the United States distribution on the map, Fig. 30. In addition to the localities shown on the map, the species has been found in Baja California, Mexico, at the following localities: 10 miles south of Punta Prieta, June 21, 1938 (Michelbacher and Ross), 44 km south of Tijuana, June, 1952 (N.L.H. Krauss), 19 miles east of Rosario, June 17, 1938 (Michelbacher and Ross), and Isla Partida, March 23, 1953 (P.H. Arnaud). It was taken in Sonora, Mexico, at Cumbre del Frente, 3 miles east of Guaymas, April 30, 1952 (J.P. Figg-Hoblyn).

DISCUSSION: Within California this species is most likely to be confused with *C. rubidum* or *C. uteanum.* Normally the dark color of the integument will distinguish it from these species, both of which, in California, at least, have elytra that are apically rufous or entirely rufous or mahogany brown. Occasional specimens of *C. fusculum,* which I take to be teneral, have rufous elytra. In these cases males may be distinguished by the greater width of the hypomeron behind the lateroposterior angle of the antennal fossa in *C. fusculum,* but I know of no satisfactory way of distinguishing such females.

ECOLOGY: In desert areas adults have been collected commonly on flowers of the legumes *Prosopis juliflora* (Swartz) DC., *Acacia greggii* A. Gray, and *Cercidium microphyllum* (Torr.) Rose and Johnston, on flowers of *Tamarix gallica* L., on *Eriogonum* spp., and on mustards of the genus *Stanleya*. Across the entire range of the species, single collections have been recorded from the flowers of each of the following: Chenopodiaceae: *Atriplex hymenelytra* (Torr.) Wats.; Rosaceae: *Pyracantha* sp.; Rhamnaceae: *Condalia* sp.; Asclepiadaceae: *Asclepias* sp.; Compositae: *Aster spinosus* Benth. It was also recorded "in apricots" in Sacramento, California. In the Spring Mts. of Clark County, Nevada (near Bonnie Springs), I collected specimens in moderate abundance on flowers of *Eriogonum* sp. but no individuals could be found on flowers of *Salix* sp. or *Vitus* sp. in the same vicinity.

Cryptorhopalum filitarse Casey

Cryptorhopalum filitarse Casey 1900, p. 156.

DESCRIPTIONS

ADULT MALES: Dorsal integument with head black to light reddish brown, pronotum and elytra mahogany to light reddish brown. Dorsal pubescence consisting of closely appressed, light or dark golden brown hairs and golden white to whitish hairs. Antennal club ovate, rufous.

Pronotum with golden white or whitish pubescence on sides and on basal lobe and golden brown or mixed golden brown and whitish hairs on disc; punctures of disc about as wide as diameter of facet of compound eye and separated by 2 to 3 diameters of single puncture. Elytra with golden-brown hairs, except for light-colored hairs distributed as follows: few hairs or dense band of hairs (as dense as submedian band) along basal margin, narrow submedian band, narrow or broad subapical band, light-colored hairs along lateral margin between submedian and subapical bands present or absent, small or large apical patch; subapical band of light-colored hairs and apical patch occasionally confluent. Antenna with ratio of width to length of segment 10 varying from 1:1.1 to 1:1.2; ratio of length of segment 11 to length of segment 10 varying from 1:1.0 to 1:1.3. Process of prosternum without median carina. Plane of hypomeron behind antennal fossa as wide at narrowest point as 1½ times width of antennal segment 3. Metasternum with or without short, oblique stria originating at posterior margin of mesocoxal cavity. Front tibia widest at middle and tapering gradually toward apex. Eighth (morphological) abdominal sternum as illustrated (Fig. 14); lateral process well developed with terminal seta slender; tuft of simple setae present at apex of slightly expanded median area. Aedeagus and lateral lobes as illustrated (Fig. 23); genital pore simple with small dorsal lobe but without proximally directed hook (Fig. 32). Ratio of width (across humeri) to length (of pronotum and elytra) varying from 1:1.58 to 1:1.64. Length ranging from 1.70 mm to 2.06 mm.

ADULT FEMALES: As males except that antennal fossa occupying about half of hypomeron, and 5th visible abdominal sternum with 2, circular, very slightly depressed foveae, each with diameter about equal to half greatest length of segment and each bounded by feeble, interrupted, thread-like carina (Fig. 33). Ratio of width (across humeri) to length (of pronotum and elytra) varying from 1:1.58 to 1:1.70. Length ranging from 1.74 mm to 2.11 mm.

LECTOTYPE DESIGNATION: The NMNH specimen bearing type label No. 37552, a female, is herewith designated as the lectotype. The specimen bears a label with the letters "Cal," which are underlined. According to the original description, the locality is Santa Barbara, California. One male and 5 females next to it bear the same label. The male was dissected and found to have genital structures similar to those figured here for the species.

GEOGRAPHIC DISTRIBUTION: CALIFORNIA: Imperial County: Santa Rosa Mts., July 4, 1946 (D.J. and J.N. Knull). Inyo County: Inyo Mts., 7,000 to 8,000 ft. elev., July 7–11 (Wickham); Westgard Pass, July 22, 1961 (J.S. Buckett); 3 miles southwest of Westgard Pass, July 18, 1964 (C.D. Johnson). Los Angeles County: San Gabriel Canyon, August 8, 1960 (Fred G. Andrews). Orange County: Fullerton, August 2, 1930 (Bartholomew). Riverside County: San Jacinto Mts., July 21, 1929 (L.D. Anderson). Tulare County: Giant Forest, July 28, 1929 (R.H. Beamer). Tuolumne County: Elizabeth Lake [Yosemite National Park], July 10, 1924 (W. Benedict). Ventura County: Ojai, August 29, 1950 (F.W. Furry). See map, Fig. 31.

DISCUSSION: This species and *C. balteatum* are readily distinguishable from all the preceding species by the presence of 3

FIGURE 39. Nearctic distribution of *C. fusculum.*

or 4 distinct bands of light-colored pubescence across the elytra, by the ovate rather than subcylindrical antennal club, and by the presence of 2 round foveae on the 5th visible abdominal sternum of the female. However, the 2 species are very difficult to separate from each other on the basis of external characters. Genitalic characters easily separate the males. The sternum of the 8th abdominal segment of *C. filitarse* has a tuft of setae at the middle of the apical margin, but these are lacking in *C. balteatum*. The lateral process of the sternum of the same segment of *C. filitarse* bears a slender apical seta, whereas the lateral process of *C. balteatum* bears an apical seta that is about as wide as the apex of the process itself. The aedeagus of *C. filitarse* has a genital pore that is more or less apical with a small proximal lobe but without a proximally directed hook as found in *C. balteatum*.

ECOLOGY: Adults have been collected on flowers of *Eriogonum* sp. and *Asclepias* sp.

Cryptorhopalum balteatum LeConte

Cryptorhopalum balteatum LeConte 1854, p. 111. Reitter 1880 (1881), p. 43. Jayne 1882, p. 365.

DESCRIPTIONS

ADULT MALES: Dorsal integument with head and thorax piceous to black and elytra dark mahogany brown to rufous. Dorsal pubescence consisting of piceous and golden, depressed hairs. Antennal club ovate, rufous.

FIGURE 40. Dots, distribution of *C. filitarse*. Circles, distribution of *C. balteatum*. Question mark, record of *C. balteatum* for county only.

Pronotum with golden hairs on sides and on basal lobe and with piceous hairs covering disc; punctures of disc about as wide as diameter of facet of eye and separated by 3 to 5 times diameter of single puncture. Elytra with piceous hairs except for golden hairs distributed as follows: few or none along basal margin, patch on humerus coalescing with narrow submedian band, narrow or broad subapical band with none along lateral margin between submedian and subapical bands except for single line of hairs on lateral carina, patch on apex. Antennal club with ratio of width to length of segment 10 varying from 1:0.8 to 1:1.5; ratio of length of segment 11 to length of segment 10 varying from 1:1.2 to 1:1.5. Prosternal process without median carina. Hypomeron behind antennal fossa at narrowest point about 1½ times as wide as antennal segment 3 (Fig. 4). Metasternum with fine, sometimes short stria extending obliquely outward from lateroposterior margin of mesocoxal cavity. Front tibia widest at apical 3/5 and tapering gradually toward apex. Eighth (morphological) sternum with stout, evenly curving seta inserted at apex of lateral process; seta terminating abruptly rather than gradually becoming filamentous; middle of apical margin of sternum without process or cluster of setae (Fig. 15). Aedeagus with ventrally directed hook-like process at apex (Fig. 21); lateral lobes with moderately broad bridge. Ratio of width (across humeri) to length (of pronotum and elytra) varying from 1:1.50 to 1:1.65. Length 1.79 mm to 2.28 mm.

ADULT FEMALES: As males except that antennal fossa occupying about ½ area of hypomeron and antennal club correspondingly smaller. Fifth visible abdominal sternum with 2, circular, very slightly depressed foveae, each with diameter about equal to ¾ greatest length of segment, not or indefinitely margined by thread-like carina. Ratio of width (across humeri) to length (of pronotum and elytra) varying from 1:1.54 to 1:1.66. Length ranging from 2.18 mm to 2.47 mm.

DISTRIBUTION: CALIFORNIA: Kern County, May, 1934 (A.T. McClay). Los Angeles County: Mint Canyon, June 24, 1949 (L.W. Isaac); 2 miles north of Valyermo, June 4, 1970 (R.S. Beal).

SYSTEMATICS: The female holotype (MCZ type No. 6875) from San Diego, California, appears to be within the limits of the species described here, but the overlapping range of external characters between this species and *C. filitarse* leaves a small margin of doubt. Two specimens stand under the name in LeConte's collection, but the second, which is *C. pruddeni* Casey, is dated 1879, so is not part of a type series.

As with many other closely related allopatric forms in which there is no evidence of a genetically controlled barrier to reproduction, *C. balteatum* and *C. reversum* Casey could be treated with equal propriety as distinct species or as subspecies. There are consistent differences between the two in setal color, but these seem relatively insignificant in view of the variations of setal color and pattern found across the range of *C. reversum*. Nevertheless, the forms are treated here as distinct species, since consistent differences, however small, do exist and since a relatively wide barrier of desert seems to separate them. Future collecting, particularly along the Mexican border, might necessitate a new interpretation of their status. *C. reversum* presently is known to occur from the Chiricahua Mountains in the southeastern corner of Arizona east to Brownsville, Texas.

DISCUSSION: This species is in the same species group as the sympatric *C. filitarse*. For a discussion of the differences between the two, refer to the discussion under *C. filitarse*. Externally the species is quite similar to *C. pruddeni* Casey (1900), which extends from Yavapai and Coconino Counties in Arizona southeast to Brewster County, Texas, and northeast to Garfield County, Colorado. Externally the two may be distinguished by the fact that the dorsal integument of *C. pruddeni* is more or less unicolorous, in distinction to the contrasting darker pronotal and lighter elytral integument of *C. balteatum*. Also in *C. balteatum* the light-colored dorsal setae are a deep golden color rather than golden-white or whitish as in *C. pruddeni*. The 8th (morphological) abdominal sternum of the males of each is provided with lateral processes which bear at the apex a stout, curved seta. In *C. balteatum* this seta is relatively stout for its entire length and terminates rather abruptly. In *C. pruddeni* the seta is stout at the base but gradually becomes finely filamentous.

C. reversum and *C. balteatum* have apparently identical male genitalic characters. The light-colored dorsal setae of *C. balteatum* are a deep golden color. Specimens of *C. balteatum* lack light-colored setae between the subbasal band and the submedian band of light pubescence. Most specimens of *C. reversum* have a mixture of light and dark setae between these two bands as well as a number of light-colored setae between the basal band and the subbasal band. However, a few specimens of *C. reversum* approach the situation found in *C. balteatum*.

ECOLOGY: The only information is that adults were collected 2 miles north of Valyermo, California, in flowers of *Yucca* sp.

Cryptorhopalum haplotes NEW SPECIES

DIAGNOSIS: Ratio of width (across humeri) to length (of pronotum and elytra) greater than 1:1.86. Eighth (morphological) sternum of male with sublateral papillae on apical margin but without lateral processes or median process; cluster of simple setae inserted along apical margin at middle.

DESCRIPTIONS

ADULT MALE: Dorsal integument with head and pronotum dark mahogany brown; elytra rufous; each elytron with suffused, slightly darker area at about basal ¼ and median ⅓. Dorsal pubescence mahogany brown, suberect; ventral pubescence golden brown, recumbent.

Pronotum with punctures of disc minute, about ⅔ times as wide as width of facet of compound eye and separated by 2 to 4 times diameter of single puncture. Antenna and hypomeron as illustrated (Fig. 3); antennal club reddish brown. Antennal fossa bounded behind by thread-like carina; width of plane of hypomeron at narrowest point behind fossa (exclusive of width of carina) about as wide as ½ width of segment 3 of antenna. Prosternal process without median or lateral carinae, transversely flat. Metasternum without oblique striae. First visible abdominal sternum with single, oblique stria originating beneath trochanter and extending ¾ distance to posterior margin of segment. Tibia of foreleg as illustrated (Fig. 28). Eighth (morphological) abdominal sternum with cluster of setae at middle of apical margin and with small papilla-like sublateral process bearing long, slender setae (Fig. 12). Lateral lobes with somewhat rounding, not truncated, apices; bridge moderately narrow (Fig. 16). Aedeagus with small, proximally directed hook at apex. Length (of pronotum and elytra): 2.38 mm. Width (across humeri): 1.27 mm.

ADULT FEMALE: Integument of head dark mahogany brown; pronotum rufous with suffused darker areas across disc; elytra rufous; each elytron with suffused darker area at about basal ¼ and median ⅓. Antenna and hypomeron as illustrated (Fig. 5). Visible abdominal sternum 5 without foveae. Length (of pronotum and elytra): 3.07 mm. Width (across humeri): 1.54 mm.

RANGE OF OBSERVED VARIATIONS: Pronotum ochreous to dark mahogany with or without light and dark mottled appearance; elytra ochreous to light brown with or without darker, suffused subbasal areas. Length (of pronotum and elytra) ranging from 2.23 mm to 3.07 mm. Ratio of width (across humeri) to length (of pronotum and elytra) varying from 1:1.86 to 1:2.07.

TYPE MATERIAL: *Holotype* male, allotype female, and 7 paratypes: Jacumba (San Diego County), California, June 19, 1951 (D.J. and J.N. Knull). Holotype and allotype deposited in the collection of Ohio State University; paratypes deposited in the collections of the CAS, the LACM, the NMNH, and the collection of the author.

ETYMOLOGY: The specific epithet is formed from the Greek noun ἁπλότης standing in apposition with *Cryptorhopalum* and meaning "simplicity." This is in reference to the simple structure of morphological abdominal segment 8 of the male.

DISCUSSION: The elongated form will easily distinguish this species from any other member of the Nearctic fauna. At least one other species belonging to the same species group occurs in Mexico in the state of Tlaxcala. Whether this species is among those presently described and assigned to *Hemirhopalum* is not known. The Mexican species seems to be readily distinguishable from *C. haplotes* by male genitalic characters as well as by the color of the dorsal pubescence, the shape of the antennal club, and other external features.

ECOLOGY: Quite a few pollen grains were found adhering to the ventral surfaces of each of the specimens, indicating that they were taken in flowers. An examination of the pollen showed it to have come from a plant within the order Rosales, but a species for which the pollen characteristics appear to be undescribed. Other details of the biological relationships of the species are unknown.

SYNONYMIES AND LECTOTYPE DESIGNATIONS FOR *C. REVERSUM* AND *C. PRUDDENI*

Since these two species are very closely allied to *C. balteatum* and since a further understanding of *C. balteatum* probably depends in part on an understanding of its relationships to these 2 species, it seems appropriate to present synonymies that have been discovered for them.

Cryptorhopalum reversum Casey

Cryptorhopalum reversum Casey, 1900, p. 156.
Cryptorhopalum festivum Casey, 1900, p. 156 NEW SYNONYMY.
Cryptorhopalum balteatum Casey, 1900, p. 156 (non *balteatum* LeConte, 1854) NEW SYNONYMY.
Cryptorhopalum pallens Casey, 1916, p. 193 NEW SYNONYMY.

A female from Ft. Wingate, New Mexico, bearing NMNH type No. 37554 is herewith designated as the lectotype of *C. reversum*.

A female from Brownsville, Texas, bearing NMNH type No.

37558 is herewith designated as the lectotype of *C. festivum*.

A female from El Paso, Texas, bearing NMNH type No. 37559 is herewith designated as the lectotype of *C. pallens*. The specimen is badly abraded, so identification with *C. reversum* is conjectural.

The single specimen which Casey identified in his collection as *C. balteatum* is a female labeled only as collected in Arizona.

Cryptorhopalum pruddeni Casey

Cryptorhopalum pruddeni Casey, 1900, p. 156.
Cryptorhopalum insigne Casey, 1916, p. 191 NEW SYNONYMY.
Cryptorhopalum anthrenoides Casey, 1916, p. 194 NEW SYNONYMY.

Three females comprise the series from which Casey described *C. pruddeni*, these taken in Arizona at the "Cañon of the Colorado River" (probably on the south rim of the Grand Canyon). The specimen bearing NMNH type No. 37550 is herewith designated as the lectotype. It appears to be a teneral individual of the species.

The female specimen bearing NMNH type No. 37553 from Jemez Springs, New Mexico, is herewith designated as the lectotype of *C. insigne*.

The unique type of *C. anthrenoides* from the Santa Catalina Mts., Arizona, is NMNH type No. 37557.

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This study could not have been completed without the generous cooperation of a number of individuals and institutions. I am indebted for the loan or gift of specimens to William F. Barr of the University of Idaho, the late Lutz Bayer of the University of Wisconsin, Frank F. Hasbrouck of Arizona State University, Charles L. Hogue of the Natural History Museum of Los Angeles County, Paul D. Hurd, Jr., formerly responsible for the California Insect Survey of the University of California, Berkeley, C. Daniel Johnson of Northern Arizona University, David H. Kavanaugh of the California Academy of Sciences, John M. Kingsolver of the Systematic Entomology Laboratory, U.S.D.A., National Museum of Natural History, Vernon L. Kirk of the Entomology and Crops Research Division of the Agricultural Research Service, Brookings, South Dakota, John F. Lawrence of the Museum of Comparative Zoology, the late A.T. McClay of the University of California, Davis, Scott McCleve of Douglas, Arizona, D.H. Pengelly of the University of Guelph, Guelph, Ontario, P.H. Raven of Stanford University, H.J. Reinhard of Texas A. and M. University, E.P. Rouse of the University of Arkansas, Jerome G. Rozen, Jr., of the American Museum of Natural History, M.W. Sanderson, formerly of the Illnois Natural History Survey, Joe Schuh of Klamath Falls, Oregon, Terry L. Seeno of the California Department of Food and Agriculture, C.A. Triplehorn of Ohio State University, Robert H. Turnbow, Jr., of the University of Georgia, Floyd G. Werner of the University of Arizona, and R.E. Woodruff of the Division of Plant Industry of the Florida Department of Agriculture. My thanks are extended to Richard H. Hevly of Northern Arizona University for some plant and pollen identifications. Additional thanks are due C. Daniel Johnson, J.M. Kingsolver, Floyd Werner, and Terry L. Seeno for a critical reading of the manuscript.

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A NEW MONOPLACOPHORAN LIMPET FROM THE CONTINENTAL SHELF OFF SOUTHERN CALIFORNIA

By James H. McLean

Published by the NATURAL HISTORY MUSEUM OF LOS ANGELES COUNTY • 900 EXPOSITION BOULEVARD • LOS ANGELES, CALIFORNIA 90007

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Prior to November 30, 1973, publications of the Natural History Museum have appeared under various titles — *Leaflet Series, Museum Graphic, Education Series, History Series, Science Series, Study Guides, Contributions in History, History Bulletin, Science Bulletin*, unnumbered catalogs of exhibitions, and other miscellaneous publications.

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Edward Ostermeyer
Editor

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CONTENTS

Systematic Account

The *Science Bulletin* and *Contributions in Science* of the Natural History Museum of Los Angeles County were merged into a single imperial octavo serial, retaining the name *Contributions in Science* and beginning with Number 301.

This serial has been newly formatted for maximum use of typography and illustrations per page, and sized for maximum use of paper. All photography has been produced utilizing a 200-line screen for detail.

Since most institutions rebind *Contributions in Science* collectively into hardbound volumes, and many researchers using them desire to photocopy material, two new features have been incorporated into the new format. A suggested citation line provides the abbreviated serial title, year, number of publication, and total pagination, and appears in the lower left corner of each page; and pages of *Contributions in Science* have been printed off-center to provide a two-inch gutter between adjacent pages for easier accessibility in photocopying.

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Contributions in Science are articles in the earth and life sciences, presenting results of original research in Natural History. *Science Bulletin* (Numbers 1–30; 28 June 1965 to 10 April 1978) and *Contributions in Science* Numbers 1–300; 23 January 1957 to 16 June 1978) were merged into a single imperial octavo serial beginning with Number 301.

A NEW MONOPLACOPHORAN LIMPET FROM THE CONTINENTAL SHELF OFF SOUTHERN CALIFORNIA[1]

By James H. McLean[2]

ABSTRACT: A new subgenus and species of monoplacophoran, *Vema (Laevipilina) hyalina,* is described from specimens with a maximum length of 2.3 mm taken on rocks from depths between 174–388 m on the Santa Rosa-Cortes Ridge of the southern California continental borderland. The shell differs from other living neopilinids in being nearly transparent and lacking clathrate sculpture. As in the genus *Vema,* there are six pairs of gills and distinct postoral tentacles. *Vema,* on the basis of six pairs of gills is here regarded as generically distinct from *Neopilina,* which has five. On shell characters the new subgenus *Laevipilina* differs from *Vema* in lacking concentric sculpture and in having its structural prisms of a depth equal to their diameter rather than twice the diameter. Radular comparisons among neopilinids are here made for the first time; the radula of the new species differs from that of three other neopilinids in having a more prominent first lateral tooth. *Vema (Laevipilina) hyalina* is the first monoplacophoran to be verified as living on a rocky substratum and the first to be found at continental shelf depths. Living specimens are accessible, suggesting that much will soon be learned about its anatomy and life history.

INTRODUCTION

Until 1952 the monoplacophoran limpets were known only from the Paleozoic fossils. On shell characters they differ from modern gastropod limpets in having the muscle scar divided metamerically. Paleontologists had regarded the fossil genera as early patellaceans. No advance was made until 1938, when Wenz (1938: 59) suggested that the symmetrically paired muscle scars of the Silurian genus *Tryblidium* might correspond to the arrangement of muscles in chitons. At that point he separated them from the Patellacea and established the superfamily Tryblidiacea for the group. Two years later he developed his idea further by considering them to represent untorted gastropods and distinguished them from prosobranch gastropods at the subclass level (Wenz 1940). He was the first to mention the name Monoplacophora but did not use it in a formal sense, stating that N. H. Odhner had suggested the name to him (see Knight, Lemche, and Yochelson, 1958). Knight (1952) enlarged upon Wenz's theory and used Monoplacophora with ordinal rank equivalent to Polyplacophora, the chitons.

Dramatic proof that monoplacophorans were untorted limpets became available in 1952 when a living species was discovered by the Danish Galathea Expedition at abyssal depths in the eastern Pacific off Costa Rica. The announcement of the discovery took place five years later when the species was described by Lemche (1957) as *Neopilina galatheae*. Its anatomy was thoroughly monographed by Lemche and Wingstrand (1959). Additional anecdotes about the original discovery were given later (Lemche 1972).

Neopilina is an untorted limpet with a posterior anus and serially repeated muscles, gills, and other organs. *Neopilina* was the most exciting malacological discovery of the century, a living fossil — a relict of a once diverse group of mollusks. An additional living class of mollusks was recognized, now apparently surviving only in the deep sea.

Further finds of *Neopilina* since the original discovery proved that living monoplacophorans are more widely distributed than was originally assumed. In recent years five more species of *Neopilina* have been described and other records of unidentified species have been published, all found at abyssal or hadal depths. The second described species, *Neopilina ewingi* Clarke and Menzies 1959, from the Peru-Chile Trench, differed from *N. galatheae* in having six pairs of gills instead of the five pairs of *N. galatheae*. Because of this difference it was made the type species of the subgenus *Vema* Clarke and Menzies 1959. Further discoveries brought the number of described species of *Neopilina* to a total of five and those of *Vema* to two.

My involvement in the study of monoplacophorans began in 1966, when, in connection with my interest in gastropod limpets, I was given the opportunity to work upon two small specimens in the S. Stillman Berry Collection. The specimens, not exceeding 2.3 mm in length, had been taken on rocks snagged on hook and

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line by a fisherman, Louis Zermatten, in the vicinity of the Cortes Bank, due west of San Diego, California, in 1965. One was from a depth of 95 fathoms (174 meters) and the other from 125 fathoms (229 meters). The rocks bearing the limpets were saved for John E. Fitch of the California Department of Fish and Game. He removed the associated mollusks and gave them to S. Stillman Berry of Redlands, California.

The dried animal of the first specimen was sacrificed for a radula preparation. Initial study of the radula (Figs. 20, 21) suggested a new group in the Patellidae, with a radula characterized by a narrow rachidian, three pairs of laterals and two pairs of flaring marginals. A minute, deep water representative of the Patellidae, otherwise known from robust intertidal forms, was unexpected, but it seemed clearly to be the case, based on the radular evidence. In the hope that more specimens would eventually be found, I delayed further work on this remarkable find. Nine years passed but no additional material came to light.

In 1975 I again turned my attention to the specimens on hand. Only then did I closely examine the specimen that still contained the dried animal. Through the dorsal surface of the nearly transparent shell I noted the circularly coiled intestine that is one of the hallmarks of the described species of *Neopilina* (Fig. 1). Then other monoplacophoran features such as metamerically paired shell muscles and a posterior anus were observed. Upon rehydrating the animal and examining it in fluid, the shell became more transparent and its structural prisms visible (Figs. 2, 3). It thereupon became clear to me that this was a monoplacophoran limpet. Contrary to all previous expectations for the group, it had come from a rocky substratum in relatively shallow water.

FIGURE 1. *Vema (Laevipilina) hyalina* new species. LACM 19149, 2.16 mm in length, dorsal view prior to rehydration of the soft parts and prior to removal of encrustations from the shell surface. The anterior apex is visible near the top and the intestine with four coils is seen through the nearly transparent shell slightly posterior to the midpoint. Photograph by Solis.

The rehydration of the specimen containing the dried animal did not fully restore the features of the ventral surface. Structures recognized were the head, mouth, velum extending laterally and posteriorly to the head, radiating pedal retractor muscles, and the posterior anus. There seemed to be no sign of gills or of postoral tentacles that also characterize the group. Moreover, the true shape of the foot could not be discerned. It seemed that it was partially missing with nothing remaining but a stump in the central area. An S-shaped structure that was clearly visible was interpreted as the radular sac, considering that the radula extracted from the other specimen was more than half the length of the shell. The shell appeared completely smooth, devoid of all traces of clathrate sculpture seen in the described species of *Neopilina*. The radula also seemed to differ considerably from that of *N. galatheae*, the only species for which a radula had been illustrated.

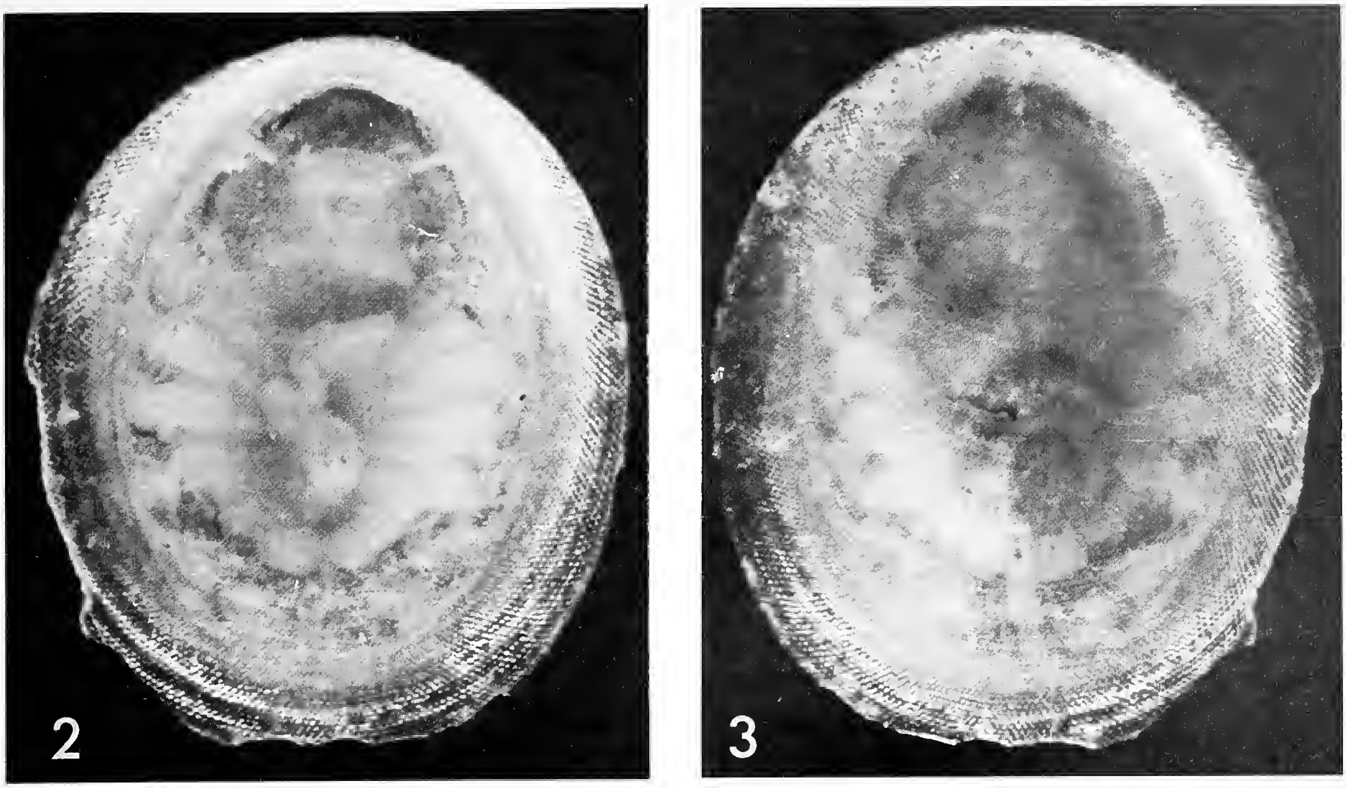
At that point in my studies I presented the preliminary findings to the American Malacological Union — Western Society of Malacologists joint meeting in San Diego, June 1975. Based on the smooth shell, radular differences, and apparent absence of gills, I considered that a new genus was indicated for the newly discovered species, and so announced an intention to propose one. The abstract resulting from my presentation was published 30 January 1976 (McLean 1976).

In the fall of 1975 an intensive offshore sampling program was initiated by the U.S. Bureau of Land Management (BLM) on the continental shelf of southern California, coinciding with the leasing of offshore tracts for oil exploitation. A group of biologists headed by Gilbert F. Jones of the University of Southern California contracted to do the biological portion of the work. Although most of the stations were made on soft bottoms, there were some box core stations from rocky areas. Sorters and technicians were alerted to watch for the new microscopic monoplacophoran, but after six months of sampling none were found.

Meanwhile, early in 1976 I decided to publish my preliminary description of the species in the hope that this notice would stimulate efforts to find other specimens. After more closely scrutinizing the rehydrated specimen with improved optics I noted swellings on the mantle margin in the position where gills could be expected. Contrary to my earlier observations, six pairs of gills seemed to be present, although no clear configuration could be seen.

No radular descriptions had been published on any monoplacophoran species since the initial monograph of Lemche and Wingstrand (1959). I was able to obtain specimens of two other neopilinid species for radular comparisons. The results, discussed herein, indicated that the two other species bridged the gap between the radula of the new form and that of *N. galatheae*.

Although many questions remained unanswered, a draft of the manuscript was completed and circulated for review. As I was preparing to submit the paper for publication, two freshly collected specimens were found in sediment from one of the BLM stations. One had been picked from the residue by the sorters and subsequently recognized by Patrick I. LaFollette, a member of the BLM project. He reexamined the residue and found another. This was the breakthrough I had hoped would occur, for I now



FIGURES 2, 3. *Vema (Laevipilina) hyalina* new species. LACM 19149, 2.16 mm in length, rehydrated and photographed in alcohol. FIGURE 2, ventral view; FIGURE 3, dorsal view. Shell prisms show at the margin, arranged in curved rows; lighter and darker concentric rings represent growth lines. Head with mouth near top center. Below the head is the S-shaped radular sac and foot stump. Tubular rectum at bottom center. Seven pairs of pedal retractor muscles radiate from the center; the first pair is narrow, the second, third, fourth and fifth pairs are long and broad, the sixth and seventh pairs are short. Beyond the lateral terminations of all but the first pair of retractor muscles are 6 pairs of gills visible as swellings that blur the shell prisms. The dorsal view shows four dark coils to the intestine in lower center. In the dorsal view, the light areas encircling the central visceral area are the terminations of the broad bands of the pedal retractor muscles. Gills represented by the blurred lighter areas between the edge of the shell and the pedal muscle terminations. Photographs by Draper.

had preserved specimens showing the true condition of the foot and the clear presence of gills (Figs. 4, 5).

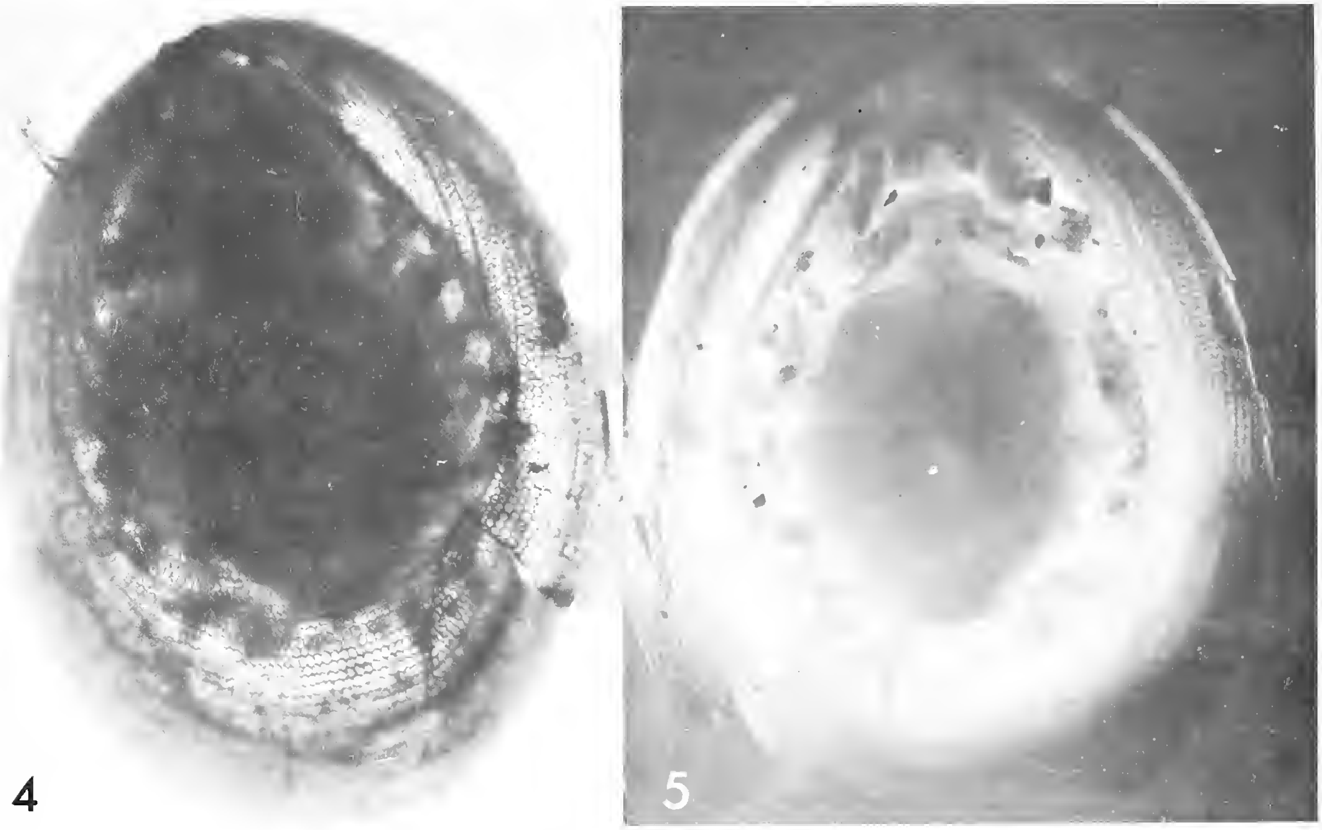
The two fresh specimens were somewhat smaller than the original two, with a maximum length of 1.75 mm. They came from a box core station on the Santa Rosa-Cortes Ridge between San Nicolas and Tanner Basins, at a depth of 388 m. Efforts to find more specimens in sediment residues from other unprocessed BLM stations from rock bottoms were unsuccessful.

Publication of the paper was withheld until I could learn more about the anatomy of the species. Although the specimens had not been fixed for histologic sectioning, it was hoped that sectioning would be possible. I asked the help of M. Patricia Morse at Northeastern University in Nahant, Massachusetts, who along with her associate, Nathan W. Riser, had work already underway on *Neopilina ewingi*.

Once again the material had limitations due to the lack of proper fixation. Many sections made by Morse and Riser from the smaller of the two specimens did not hold together and the results were disappointing. However, they prepared the larger specimen (Figs. 4, 5) by critical-point drying for viewing with a scanning electron microscope (SEM). That effort produced some highly satisfactory pictures on 11 February 1977, which are reproduced here (Figs. 6–8, 11).

In February 1977 further specimens were collected on a three day cruise of the *VELERO* led by Heinz A. Lowenstam of the California Institute of Technology, and assisted by LaFollette, now a member of the Malacology Section of the Museum. Efforts to recover the species with rock dredges and box cores were successful at the same locality as the earlier BLM station. Six living specimens attached to their rock substratum were obtained. The animals survived for several weeks at ambient water temperatures (Lowenstam 1977, abstract). A report on the behavior, ecology, and shell ultrastructure will be published elsewhere by Lowenstam. One of the living specimens was fixed for histologic sectioning to be done by Morse and Riser, who will also report separately on their results.

The rocks obtained on the cruise were examined aboard ship for living specimens and then preserved in 70% ethanol. Further examination of the rocks by LaFollette produced four more specimens that became the type lot. One of these specimens (Fig. 9), designated the holotype, is in excellent condition and shows most of the features now attributed to the species.



FIGURES 4, 5. *Vema (Laevipilina) hyalina* new species. LACM 19150, 1.75 mm in length. FIGURE 4, dorsal view, showing the regularity of the shell prisms, gills darkly outlined. FIGURE 5, ventral view, showing the 6 pairs of gills, U-shaped anterior lip of the mouth, the postoral tentacles clearly visible between the mouth and the foot. Photographs by Morse and Riser, light microscope, 4 X objective.

SUPRASPECIFIC CLASSIFICATION OF LIVING MONOPLACOPHORANS

The Monoplacophora have been recognized as a separate class of mollusks for a relatively short period. A revised classification of the Paleozoic fossil representatives was given by Knight and Yochelson (1958). Starobogatov (1970), and more recently, Runnegar and Jell (1976), have offered other versions.[3]

These classifications have been based largely upon shell form and the count and configuration of muscle attachment scars on the shell. The modern monoplacophorans have thin shells that lack readily visible muscle scars. Unfortunately, details of the musculature are known only for *Neopilina galatheae* as given by Lemche and Wingstrand (1959). There is therefore a poor basis upon which to compare diversity in the living species with the considerable diversity indicated in the fossil record.

When Lemche (1957) proposed *Neopilina galatheae* he placed it in the family Tryblidiidae, a group otherwise unknown since the Devonian. Knight and Yochelson (1958) established the subfamily Neopilininae for the species. Subsequent authors followed this scheme until Starobogatov (1970) disassociated the group from the Tryblidiacea altogether by recognizing both a separate family Neopilinidae and superfamily Neopilinoidea. However, Runnegar and Jell (1976) retained *Neopilina* in the Tryblidiidae.

A consideration of the overall classification of Monoplacophora is not within the scope of this paper; there are evidently some controversial aspects that will not readily be settled. Certainly a Recent family Neopilinidae may be justified on grounds in addition to the great disparity in age. The shells of neopilinids are thin and lack the massive development of the nacreous layer of the Devonian Triblidiidae (Erben, Flajs and Siehl 1968).

Generic criteria within the Neopilinidae are also lacking a sound basis for comparison. *Vema* Clarke and Menzies 1959, type species *Neopilina (Vema) ewingi* Clarke and Menzies 1959, was proposed as a subgenus of *Neopilina* chiefly on the presence of six pairs of gills, rather than five of *Neopilina*.

In the 18 years that have passed since the first two species were proposed, four more species of *Neopilina (Neopilina)* have been described, along with one more species of *Vema*. The number of gill pairs has proven to be a consistent character in species of each group regardless of size or growth stage. The supplementary criteria for *Vema*, thinner shell and thinner periostracum,

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[3] While this paper was in its final stage of preparation, I received a useful review paper on the Recent monoplacophorans (Cesari and Guidastri 1976). The article, in Italian, contains an extensive bibliography that includes many titles omitted here. Also, an obituary of the late Henning Lemche (Knudsen 1977) includes references to other papers by Lemche on *Neopilinia* and its affinities.

FIGURE 6. *Vema (Laevipilina) hyalina* new species. LACM 19150, 1.75 mm in length, critical-point dried, SEM micrograph. Lateral view of ventral surface, showing the 6 pairs of gills, the anterior lip of mouth, the velar ridge extending laterally around the mouth, the ridge between the mouth and foot bearing the postoral tentacles. Shrinkage of the body has revealed the pallial line midway in the exposed portion of the shell, the nacreous layer on the innermost portion thick enough to obscure the pattern of hexagonal prisms. X 80.

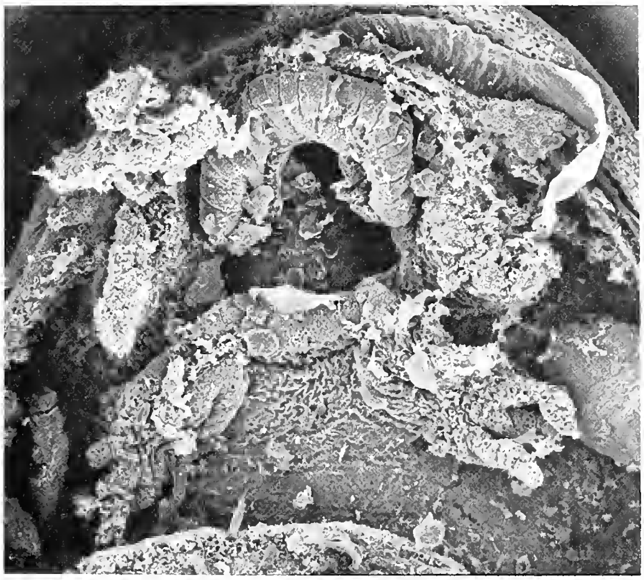

FIGURE 7. *Vema (Laevipilina) hyalina* new species. LACM 19150, length 1.75 mm, critical-point dried, SEM micrograph. Ventral aspect, enlargement of head area, showing the U-shaped anterior lip of the mouth, the radula exposed on the odontophore within. Postoral tentacles visible on the ridge below the mouth. The velum is a narrow ridge anterior to the mouth and extending laterally on both sides. X 190.

FIGURE 8. *Vema (Laevipilina) hyalina* new species. LACM 19150, critical-point dried, SEM micrograph. Radular ribbon exposed on the odontophore within the mouth cavity. This is an enlargement of the area visible in Figure 7, oriented with the anterior at the top as in the other figures. Rachidian and lateral teeth as drawn in Figure 22. One of the fringed first marginals is fully exposed, showing depth to the comblike surface. X 900.

have been maintained in the second reported *Vema, N. (Vema) bacescui* Menzies 1968. The two species of *Vema* are known only from the southern hemisphere in the eastern Pacific, whereas the species of *Neopilina* have been shown to have a broader distribution in abyssal depths at the base of the continental slope in the eastern Pacific in both hemispheres and in the Indian Ocean and mid-Pacific.

Inasmuch as the anatomy of *Vema ewingi* has not been described in detail, there is no sound basis upon which to decide whether the separation of the two groups should be at the subgeneric, generic or familial level. Starobogatov (1970:301) stated: "*Vema* can hardly be regarded as a subgenus of *Neopilina*. Moreover it cannot be stated with confidence that *Vema* is a member of the same family . . . it is in any case appropriate to await publication of detailed data on the anatomy of *Vema*." Nevertheless, for a group in which serial repetition of key structures is fundamental, other internal organs in *Vema* can be expected to have an arrangement differing from that of *Neopilina*. Once the results of comparative anatomical studies are available, there will, in my opinion, be ample reasons to consider

FIGURE 9. *Vema (Laevipilina) hyalina* new species. Holotype, LACM 1787, 1.94 mm in length, preserved and photographed in alcohol. Shell prisms show at the margin on the left side where the pallium is lifted away. The pallial fold encircles the head area and borders the outer side of the pallial cavity, in which six pairs of gills are visible. The anterior lip of the mouth is surrounded by the velum, which extends laterally into the pallial cavity. Between the velum and the foot is the ridge bearing the postoral tentacles. Foot with thickened margin, the two posterior lobes of the gonad visible through the transparent sole. The opaque area at the lower left is due to an encrusting foraminiferan on the outer surface of the shell. Photograph by Draper.

the two groups to be generically distinct. Although some might argue that it is premature to make this distinction, it is necessary to do so in order to recognize a subgenus within the six-gilled *Vema* lineage. There is a major dichotomy between the abyssally occurring species with sculptured shells and the small, smooth shelled, more shallowly occurring new species. I believe it prudent to recognize this distinction now at the subgeneric level.

The outline that follows includes all of the taxa proposed to date in the Neopilinidae[4]. As more continues to be learned about the anatomy of the living species, the diagnoses can be enlarged. Uncertainties now exist concerning the musculature and repetition of internal structures; discussion of these characters is therefore omitted.

SYSTEMATIC ACCOUNT

NEOPILINIDAE Knight and Yochelson 1958

NEOPILININAE Knight and Yochelson 1958:39; Starobogatov 1970:301 (familial rank).

DIAGNOSIS: Shell thin, cap shaped, apex anterior; shell layers consisting of a thin periostracum, a dominant prismatic layer, and a thin internal nacreous layer. Eyes lacking, mouth bordered anteriorly by a velum, posteriorly by postoral tentacles; foot sole thin, weakly muscularized; anus posterior to foot; gills 5 to 6 pairs, with simple lamellae. Radula with a narrow rachidian, three pairs of laterals and two marginals, edge of first marginal fringed.

The family is limited to the known Recent monoplacophorans. It differs from the Paleozoic families in having an extremely thin internal nacreous layer of the shell.

Neopilina Lemche 1957

Neopilina Lemche 1957:414. Type species: *N. galatheae* Lemche 1957.

DIAGNOSIS: Shell with radial and concentric ridges at least in early stages, periostracum moderately prominent; gill pairs 5.

SPECIES: *N. galatheae* Lemche 1957 (Costa Rica); *N. veleronis* Menzies and Layton 1963 (Baja California, Mexico); *N. adenensis* Tebble 1967 (Indian Ocean); *N. bruuni* Menzies 1968 (Peru); *N. oligotropa* Rokop 1972 (mid-Pacific).

OTHER RECORDS: *N. galatheae*, Parker 1962 (off Cape San Lucas, Baja California); unidentified, Menzies 1968 (Costa Rica); unidentified, Rosewater 1970 (South Atlantic east of Falkland Islands); unidentified, Filatova, Vinogradova and Moskalev 1974 (Atlantic-Antarctic); same record identified as *N. galatheae*, Filatova, Vinogradova, and Moskalev 1975.

DISTRIBUTION: Abyssal, Eastern Pacific: Baja California, Costa Rica, Peru; east of southern tip of South America; mid-Pacific; Indian Ocean.

REMARKS: Of the four species described, *N. galatheae* is the only one known from material from other than the type locality. *Neopilina veleronis* was described prior to the availability of scanning electron microscopy. No intact shells of *N. veleronis* are extant; shells of the remaining paratypes have been altered by the preservative (Figs. 14, 15). Shells of the two original specimens of *N. oligotropa* were thought to have been altered by the initial preservative (Rokop 1972). *Neopilina veleronis* and *N. oligotropa* were described from specimens not exceeding 3 mm in length; *N. veleronis* was considered mature because ripe ova were recognized by Menzies and Layton (1962); *N. oligotropa* was presumed mature, having come from an oligotropic or food-poor environment. *Neopilina adenensis* and *N. bruuni* were described from single specimens, the latter species briefly diagnosed but not described in detail.

Vema Clarke and Menzies 1959

Vema Clarke and Menzies 1959:1027. Type species: *Neopilina (Vema) ewingi* Clarke and Menzies 1959.

DIAGNOSIS: Shell thinner, periostracum thinner, sculpture weaker than that of *Neopilina:* gill pairs 6.

Subgenus *Vema s. str.*

DIAGNOSIS: Moderate in size, sculptured with fine radial ribs and raised concentric ridges especially strong in early stages; depth of structural prisms twice that of surface diameter. Gill pairs 6, gill lamellae 5–7.

SPECIES: *V. ewingi* (Clarke and Menzies 1959) (Peru); *V. bacescui* (Menzies 1968) (Peru).

DISTRIBUTION: Abyssal, Peru-Chile Trench.

REMARKS: *Vema ewingi* (Figures 12, 13) has been collected at a number of stations (Menzies 1968; Meenakshi et al. 1970) off Peru, but *V. bacescui* is known from a single station, the original number of specimens not mentioned. The latter species was said to have a distinctive reticulate pattern on the shell surface and a greater abundance of postoral tentacles. Further comparative details were not given.

Subgenus *Laevipilina* NEW SUBGENUS

Type species: Vema (Laevipilina) hyalina new species.

DIAGNOSIS: Small (under 3 mm in length), lacking concentric and radial sculpture; structural prisms hexagonal, uniform in size, their depth equal to their surface diameter. Gill pairs 6, gill lamellae 2–3.

DISTRIBUTION: Continental Shelf, southern California.

ETYMOLOGY: The subgeneric name, like that of *Neopilina*, is based on *Pilina*, a fossil (Silurian) monoplacophoran of the family Tryblidiidae. The prefix *laevi* (from *laevis*, the Latin adjective for smooth) emphasizes the unsculptured surface of the shell in the new taxon.

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[4] One published record may now be removed. Filatova, Sokolova and Levenstein (1968) and Filatova and Zenkevich (1969) reported finding a monoplacophoran at a mid-Pacific seamount northwest of Hawaii. The apex was said to be close to the center of the shell rather than near its anterior margin as in the known species. It was therefore considered to represent a new genus in the Tryblidiidae. In response to my inquiry about the current status of this specimen, she stated (Filatova, personal communication, 12 July 1976): "As to our small specimen of *Neopilina* (?) from Hawaii region it was very young one and it was difficult to decide about its true systematic position, especially for it had the central umbo, and it was only a single specimen."

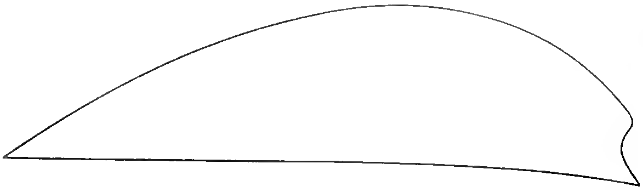

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FIGURE 10. *Vema (Laevipilina) hyalina* new species. LACM 19149, length 2.16 mm. Lateral profile, the anterior apex at the right.

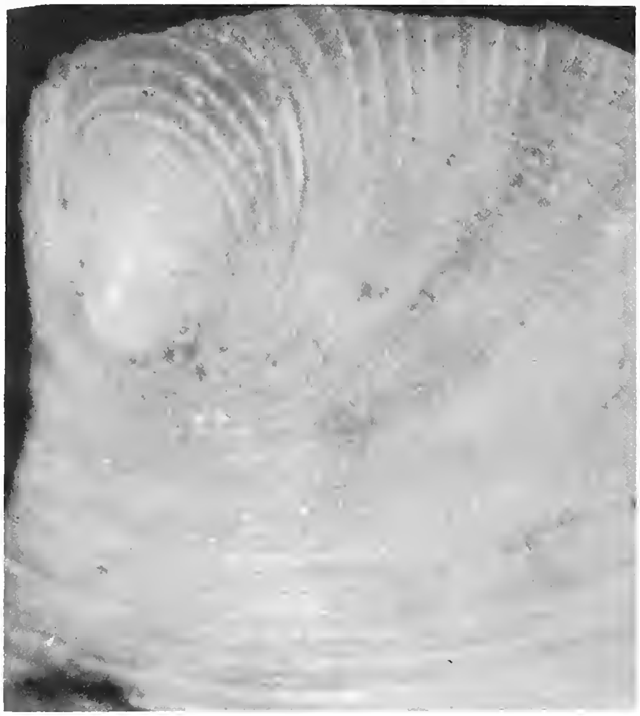


FIGURE 12. *Vema (Vema) ewingi* (Clarke and Menzies 1959). Anterior face of broken shell showing the bulbous apex at the left; strong concentric and weaker radial sculpture is visible in early growth stages. LACM 65–11, 6200 m, 110 mi. W of Callao, Peru, R/V ANTON BRUUN, 24 November 1965. Photograph by Draper. X 45.

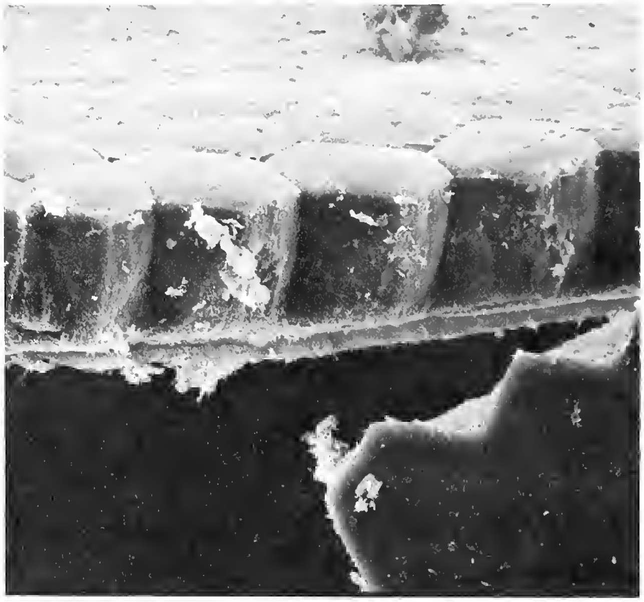


FIGURE 11. *Vema (Laevipilina) hyalina* new species. LACM 19150, SEM micrograph, fractured edge of shell. The narrow band below represents the periostracum. From an area outside the pallial line and therefore lacking the internal nacreous layer. This shows the hexagonal surface outline of the prisms and the depth approximately equivalent to the diameter. X 1100.

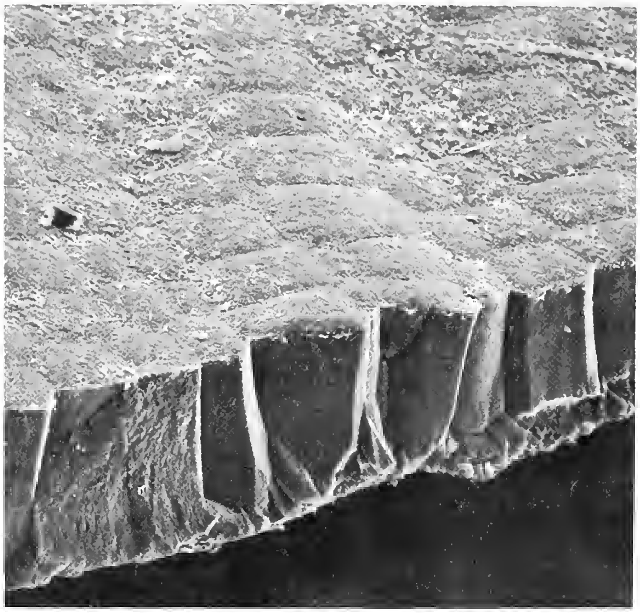


FIGURE 13. *Vema (Vema) ewingi*. SEM micrograph, fractured edge of shell near the outer margin. Some of the prisms have a hexagonal surface, while others are more irregular and elongate. Depth of prisms approximately twice the diameter of those with hexagonal surface. Compare with same view of *N. hyalina* in Figure 11, noting differences in magnifications. X 240.

Vema (Laevipilina) hyalina
NEW SPECIES
Figures 1–11, 20–22

McLean 1976:60 (abstract, not named); Cesari and Guidastri 1976:235 (review, McLean 1976); Lowenstam 1977:1076 (abstract, reporting collection of living specimens of "a new monoplacophoran species").

DIAGNOSIS: *Vema hyalina* differs from other 6-gilled neopilinids in its smaller size at maturity, lack of concentric and radial shell sculpture, shallow depth of the structural prisms and reduced number of gill lamellae.

SHELL: Small (largest known specimen 2.3 mm in length), thin, transparent, iridescent; surface smooth, clathrate sculpture lacking. Periostracum thin, visible as a yellow sheen; prismatic layer thick; internal nacreous layer thin. Pallial line visible at one-fourth the distance from the margin to the center, inside of which the thicker nacreous layer obscures the pattern of prisms. Muscle scars not apparent. Structural prisms visible under magnification, irregular in shape, usually hexagonal, some pentagonal, not elongate on surface; depth of prisms approximately equal to their diameter; prisms arranged in concentric rows corresponding to growth lines at the shell margin and also showing a pattern of curved lines radiating from the mid-dorsal region. Base of shell in one plane, outline evenly elliptical, length 1.2 times that of width; maximum shell height anterior to mid-point. Apex smoothly papillate, positioned slightly behind anterior margin at half the shell height, projecting and rendering anterior face slightly concave. Apical area completely transparent, not showing defined structural prisms, clear area extending for approximately 10% of shell length.

EXTERNAL ANATOMY: Foot large, thin, oval, nearly transparent, its base outlined by a thickened ridge. Gills six pairs; in mature specimens the first two pairs bilobate, next four with three fleshy fingerlike lobes; located in pallial groove between foot and pallial fold. Pallial fold a well-defined ridge in front of head and extending on sides halfway between foot and shell edge, its position corresponding to pallial line on shell interior. Pallium of thin mantle tissue extending to shell margin outside of pallial fold. Mouth surrounded on front and sides by thick U-shaped anterior lip. Velum a narrow ridge in front of anterior lip, extending laterally on either side, terminating in large triangular flaps that extend into pallial groove. Postoral tentacles located on both ends of a ridge extending laterally between mouth and foot; tentacles prominent and finely branched into at least six branches. Anus posterior to foot, close to mantle margin.

INTERNAL ANATOMY: Gut coils four, visible through transparent shell, coils filling space between midpoint and half the distance to posterior edge of shell, final coil extending to anus. Gonad visible through semi-transparent foot sole, divided posteriorly into two broad lobes. Radula sac S-shaped, prominent. Pedal retractor muscles tentatively seven pairs; first pair narrow; second, third, fourth, and fifth relatively broad and long; sixth and seventh pairs broad and short. Gills positioned just outside terminations of retractor muscles on shell, terminations of first pair of muscles without corresponding gills.

RADULA: Ribbon of original specimen 1.6 mm long, about 70% of shell length, with 25 rows of fully developed teeth and 17 rows in developmental stages. Each inverted V-shaped row approximately .08 mm wide, containing a rachidian, 3 pairs of lateral teeth, and 2 pairs of marginal teeth. Rachidian tooth long and slender, four times longer than wide, with a slightly swollen and overhanging tip. Shaft of first lateral tooth of similar diameter, its tip more than twice the width and with a smooth overhanging edge. Second lateral similar to the first, its free end nearly three times width of the shaft. Third lateral smaller, free end about twice its width, positioned below the second lateral. First marginal large, positioned well below the lateral teeth, broadly triangular, basal outline faintly visible, free edge broadly curved and finely fringed; extending past midpoint of ribbon and overlapping with opposite tooth, extending on outside well beyond basal membrane. Second marginal small, free edge smooth, extending beyond edge of basal membrane.

TYPE MATERIAL: Holotype, Los Angeles County Museum of Natural History (LACM) 1787, 2 paratypes LACM 1788, 1 paratype National Museum of Natural History (USNM) 758556. Other specimens from the vicinity of the type locality retained by Heintz A. Lowenstan, California Institute of Technology.

TYPE LOCALITY: Santa Rosa-Cortes Ridge (32°59.0′ N, 119° 32.8′ W), depth 373–384 m. Collected by Heinz A. Lowenstan and Patrick I. LaFollette, R/V Velero IV sta. 25765, 14 February 1977.

ADDITIONAL RECORDS:

1) LACM 19148, radula slide (Figs. 20–22) and shell fragments on SEM stub. One specimen, 95 fm (174 m), between Cortes and Tanner Banks, California (32° 41′ N, 119° 17.3′ W), February 1965, collected by Louis Zermatten, ex S. S. Berry Collection, no. 33351. Shell used for SEM analysis by Lowenstam.

2) LACM 19149, rehydrated specimen (Figs. 1–3). One specimen, 125 fm (229 m), Cortes Bank, California (32° 25.8′ N, 119° 13.5′ W), April 1965, collected by Zermatten, ex Berry Collection no. 33333. Specimens from these two localities were attached to rocks brought up by hook and line; the hooks had been snagged in bore holes made by pholad bivalves. The dried specimens were removed by John E. Fitch and given to Berry. Coordinates were supplied by Fitch in 1976 after consulting with Zermatten. Both localities were productive fishing sites for the red rock cod *Sebastes miniatus* and were regularly fished by Zermatten.

3) LACM 19150, scanned specimen (Figs. 4–8, 11). Two specimens, 388 m, Santa Rosa-Cortes Ridge, California (32° 58.85′ N, 119° 33.05′ W), 1 May 1976, R/V VELERO IV sta. 24904, BLM sta. 569 (Figure 16, bottom photograph). This was the first record of the species at the type locality. The specimens were found in the alcohol-preserved rock and gravel residue by LaFollette. One specimen was used in an attempt at sectioning by Morse and Riser, the other remaining specimen was critical-point dried and examined with SEM.

DIMENSIONS:

	length	width	height
LACM 1787 (holotype)	1.94	1.62	0.55
LACM 1788a (paratype)	1.54	1.22	0.41
LACM 1788b (paratype)	0.81	0.66	0.26
USNM 758556 (paratype)	1.94	1.62	0.59
LACM 19148 (radula)	2.16	1.70	0.70
LACM 19149 (rehydrated)	2.28	1.93	0.64
LACM 19150 (scanned)	1.75		

ETYMOLOGY: The specific name is an adjective based on the Greek noun *hyalos* (glass), to denote the glassy, transparent nature of the shell.

DISCUSSION

The discovery of a monoplacophoran living at a depth considered to be the approximate boundary between the continental shelf and the continental slope is remarkable and unanticipated on the basis of previous knowledge of living monoplacophorans.

Prior to the discovery of this species, there had been none of the abyssal species recovered alive, nor had it been possible to obtain specimens without the use of an oceanographic vessel capable of trawling in great depths. Now, 20 years following the announcement that a group of mollusks supposed extinct in the early Paleozoic survives today, it is possible to obtain living specimens and observe them under laboratory conditions.

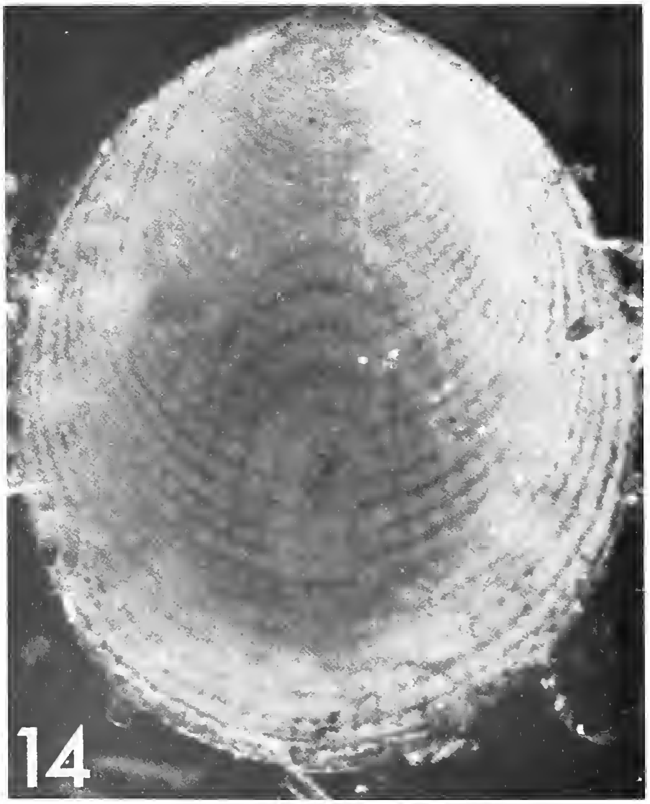
Vema hyalina is small and therefore is not an ideal laboratory animal. Nevertheless, interest in the species should enable future investigators to surmount the inherent difficulties.

SIZE AND STRUCTURE

The maximum length known for the species is 2.3 mm. A sufficient number of specimens are known of less than that size, so that it now seems unlikely that larger ones will be found. The sectioned specimen, which measured 1.6 mm in length, showed mature sperm and was therefore considered sexually mature. Shells of *Vema hyalina* have a mature look; they do not have a disproportionately large apical area as would be the case with immature specimens. The shell structure is so fragile that larger specimens would be unlikely.

Vema hyalina, the third species of *Vema* to be described, is the smallest of the genus, being about one-tenth the size of the others. Two small-shelled species of *Neopilina s. str.* are known: *N. veleronis* and *N. oligotropa.* That *N. veleronis* (Figs. 14, 15) was described from mature specimens is reasonably certain from the fact that mature ova were observed in histologic sections, as noted in the original account of the species. *Neopilina oligotropa* was considered likely to be mature because it came from a mid-ocean environment with limited food sources. The other associated fauna was represented by similarly small forms. Size differences of this magnitude within genera are somewhat unusual in mollusks, but are not unknown.

The lack of surface shell sculpture distinguishes *Vema (Laevipilina) hyalina* from other described neopilinids. The shells of all the other species are reinforced, at least in their young stages, by concentric and radial sculpture, which strengthens without greatly increasing weight or bulk. Although all neopilinid shells are thin and fragile, they apparently provide sufficient support for the moderately large species *(N. galatheae* reaches 37 mm in length) living at abyssal depths where the physical conditions are rela-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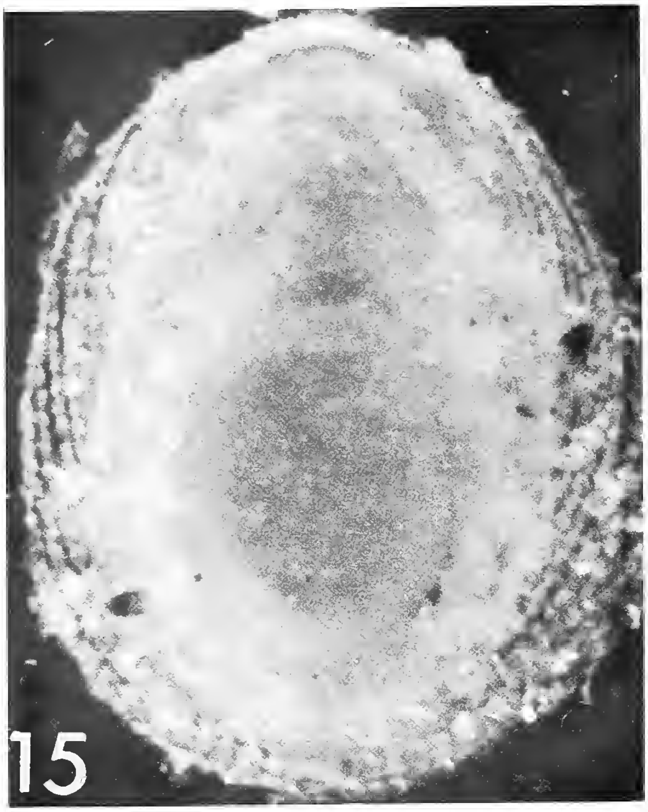
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FIGURES 14, 15. *Neopilina veleronis* Menzies and Layton, length 2.1 mm. Recent photographs of holotype in alcohol. FIGURE 14, dorsal view. FIGURE 15, ventral view. The anterior apex is at the top. Five coils of the intestine are visible through the translucent shell. The shell is now considerably decalcified; the visible nodular structures that remain are the intersections of the radial and concentric sculpture. Photographs by Draper.

tively stable. A shallow water counterpart would be expected to have a stronger shell, one better suited to an environment in which physical stresses are greater. The habitat of *V. hyalina* at the edge of the continental shelf is more variable than that of the deep sea but is far less rigorous than that of intertidal or sublittoral zones. *Vema hyalina* has, however, the most fragile shell of any of the species. Its existence in a somewhat more variable environment seems to be at the cost of a major reduction in size.

Shell structure of *Vema hyalina* follows the basic neopilinid plan, summarized most recently by Meenakshi et al. (1970). Present are the periostracum, prismatic, and nacreous layers. The periostracum is extremely thin. The prismatic layer forms the major component of the shell, with the diameter and depth of the prisms nearly equal. In *Vema ewingi* (Figs. 12, 13) there are hexagonal prisms and also some prisms with a more elongate surface. The depth of the prisms in *V. ewingi* seems to be about twice the diameter at the surface of the regular hexagonal prisms. In *V. ewingi* there are also some prisms with surface area smaller than in the regular hexagons. Small prisms are not found in *V. hyalina*. These differences are regarded as more than specific differences between the two species of *Vema;* the differences are regarded as supraspecifically diagnostic of the subgenera *Vema* and *Laevipilina*.

The internal nacreous layer of neopilinids is very thin (Meenakshi et al. 1970:211) and this is also true for *V. hyalina*. Shells of *V. hyalina* show a pallial line corresponding to the position of the pallial fold of the mantle, inside of which the nacreous layer is thick enough to slightly obscure the pattern of prisms when viewed from within.

The early developmental stages in neopilinid monoplacophorans are largely unknown. Lemche and Wingstrand (1959:16, 64, figs. 34, 49) described and illustrated a coiled protoconch for *Neopilina galatheae*. No subsequent author has reported a coiled protoconch in other specimens of *N. galatheae* or any other species. Menzies (1968:7, figs. 8a–d) illustrated an unidentified juvenile *Neopilina* shell, showing a bulbous, transparent protoconch with an abrupt transition to the adjacent shell area, which is structured with prisms that are elongate on the surface. As discussed by Menzies, the loss of such a protoconch and subsequent repair to the area would produce a circular scar like that originally reported by Clarke and Menzies (1959: fig. 1d) at the apex of *V. ewingi*. The apical profile of *V. hyalina* (Fig. 10) is similar to that of the unidentified species illustrated by Menzies (1968: fig. 8c), and it is possible that the protoconch is missing and the area sealed over. However, in *V. hyalina* there is no sharp transition line between the apical tip and the area where prismatic structure begins; the prismatic structure becomes apparent, faintly at first, some distance away from the apex. It is to be hoped that future workers will investigate the early development of the species.

HABITAT AND ECOLOGY

The localities known for *Vema hyalina* are on the western edge of the "southern California continental borderland" (see Emery 1960). Unlike continental shelves in most other areas of the world, the submarine topography is complex, with high and low areas, and ridges and troughs running roughly parallel to the adjacent land mass and its mountain ranges. Some of the topographic highs form islands, others form shallow banks, and the lows form a number of deep, closed basins. Patterns of currents at the surface and at intermediate depths are complex. The localities known for *V. hyalina* are on the Santa Rosa-Cortes Ridge, a submarine range that includes Santa Rosa Island, Begg Rock, San Nicolas Island, Tanner Bank and Cortes Bank. East of the area is the San Nicolas Basin, to the south are the East and West Cortes Basins and to the west the Tanner Basin. Further to the west is another ridge of lesser elevation and beyond that is the Patton Escarpment, a steep mud slope that drops to abyssal depths.

Bottom temperatures at continental shelf depths in southern California vary but little throughout the year. Joseph L. Reid of the Scripps Institution of Oceanography informs me that at a depth of 400 m at positions near the type locality the estimated range of temperatures is 6.4° to 7.5° C, based on data of the California Cooperative Oceanic Fisheries Investigations, summarized in data reports from Scripps Institution. The shallowest of the original records for the species was 174 m. Temperatures at 200 m in southern California are in the vicinity of 8° to 9° C (Emery 1969: 98). The known bathymetric range for *Vema hyalina* is 174 to 388 m; bottom temperatures correspondingly range from a maximum of 9° to a low of 6.4° C.

It is unlikely that the species will be found at shallower depths, considering the extent to which sampling at shallow depths has been done in southern California. However, the lower limit of the bathymetric range is unknown; we may have sampled only the upper limits of the species' bathymetric range. The scarcity of rocky substrata at greater depths may well be the limiting factor.

There is considerable information available on the bottom conditions at the type locality. When the first two specimens from the type locality were collected on 1 May 1976 the station was sampled with a box core and the bottom was photographed just before the sample was taken (Fig. 16). Bottom conditions were recorded as follows: "Smooth bottom with pebbles and small rocks, sparse shell debris." The photograph shows small rocks somewhat obscured by fine sediment and some moderately large invertebrates, including the seastar *Rathbunaster californicus*, another seastar, the echinoid *Allocentrotus fragilis*, a gorgonian, a massive sponge, and brittle stars. Rocks from the station are of moderately hard shale and were partially encrusted with several different species of bryozoans. The chiton *Hanleyella oldroydi* was common.

The species composition is therefore diverse and includes molluscan predators such as seastars and muricid gastropods *(Boreotrophon* spp.) that bore through shells. *Vema hyalina* must have some methods enabling defense against predators, whether it be a rapid escape response as used by many shallowly occurring limpets, or seclusion in deep crevices. Study of living animals should answer these questions.

The histologic sectioning by Morse and Riser of one of the specimens showed the presence of diatom frustules and sponge spicules in the gut, suggesting that the species browses upon the detrital material that accumulates in crevices. For neopilinids from abyssal depths, Menzies et al. (1959:179) reported that: "A fecal pellet removed from the hindgut of a specimen of *Neopilina (Vema)* showed the presence of diatom frustules, radiolarian skeletons, pelagic foraminiferal tests and innumerable bacteria-size particles as well as sponge spicules. This evidence suggests that *Neopilina* is a mud-ingesting animal or at least an unselective detritus feeder." Thus the feeding habits of all modern neopilinids are probably similar. This is also suggested by the similarity of radular structure among the neopilinids, as discussed in

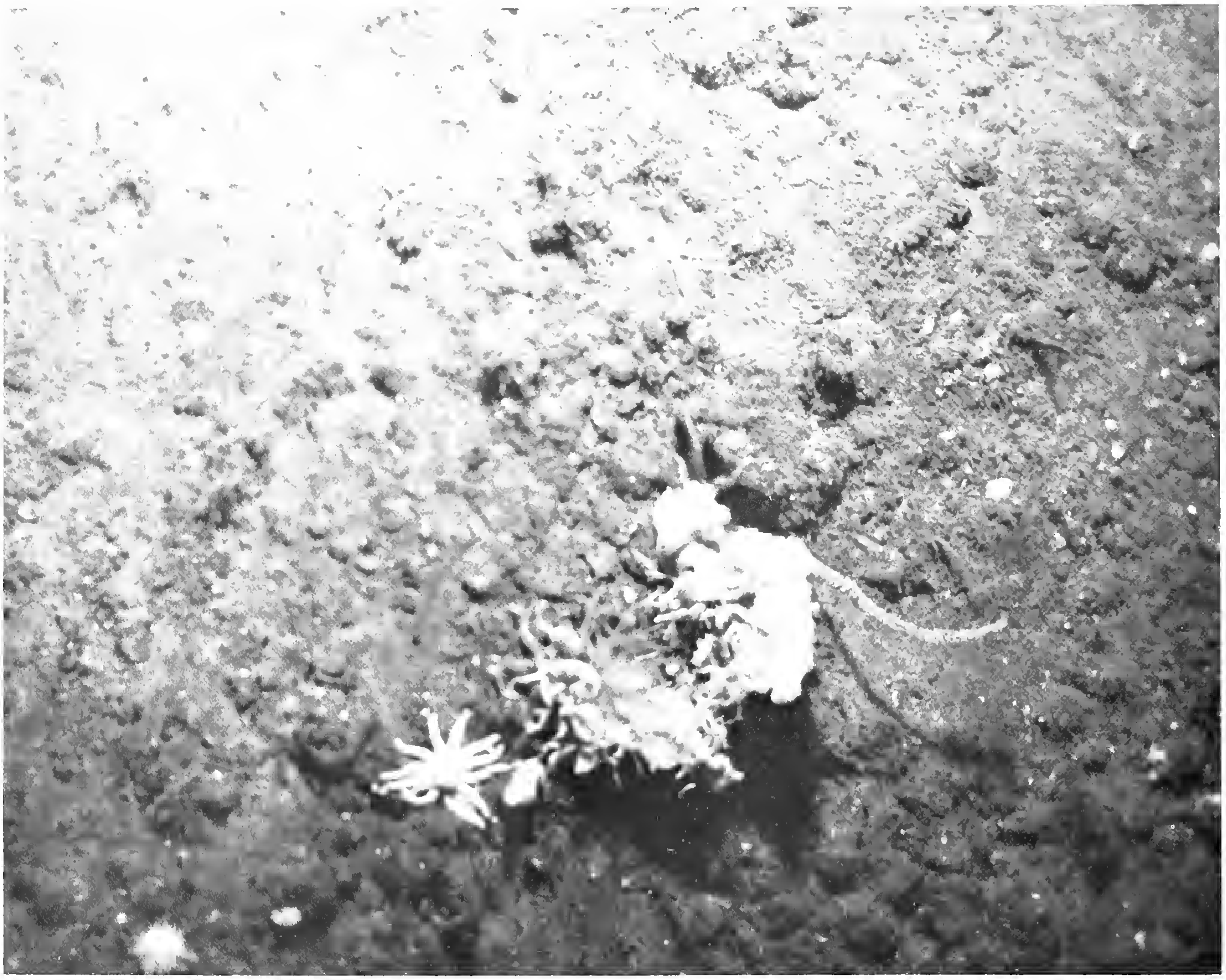


FIGURE 16. Bottom photograph near type locality taken just before sampling with box core. Depth 388 m, Santa Rosa-Cortes Ridge, California (32° 58.85′ N, 119° 33.05′ W), 1 May 1976, R/V VELERO IV sta. 24904, BLM sta. 569. Bottom consists of small rocks obscured by sediment. See text for description of the invertebrates pictured. Photograph courtesy of Gilbert F. Jones, BLM project.

detail below. The neopilinid radula has a feathery appearance, and is not sufficiently robust to enable feeding by rasping or piercing of prey organisms.

Vema hyalina is the first neopilinid definitely known to be associated with a hard substratum. The first described species of *Neopilina* and *Vema* were assumed to be free living on soft bottoms of ooze on the abyssal sea floor. No rocks or hard-surfaced objects were reported in dredge hauls. Menzies, Ewing, Worzel, and Clarke (1959) included bottom photographs of tracks presumed made by *Neopilina,* but this observation was later questioned by Wolff (1961), who suggested that the tracks were made by a bivalve. No photographs are yet available that actually reveal the life mode of any of the abyssal species of *Neopilina* or *Vema*.

Not until 1972 with the description of *N. oligotropa* was the availability of hard substratum documented along with the taking of a neopilinid. Rokop (1972) reported the presence of manganese nodules in the vicinity of *N. oligotropa* but had no evidence to suggest that the species was attached to the nodules. In 1974 Filatova et al. reported that their unidentified *Neopilina* from the Atlantic sector of the Antarctic came from a bottom of mud with sand and pebbles. They considered it a foregone conclusion that all *Neopilina* require a hard substratum: "The hard substratum to which *Neopilina* adheres (stones, manganese nodules or pebbles) is dispersed in good quantity in the Antarctic region by the action of floating ice."

Doubts about the habitat of the abyssally occurring species of *Neopilina* will persist until some way is found to photograph or observe living specimens. In view of the apparent absence of hard surfaces in the abyssal depths off Costa Rica (type locality of *N. galatheae*), in the Peru-Chile Trench (type localities of *V. ewingi, V. bacescui,* and *N. bruuni*) and in the Cedros Trench off Baja California, Mexico (type locality of *N. veleronis*), it seems to me that the weight of evidence would associate the abyssal species with soft bottoms.

Yet this remains an anomaly because all other limpets (gastropods of several families) are, without exception, attached to hard surfaces. However, the foot of *Neopilina* is somewhat unusual compared to that of gastropod limpets. Lemche and Wingstrand (1959:31) prefaced their detailed description of the foot of *N. galatheae* as follows:

> "The circular foot occupies the central parts of the ventral side of the animal. Being strongly contracted in the preserved specimens, its diameter is about half that of the shell. For descriptive purposes the foot is here regarded as the central body wall underlying the large peri-intestinal blood sinus. Its central part forms a circular membraneous disc, which, at places, is little more than 0.1 mm thick and therefore somewhat transparent even in the preserved material. The periphery of the foot is developed as a prominent muscular foot margin all round the organ."

Thus the foot of *Neopilina* is characterized by its small diameter, extremely thin sole, and highly muscularized margin. Lemche (1957) had originally postulated that *N. galatheae* lived upside down, but that idea was immediately challenged by Yonge (1957), who considered it possible that the foot could indeed be too weakly muscularized for creeping on a hard surface, but that it could prevent the animal from sinking into the bottom ooze. Clarke and Menzies (1959) reported that the original specimens of *V. ewingi* were coated with mucus on the ventral surface and this was considered to function as an aid to locomotion on soft bottoms.

Perhaps the forthcoming histological work with *V. hyalina* will yield some insight. If the foot of *V. hyalina* proves to be more highly muscularized than that of the other species, it will suggest that the other species are adapted for existence on soft bottoms, whereas *V. hyalina* is better adapted to adhere to rocks.

RADULAR COMPARISONS

The neopilinid radula has not been discussed since the original treatment by Lemche and Wingstrand (1959:27, fig. 88) of *Neopilina galatheae*. Subsequent authors have apparently been hesitant to sacrifice part of their material for whole-mount radular studies. The radula of *V. hyalina* differs considerably from that of *N. galatheae,* although the basic plan is similar. In order to make further comparisons I prepared slides from a single specimen of *V. ewingi* in the LACM collection and a paratype of *N. veleronis* from the Hancock Collection. Because of the scarcity of material of all species, I had had to base my observations on single specimens of each, using standard whole mounting methods. Future studies should use SEM with its much finer resolution and depth of field.

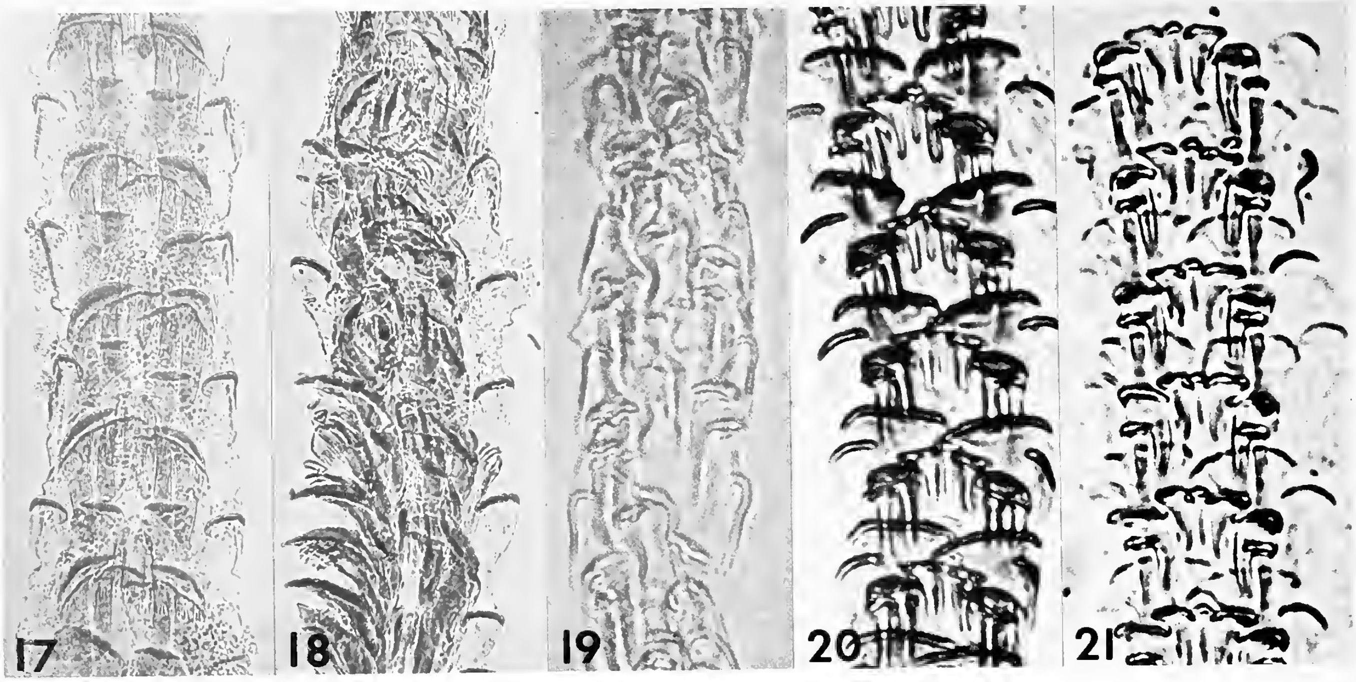
The neopilinid radula consists of a narrow rachidian and five pairs of additional teeth arranged in an inverted V-shaped row across the ribbon. Lemche and Wingstrand called all five pairs lateral teeth but gave no reasons for doing so. I regard the innermost three pairs as lateral teeth and the outer two pairs as marginal teeth for two reasons: (1) the fourth tooth, here called the first marginal, has a fringed edge unlike that of the preceding laterals; (2) the marginals did not stain as darkly as the laterals in my preparations using stained, non-resinous mounting medium, suggesting that the marginals differ from the laterals in thickness and composition.

Figure 25 herein is redrawn from Lemche and Wingstrand's illustration of the radula of *Neopilina galatheae.* The rachidian tooth is slender, with no overhanging cusp, resembling the reduced, vestigial central tooth of some Patellidae. The first lateral tooth is only slightly larger, and has a blunt, overhanging edge. The second lateral is longer and broader, with a broad overhanging edge; and the third is similar but placed considerably below the first. The next tooth, here called the first marginal, was described as a "membranous tooth" or "comb tooth," with its overhanging edge "slit up into some 40 long and curved denticles pointing aborally." The final tooth, here called the second marginal, is triangular and projects beyond the edge of the ribbon. It has a narrow, overhanging edge.

The radula of *Vema ewingi* (Figs. 17, 18, 23) differs from that of *N. galatheae* in minor ways. One portion of the ribbon (Fig. 17) was stained and mounted in non-resinous medium after slight treatment with NaOH in an effort to clean it. The teeth remained aligned as in figure 17. Further cleaning was attempted on another portion of the ribbon, but the teeth folded over in the resulting mount (Fig. 18), suggesting that the teeth are more delicate than those of various gastropod radular ribbons with which I am familiar. However, the latter preparation does show the teeth in side view. In *V. ewingi,* as in *N. galatheae,* the first lateral is small, although somewhat larger than the central tooth. The most significant difference is that the second lateral of *V. ewingi* extends well above the position of the first lateral, rather than to approximately the same level. The second and third laterals seem to be longer than those of *N. galatheae,* and show an overhanging tip when viewed in the aligned position, whereas in side view they are shown to be long and evenly curved (Fig. 18). It is possible that Lemche and Wingstrand missed the overhanging tip in their drawing of *N. galatheae;* the second and third lateral teeth might therefore be larger than they indicated. The fringed first marginal of *V. ewingi* resembles that of *N. galatheae* and the second marginal is similar, except that its outer edge is thicker.

I had difficulty interpreting the radula of the only small-sized species of *Neopilina* available, *N. veleronis,* because I was unable to mount in an aligned position any of five separate pieces of the ribbon. Here again, this may indicate that neopilinid radulae are more fragile than gastropod radulae of similar size. However, all of the teeth may be recognized in the portion photographed (Fig. 19), even though the rachidian and the fringed first marginal are not clearly shown. In *N. veleronis* (Fig. 24) the first lateral is more prominent than in either *N. galatheae* or *V. ewingi,* and extends slightly above the position of the rachidian. In addition, the fringed first marginal is broader than in either *N. galatheae* or *V. ewingi.* These differences place the radula of *N. veleronis* closer to that of *V. hyalina* than to that of the two relatively large-sized neopilinids. However, the second marginal is more than twice as long as that in any of the other species. *Neopilina veleronis* is unique among the species studied in the length of the second marginal.

A detailed description of the radula of *V. hyalina* is included in the species description above. The whole-mounted ribbon of the original specimen is shown in figure 20, focused on the shaft of the lateral teeth, and in figure 21, focused on the fringed edge of the first marginal. The teeth are drawn in figure 22. After the drawings were finished I received an SEM view of the radula in place within the mouth cavity (Fig. 8). The radula differs from that of both *N. galatheae* and *V. ewingi* in having the first lateral fully developed and about equal in size to the second lateral,



FIGURES 17–21. Neopilinid radular ribbons, magnifications adjusted to show a similar number of teeth rows. FIGURE 17, *Vema (Vema) ewingi*, intact ribbon with teeth aligned (LACM 65–11, 6200 m, 110 mi. W of Callao, Peru, R/V ANTON BRUUN, 24 November 1965). FIGURE 18, *Vema (Vema) ewingi*, another portion of same ribbon with lateral teeth turned to the side. FIGURE 19, *Neopilina veleronis*, intact ribbon of paratype, teeth not aligned (AHF 603, 2730–2769 m, 30 mi. W of Natividad Island, Baja California, Mexico). FIGURE 20, *Vema (Laevipilina) hyalina* new species, intact ribbon with teeth aligned, focused on shafts of lateral teeth (LACM 19148). FIGURE 21, *Vema (Laevipilina) hyalina*, same ribbon, focused on fringe of first marginal teeth.

instead of the highly reduced condition in these two species. Although the first lateral of *N. veleronis* is somewhat larger than it is in the other two species, that of *V. hyalina* is still the larger. The fringed first marginal of *V. hyalina* is much broader than in *N. veleronis*. Only in *V. hyalina* is the fringed tooth so broad that it overlaps the opposite member in the central part of the ribbon. The second and third laterals of *V. hyalina* are not significantly different from those of the other three species, whereas the second marginal is similar to those of *N. galatheae* and *V. ewingi*, but not the exceptionally long second marginal of *N. veleronis*.

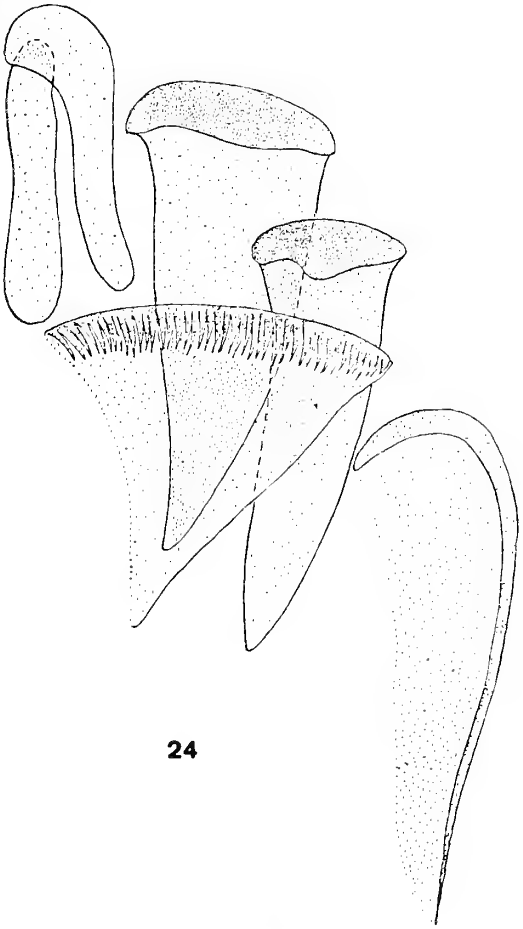
To summarize the radular differences noted among the four species: *Vema hyalina* exhibits major differences in two of the five teeth compared to the two rather similar species *N. galatheae* and *V. ewingi*, whereas the condition of these two teeth in *N. veleronis* is intermediate between these two species and *V. hyalina*. The radula of *N. veleronis* is unique in the extreme elongation of the second marginal.

The radular differences noted in the four species do not correlate with the existing generic division based on number of gill pairs, five in *Neopilina* and six in *Vema*. The only correlation is in size. Both large-sized species have similar teeth and the two small-sized species have similar teeth. Radular differences among the species examined are quantitative rather than qualitative, supporting placement of the four species in the same family. A study of the radulae of the other three living species of neopilinids should reveal further specific differences.

The radula of neopilinid monoplacophorans is very similar to that of chitons and patellacean limpets having the docoglossate radula. In the three groups the radula has in common: a reduced or absent rachidian; strong, hook-shaped lateral teeth; and few, weakly developed marginal teeth. Lemche and Wingstrand (1959) found major similarities in the radular supportive mechanism in *Neopilina* and chitons. Golikov and Starobogatov (1975) discusssed the similarities in form and function of the docoglossate radula with that of chitons and neopilinids.

The docoglossate radula has long been known to function in a way that differs from that of other gastropods. Fretter and Graham (1962:200) gave a detailed comparison of radular function in the two kinds of radulas. In the docoglossate radula there is no longitudinal bending; the entire ribbon works as a rasp with numerous rows functioning at once. In the rhipidoglossate and other non-docoglossate radulae, rows of teeth bend longitudinally

FIGURES 22–25. Radular dentition of neopilinids, drawn from slides photographed in figures 17–21. FIGURE 22, *Vema (Laevipilina) hyalina* new species. FIGURE 23, *V. (Vema) ewingi*. FIGURE 24, *Neopilina veleronis*. FIGURE 25, *N. galatheae*, after Lemche and Wingstrand, 1959. Teeth from left to right are the rachidian; first, second, and third laterals; fringed first marginal; and the outermost, second marginal. Drawings by Mary Butler.



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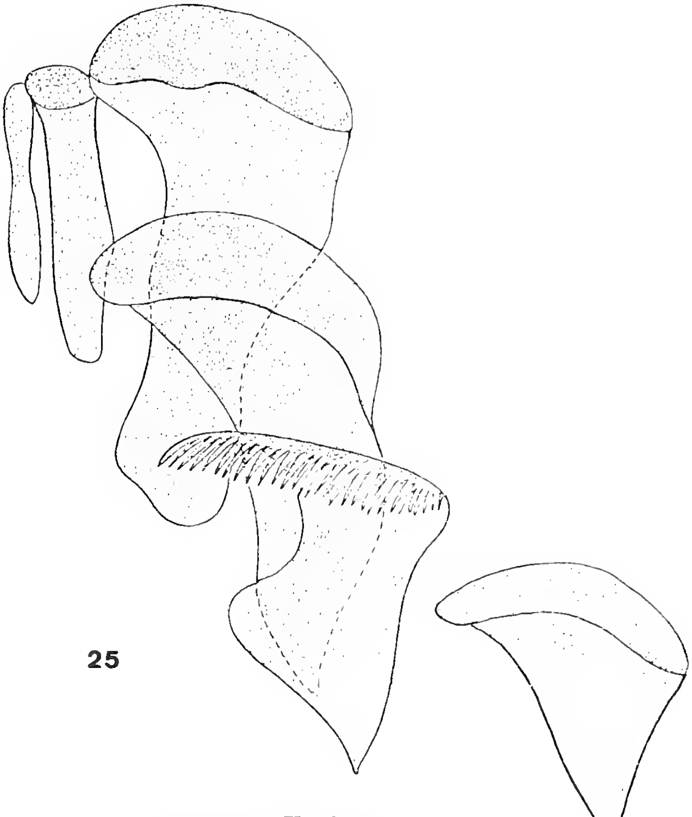

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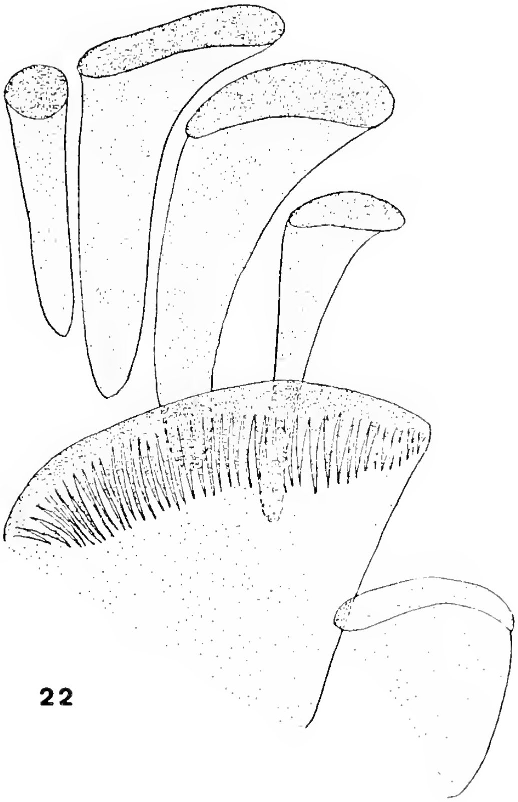

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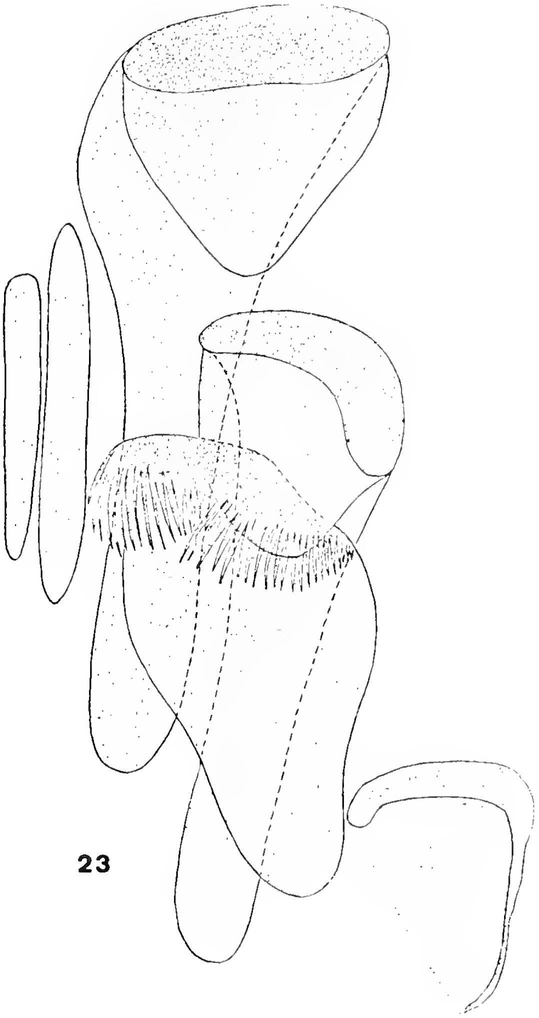

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and the teeth are most effective at the "bending plane."

Golikov and Starobogatov consider the rasp type of radula — for which a more technical term has not been proposed — as the most archaic in the Mollusca. Most other authors, such as Fretter and Graham (1962), consider the rhipidoglossate radula as the most primitive and the docoglossate radula derived from it in an as yet unexplained way. The matter remains controversial because there is no apparent affinity between these two kinds of gastropod radulae.

A comblike fringe, similar to that on the neopilinid first marginal tooth, occurs on the marginal teeth of some genera of the docoglossan limpet family Lepetidae. In the Neopilinidae the fringe is found only on the first marginal tooth, but in the Lepetidae the very similar appearing fringe is found on both pairs of marginal teeth. The origin and significance of these comblike teeth remains to be explained. Could the fringe be a clue to a more direct affinity between the Monoplacophora and the Docoglossa?

The Paleozoic monoplacophorans are found in shallow water deposits. They were probably grazing animals like modern patellacean limpets and chitons. The large and robust radular teeth in modern limpets and chitons are opaque and mineralized (Lowenstam 1967, 1971). The neopilinid radula is probably less robust than that of its fossil predecessors, but is probably similar to what was present in the extinct families of Monoplacophora. As in the chitons and docoglossan limpets, the neopilinid radula is large in proportion to body size. Its mineral content should be investigated.

The radula of the Polyplacophora, the chitons, is not especially diverse from family to family. I would expect Monoplacophora as a whole, to have had a diversity similar to that of the Polyplacophora, in which the level of organization is primitive, the family distinctions are not profound, and the species are relatively few in number.

ORIGINS

When the discovery of *Neopilina galatheae* was announced, who could have predicted that it represented but one of a small number of species of this relict group? Can it be that the *Laevipilina* branch in the Neopilinidae is represented elsewhere in the world? The possibility should be considered by those who have opportunity to dredge rocks at the edge of the continental shelf. The offshore fauna of southern California is one of the most often sampled and best known in the world. This discovery comes at a time when there are rather few new species being discovered in the area. Experienced collectors have no doubt had it on hand before, but have missed it. Many years may pass before the faunas of rocky bottoms on the outer continental shelves will be sufficiently known to answer the question.

Unfortunately, a fossil record of the abyssal fauna is not accessible. Many families of modern mollusks seem to have centers of origin in which extensive speciation has taken place. One might consider the eastern Pacific as the place of origin of the neopilinid stock, since most of the species and records are from that region. This might seem to be a foregone conclusion were it not for those species described from single records in the Indian Ocean and the mid-Pacific. The most likely explanation seems to be that accepted by most authors (e.g. Parker 1962) that the neopilinid line is a monoplacophoran offshoot that happened to invade the deep sea and has existed there in the absence of severe competition and predation since the Paleozoic. The shallow occurrence of *Vema (Laevipilina)* would thereby represent a reinvasion of the shallow water habitat from an abyssal stock.

Yet there is now an alternative theory: there is a possibility that the monoplacophorans have continued to survive at intermediate depths since the Paleozoic and that the deep-sea invasion is of relatively recent occurrence. The discovery of other monoplacophorans from intermediate depths would support this idea. However, the lack of eyes in *Vema (Laevipilina) hyalina,* a species that lives at a depth where considerable light is available, suggests that it is a derivative from forms existing in deep, lightless environments.

ACKNOWLEDGEMENTS

The original discovery of this remarkable new species was due to the combined efforts of Louis Zermatten, John E. Fitch and S. Stillman Berry, those who collected, found, and curated the specimens. I am especially grateful to Dr. Berry for enabling me to work with the material.

The second find of the species was a supplementary dividend from the project: Southern California Baseline Studies and Analysis (FY 1975–1976), under subcontract to Science Applications, Inc., La Jolla, California (funded by the Bureau of Land Management, U. S. Department of the Interior). I am grateful to Gilbert F. Jones of the University of Southern California and the project staff, especially Patrick I. LaFollette, for the efforts that eventually produced the specimens.

I thank Heinz A. Lowenstam of the California Institute of Technology, Pasadena, California, for the donation of four specimens in the type series. He, along with my assistant Patrick I. LaFollette, returned to the BLM locality on the R/V VELERO IV and collected living specimens.

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Photographs are largely the work of Bertram C. Draper, Museum Associate, with several others by Armando Solis, Museum Photographer. Radular slides were prepared and photographed by Jo-Carol Ramsaran, Museum Volunteer, and drawn by Mary Butler, Museum Illustrator.

NOTES ADDED IN PROOF: 1) An account of the role of N.H. Odhner in introducing the name Monoplacophora was provided by that author (Odhner 1961). 2) In a paper just received Lowenstam (1978) has described the behavior and illustrated a living specimen of *Vema hyalina,* which he referred to as "McLean's *Vema* sp." 3) Recent efforts to find rocky bottom at the two positions mentioned for the original specimens from the Berry Collection have not been successful.

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A NEW SALAMANDER, GENUS *BATRACHOSEPS*, FROM THE INYO MOUNTAINS OF CALIFORNIA, WITH A DISCUSSION OF RELATIONSHIPS IN THE GENUS

By Ronald William Marlow, John M. Brode, and David B. Wake

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Edward Ostermeyer
Editor

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The *Science Bulletin* and *Contributions in Science* of the Natural History Museum of Los Angeles County were merged into a single imperial octavo serial, retaining the name *Contributions in Science* and beginning with Number 301.

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Since most institutions rebind *Contributions in Science* collectively into hardbound volumes, and many researchers using them desire to photocopy material, two new features have been incorporated into the new format. A suggested citation line provides the abbreviated serial title, year, number of publication, and total pagination, and appears in the lower left corner of each page; and pages of *Contributions in Science* have been printed off-center to provide a two-inch gutter between adjacent pages for easier accessibility in photocopying.

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Contributions in Science are articles in the earth and life sciences, presenting results of original research in Natural History. *Science Bulletin* (Numbers 1–30; 28 June 1965 to 10 April 1978) and *Contributions in Science* (Numbers 1–300; 23 January 1957 to 16 June 1978) were merged into a single imperial octavo serial beginning with Number 301.

A NEW SALAMANDER, GENUS *BATRACHOSEPS*, FROM THE INYO MOUNTAINS OF CALIFORNIA, WITH A DISCUSSION OF RELATIONSHIPS IN THE GENUS[1]

By Ronald William Marlow,[2] John M. Brode,[3] and David B. Wake [2, 4]

ABSTRACT: A newly discovered species of plethodontid salamander from the Inyo Mountains in the northern Mojave Desert, California, is described as *Batrachoseps campi*. This new species helps bridge the gap between *Batrachoseps* and members of the tropical supergenus *Bolitoglossa*, and may well be the most generalized of all bolitoglossine salamanders. *Batrachoseps campi* and *B. aridus* are the only plethodontid salamanders known to be restricted to localized mesic microhabitats surrounded by desert. The new species is very generalized in morphology. In some respects it resembles *B. wrighti* of Oregon, but it also shares some features with *B. aridus*. On the basis of its distinctive morphology and distribution, *B. campi* is thought to be a survivor of an early stage in the evolution of the genus. The Inyo Mountains region may have served as the habitat of the species throughout much of the Tertiary. Recommendations are made for preservation of the fragile habitats in which the species lives.

In 1970 Brame described the first terrestrial salamander endemic to desert habitats. *Batrachoseps aridus* occurs in a highly restricted, mesic microhabitat in the desert of southern California. We now announce the discovery of a second species of lungless salamanders, family Plethodontidae, known from desert regions. The new species was discovered in the fall of 1973 in two canyons along the west slope of the Inyo Mountains at the northern edge of the Mojave Desert near the Owens Valley, California. This strikingly distinct form is so different from other *Batrachoseps* in its robustness and coloration that we initially thought it to be a species of *Hydromantes*, or even of a new genus. Upon further examination it proved to be a structurally generalized member of the genus *Batrachoseps*, very similar to a postulated ancestor of the entire genus and not much removed from the ancestral stock of the tribe Bolitoglossini (including *Hydromantes* and all of the neotropical plethodontid salamanders, in addition to *Batrachoseps*). Like *B. aridus*, the species seems to occur only in restricted, mesic microhabitats in a setting that is seemingly harsh and inhospitable for salamanders. Yet, the apparent absence of any populations even remotely similar to this species in areas more favorable for salamanders suggests that the Inyo Mountains have long been the home of the species. These mountains are relatively ancient, and in fact may represent remnants of the original crest of the Sierra Nevada before the modern mountains were uplifted to the west (Bateman and Wahrhaftig 1966). Possibly these salamanders have been in the Inyo Mountains throughout Cenozoic times.

The new species is named in honor of the late Charles L. Camp, herpetologist, paleontologist, and historian, who contributed greatly to our knowledge of the American West. Professor Camp discovered the genus *Hydromantes* in the New World, described *H. platycephalus*, participated in the discovery and description of *H. shastae*, and very early recognized the diversification within the genus *Batrachoseps* in his description of *B. major*. The species shall be known as:

Batrachoseps campi NEW SPECIES

Figures 1, 6, 7, 8, 11

Suggested common name: Inyo Mountains Salamander.

HOLOTYPE: MVZ 122993, an adult female from Long John Canyon, W slope of the Inyo Mountains, elevation 1695 m (5560 ft), 3.2 km (2 mi) (airline) N, 5.3 km (3.3 mi) E Lone Pine, Inyo County, California, USA; collected by John M. Brode and Ronald William Marlow on September 26, 1973.

PARATYPES: MVZ 122994–122996 (3 specimens), same data as the holotype; MVZ 123011–123015 (5 specimens), same locality as holotype, collected October 20, 1973; MVZ 122997 – 123009, 123017 – 123031 (28 specimens), LACM 122004 – 122011 (8 specimens), French Spring, W slope of the Inyo Mountains, elevation 1829 m (6000 ft), 6.4 km (4 mi) N, 5.7 km (3.6 mi) E Lone Pine, Inyo County, California.

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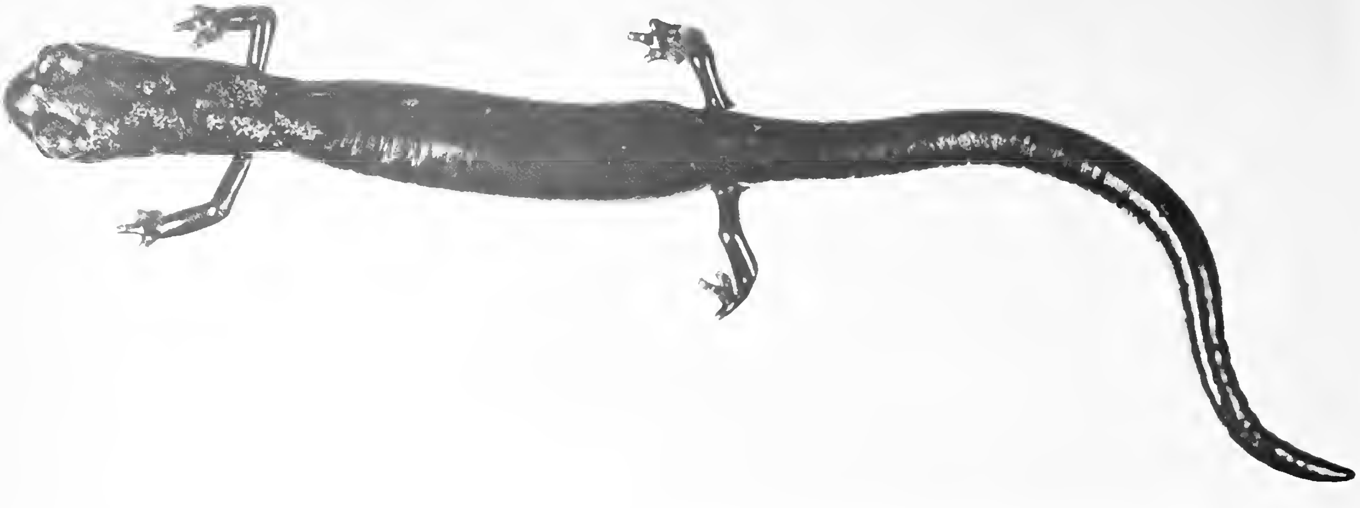

FIGURE 1. *Batrachoseps campi* (MVZ 123023), an adult female (40.4 SL) from Long John Canyon, Inyo Mountains, Inyo County, California. Photograph by James Hendel, Scientific Photography Laboratory, University of California, Berkeley. Scale is 25 mm.

DIAGNOSIS: A large, robust species of *Batrachoseps* (individuals identifiable to sex, 16 males: 41.3–53.3, mean 45.3 SL[5]; 23 females: 32.0–60.7, mean 45.5 SL) with a short tail, broad head and large feet; distinguished from all members of the genus by these characters and by its distinctive coloration (dark brown-black ground color with moderate to large patches of light gray iridophores on upper eyelids and irregularly spread over head and anterior part of trunk, and lacking a dorsal stripe or band that is lighter than the ground color); distinguished from *B. aridus* by its much larger size (largest known *B. aridus* are less than 40 mm SL), relatively shorter tail, and fewer vertebrae (19–20 versus 17–19); further distinguished from species which approach it in adult size by its much broader head, fewer trunk vertebrae (except *B. wrighti*) and much shorter tail. *Batrachoseps campi* is the only member of the genus that has paired prefrontal bones and divided premaxillary bones from early juvenile stages throughout adult life.

DESCRIPTION: *Batrachoseps campi* is the most generalized member of the genus in its morphology. The species is relatively large and has a large, broadly rounded snout. Nostrils are small and typical of the genus. There are no protuberances associated with the distinct nasolabial grooves. No mental hedonic glands have been observed in males. The head is very broad (SL 6.6–7.1, mean 6.8 times head width in 6 males and 6.3–7.5, mean 7.0 in females over 45 SL). Grooving patterns of head, throat and neck are typical of the genus. Eyes are relatively large and moderately protuberant. Vomerine teeth are borne in long series (mean total 16.5); frequently the teeth extend nearly to the lateral edge of the internal nares. Small maxillary teeth extend beyond the center of the eyeball; they increase in number with increasing size and are relatively numerous (mean total 46). Premaxillary teeth are small and numerous (8–10 in adult males; 6–17 in adult females); they are in an advanced position in the males, but barely protrude through the lip. Costal grooves between appressed limbs (counting one each in axilla and groin) range from 16–18 with a strong mode of 17. The tail is short for this genus and tapered; tail length in 20 adults over 45 SL is 0.62–0.88, mean 0.76 (± 0.06) times SL, with no discernible sexual dimorphism. The tail has no basal constriction, and is nearly round. However, an irregular row of enlarged glands is present on the dorsal surface of the tail. These glands form pustule-like protuberances that are more lightly colored than surrounding surfaces. The postiliac gland is a small, grayish spot that is not conspicuous. Limbs are long for the genus, and leave from 2–5 intercostal folds uncovered when appressed (mean 3.66 ± 0.89; n = 47). Standard length ranges from 4.2–5.3 (mean 4.8 ± 0.3) times hind limb length in 16 females, and from 4.5–5.1 (mean 4.8 ± 0.25) in males. The hands and feet are large for this genus. Webbing is insignificant, and the four fingers and four toes are all discrete. The third digit of both manus and pes is far longer than the others. All digits have bulbous tips and large subdigital pads. Fingers in order of decreasing length: 3, 2, 4, 1; toes in order of decreasing length: 3, 2, 4, 1.

MEASUREMENTS (OF HOLOTYPE): Head width, 8.4; snout to gular fold (head length), 12.8; head depth at posterior angle of jaw, 2.9; eyelid length, 3.3; eyelid width, 2.0; anterior rim of orbit to snout, 1.7; horizontal orbital diameter, 1.9; interorbital distance, 3.8; distance between vomerine teeth and paraspheroid tooth patch, 0.2; snout to fore limb, 5.7; distance separating internal nares, 2.4; distance separating external nares, 2.6; snout projection beyond mandible, 0.9; snout to posterior angle of vent (standard length), 60.7; snout to anterior angle of vent, 56.1; axilla to groin length, 32.5; tail length, 48.5; tail width at base, 4.3; tail depth at base, 3.7; fore limb length, 11.1; hind limb length, 12.1; width of right hand, 3.4; width of right foot, 4.0.

COLORATION: This is a dark salamander that differs from all other *Batrachoseps* in lacking a dorsal stripe at all ages. The ground color is very dark brown-black in most individuals, but a lighter brown-black in some. This is the result of a dense network of melanophores, covering the whole body with few or no gaps. The only additional color is a scattering of silvery iridophores which when grouped together form patches with a slightly greenish hue. Patches of iridophores are concentrated on the upper

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[5] SL = standard length, the distance from the snout to the posterior angle of the vent; all measurements in this paper are in millimeters, unless stated otherwise.

FIGURE 2. Type locality of *Batrachoseps campi*, Long John Canyon, Inyo Mountains, Inyo County, California. Camera is aimed southeast. Salamanders were found inside the mouth of the canyon, under surface objects in the shaded area.

eyelids of most individuals, and in a series of spots of varying size lying mainly on the posterior part of the head, the neck, and the dorsum in the vicinity of the insertion of the hind limbs. Elsewhere, including the nearly immaculate venter, the iridophores are scarce and small. These cells fade and disappear after a short time in alcohol. The dorsal glands of the tail are prominent near the tail base in many of the individuals. They appear to be brown-tan in color, the result of a thinning of the ground color. The iris is dark and featureless.

REMARKS: There is little sexual dimorphism in this species. Mean SL of males and females in the sample is similar, but females appear to reach larger sizes than males. Females have vertically folded vent margins, whereas males have dense, short papillae in the anterior half of the vent.

Some large females in the sample have enlarged, yellow ovarian eggs. Testes of most adult males are large and unpigmented. Vasa deferentia are heavily pigmented in most adult males. The two largest males (50.4, 53.3) have bilobed testes. The smallest male with bilobed testes is 45.0 SL, and the largest male with unilobed testes is 47.4 SL. Males 43.3 and 49.0 SL have a second lobe forming, and a male 48.6 SL has two lobes.

When uncovered, individuals of *B. campi* displayed no special defensive behavior of the kind observed in other species of the genus (Stebbins and Lowe, 1947; Brame, Long, and Chiri, 1973). Apparently immobility is the sole defensive behavior.

HABITAT: The western slopes of the Inyo Mountains receive approximately 22 cm of precipitation each year, much of it coming in snowfall. Vegetation on the slopes is sparse and stunted with extensive areas of open, rocky substrate. Long John Canyon is narrow and winding with rock walls rising almost vertically for about 150 m. At the type locality the canyon axis is east-west and the canyon floor is about 10 m wide (Fig. 2). The floor of the canyon is strewn with boulders and flood-carried rubble. A permanent spring at the type locality provides enough moisture for a dense, nearly impenetrable growth of woody shrubs (average height about 2 m) filling the canyon floor and extending approximately 100 m. This appears to be the extent of the available surface habitat, though crevices and subterranean water courses may provide extensive underground habitat.

Salamanders were found under rocks in fine, dark soil (a sandy loam) that was wet enough that a cast formed in the hand withstood taps with the finger. As many as four animals were taken under a single large rock (25 x 40 cm). This is a heavily shaded canyon. On October 20 the sun shone on the canyon bottom at 10:30, but by noon the canyon was entirely shaded.

The flora of the canyon floor is dominated by dense stands of *Salix* sp., *Forestiera neomexicana* and *Rosa Woodsii*. Also present were *Erodium* sp., *Artemisia Dracunculus*, *A. ludoviciana*, *Clematis ligusticifolia*, *Aquilegia formosa*, *Gutierrezia microcephala*, *Philadelphus microphyllus*, *Chrysothamnus teretifolius*

Table 1. Classification matrix based on discriminant analysis of 229 specimens of nine species of *Batrachoseps*, including juveniles and adults of both sexes. Entries along the main diagonal are "correct" matches of individuals to their source populations based on twelve morphological characters.

	Number of Individuals Classified into Group							
Group	1	2	3	4	5	6	8	9
1 *aridus*	13	0	0	0	0	0	0	1
2 *stebbinsi*	0	29	1	0	0	0	0	0
3 *simatus*	0	3	23	0	2	0	0	1
4 *attenuatus*	0	0	0	27	3	0	0	0
5 *major*	0	0	1	1	26	0	0	2
6 *campi*	0	0	0	0	0	46	0	0
8 *wrighti*	1	1	0	0	0	0	18	0
9 *pacificus*	0	1	0	0	0	0	0	29

and *Haplopappus cuneatus*.

The second locality, French Spring, is 6.4 km (4 mi) (airline) north and 5.7 km (3.6 mi) (airline) east of Lone Pine, Inyo Co., California, at an elevation of about 1800 m. The water flow of this spring is much more extensive than in Long John Canyon. The flow from the spring cascades down approximately 300 m of naturally terraced rocky hillside and approximately 300 m of canyon floor, before disappearing in the sand. Vegetation is similar to that at the type locality (Fig. 3).

COMPARISONS: Both bivariate and multivariate morphometric analyses have been used to compare *B. campi* with other described species of *Batrachoseps*. For these comparisons the following juvenile and adult specimens were used (all deposited in LACM and MVZ, catalogue numbers and measurements on file at MVZ): 14 *B. aridus* (type locality); 30 *B. stebbinsi* (type series); 29 *B. simatus* (type series); 30 *B. attenuatus* (San Francisco, Calif.); 30 *B. major* (vicinity of Los Angeles, Calif); 46 *B. campi* (type series); 20 *B. wrighti* (central Oregon); 30 *B. pacificus* (Santa Cruz Island). Only *B. relictus*, a highly variable species currently under study by Kay Yanev, was omitted. The latter species is small and slender, and is most similar in morphology to *B. attenuatus*. Data for the following characters were used: SL, head width, hind limb length, front limb length, limb interval, total maxillary teeth, total vomerine teeth, tail length, front foot width, hind foot width, head length, number of trunk vertebrae. Bivariate plots of head width, limb length and foot width against standard length were produced for comparison with the results of Brame and Murray (1968), and tooth number and tail length were also plotted against standard length. The results of the bivariate analysis indicated that most characters distinguish *B. campi* from some other species and some characters (head width, Fig. 4) distinguish *B. campi* from nearly all other *Batrachoseps* (compare with Fig. 9, Brame and Murray 1968). The species differ greatly in adult size, thus making direct comparison of individual features and even bivariate analysis difficult. However, the species of *Batrachoseps* are readily distinguished by combinations of three characters or more, and we believe multivariate discrimination is the method of choice. Canonical variate analysis was chosen to discriminate between the species. In particular, we wished to determine how distinct *B. campi* was relative to species it resembled most closely, based on bivariate analysis. The University of California, Berkeley, version of the BMD07M program for stepwise discriminate analysis was used (see Lynch and Wake 1975, for description).

The main result of the discriminate analysis is the demonstration of the distinctiveness of *B. campi* relative to other species of *Batrachoseps*. Even among the remaining species of the genus there is a moderate amount of discrimination, but we emphasize that we are not considering geographic variation here. A feature of the program used is a classification matrix which gives the number of "correct" and "incorrect" assignments of individuals to their proper populations on the basis of morphological criteria alone (see Lynch and Wake 1975). The classification matrix (Table 1) assigned all 46 specimens of *B. campi* to the correct population on morphological grounds. There are from one *(B. pacificus, B. aridus, B. wrighti)* to six *(B. simatus)* mis-classifications in the other species, but overall 92 per cent of the classifications are correct. The first three canonical variables account for 93 per cent of the observed interspecific variance. The first two canonical axes are illustrated in Figure 5.

Along the first axis (accounting for 69 per cent of the interspecific variance) species are separated mainly by factors related to size (standard length, head width). Limb interval and tail length also contribute importantly. *B. campi* is well separated from all other species. *B. aridus, B. stebbinsi, B. wrighti* and *B. pacificus* are relatively close to *B. campi* along this axis; *B. attenuatus, B. major*, and *B. simatus* are relatively remote.

The second axis (accounting for 16 per cent of the total interspecific variance) separates *B. wrighti* from all other species, but seems to add little to discrimination among remaining species. Based on the magnitude of standardized coefficients of the canonical variables, head width, numbers of trunk vertebrae and foot width contribute most to discrimination along this axis.

The third axis accounts for only about 8 per cent of the total interspecific variance. It allows separation of *B. stebbinsi* and *B. simatus* from all other species, with *B. aridus* being on the extreme end of the axis from *B. stebbinsi*. Other axes contribute little additional discrimination.

COMPARATIVE OSTEOLOGY: Osteological comparisons to other *Batrachoseps* are based on study of an adult female (49.4 SL) and a juvenile female (37.6 SL) of *B. campi*. These were cleared and stained using standard techniques. Radiographs of the type series and both cleared and stained specimens and radiographs of all other species of the genus were utilized.

Batrachoseps campi is similar to other species of *Batrachoseps* in some features of skull structure, but it is highly distinctive in others. The skull of *B. campi* is typical of the genus in proportions (Fig. 6). The characteristic dorsal fontanelle between the paired frontals and parietals is especially prominent. The fontanelle is proportionately of similar size in all species of *Batra-*

choseps, with a slightly smaller fontanelle in *B. wrighti* than in other species. Only *Batrachoseps* among all genera of salamanders has a fontanelle of this shape. In all *Batrachoseps* the skull is relatively short and broad; total skull width is 70 to 75 per cent of skull length, and *B. campi* falls about in the middle of the range of measurements.

The relatively short maxillary bones seen in *B. campi* are widespread in *Batrachoseps*. Characteristically the frontals are narrowed, appearing "pinched" between the orbits, and this is seen in *B. campi*. In all species the skull is lightly built and rather weakly articulated. However, *B. campi* has notably stronger and more extensive cranial articulations than other species.

Premaxillary bones of *B. campi* are separated in both juvenile and adult specimens. In most of the radiographed individuals, including juveniles, the divided premaxillaries can be seen clearly. In some individuals the appropriate region of the skull is obscure on the radiographs. Divided premaxillary bones are found elsewhere in the genus only in large adult *B. wrighti* (Bishop 1937, Stebbins and Lowe 1949, Wake 1966). Smaller *B. campi* than those available to us (28.5 SL) probably have a single premaxillary bone, the typical plethodontid situation; fused larval and juvenile premaxillaries separate at metamorphosis or early in life in the primitive plethodontid condition, but remain fused in a variety of derived conditions (Wake 1966).

In *B. pacificus*, *B. simatus*, *B. stebbinsi*, *B. major*, *B. aridus* and some populations of *B. attenuatus* and *B. relictus*, the frontal processes of the premaxillary arise separately, then fuse for a distance before again separating near their tips. We see no evidence of such fusion in either *B. wrighti* or *B. campi*. The posterior tips of the frontal processes diverge greatly in *B. campi*, to a lesser degree in *B. wrighti* and only slightly in other species. As in all species of *Batrachoseps* the premaxillaries of males are larger and more protuberant than those of females, but sexual dimorphism is apparently less marked than in such species as *B. pacificus* and *B. major*, and probably less than in the other species as well.

The maxillary bones are not well articulated with other bones in *Batrachoseps*, but in *B. campi* the elements are relatively stouter than in any other species of the genus. The facial lobe of the maxillary in *B. campi* is relatively large, equalling the proportions in such large species as *B. pacificus*. Palatal portions of the maxillaries are very small. The large nasal bones are the dominant facial elements. They have a narrow spinous projection paralleling the frontal processes of the premaxillaries in *B. campi* and in other *Batrachoseps*, but these are especially pronounced in *B. campi*. Rather well developed septomaxillaries are present in all species of *Batrachoseps*.

Prefrontal bones have previously been reported only in *B. wrighti*, in which individuals over 45 mm body size have very tiny but discrete elements (Wake 1966). Well developed prefrontals are present in both the juvenile and adult *B. campi*, and, while the radiographs are not suitable for finding these elements in all instances, they can be seen in a number of the X-rayed specimens. The bones are about the size of the facial lobes of the maxillaries and are distinctly larger than the septomaxillaries. In contrast, the prefrontals which develop in large *B. wrighti* remain much smaller than the septomaxillaries.

Preorbital processes of the vomers are typically absent in *Batrachoseps*. In *B. campi* small processes that extend to the lateral margin of the internal nares (adult) or to the center of the nares (juvenile) are evident. These tooth-bearing processes are prominent in the radiographs. In other species of *Batrachoseps* the

FIGURE 3. French Spring, Inyo Mountains, Inyo County, California. Camera is aimed southeast. Salamanders were found under rocks along the stream course in the center of the photograph.

Table 2. Quantitative characteristics of the chromosomes of *Batrachoseps campi* based on haploid set of Figure 12.

Chromosome No.	Relative length[a]	Arm ratio[b]	Centromere index[c]
1	11.0	1.05	49
2	10.0	1.28	44
3	9.8	1.05	49
4	9.0	1.21	45
5	8.8	1.10	48
6	8.4	3.35	23
7	7.8	1.00	50
8	7.1	1.04	49
9	6.0	1.38	42
10	6.0	1.06	48
11	5.8	1.31	43
12	5.7	1.14	47
13	4.8	2.13	32

[a] Length of chromosome/total length of haploid genome x 100.

[b] Length of long arm/length of short arm.

[c] Length of short arm x 100/length of whole chromosome.

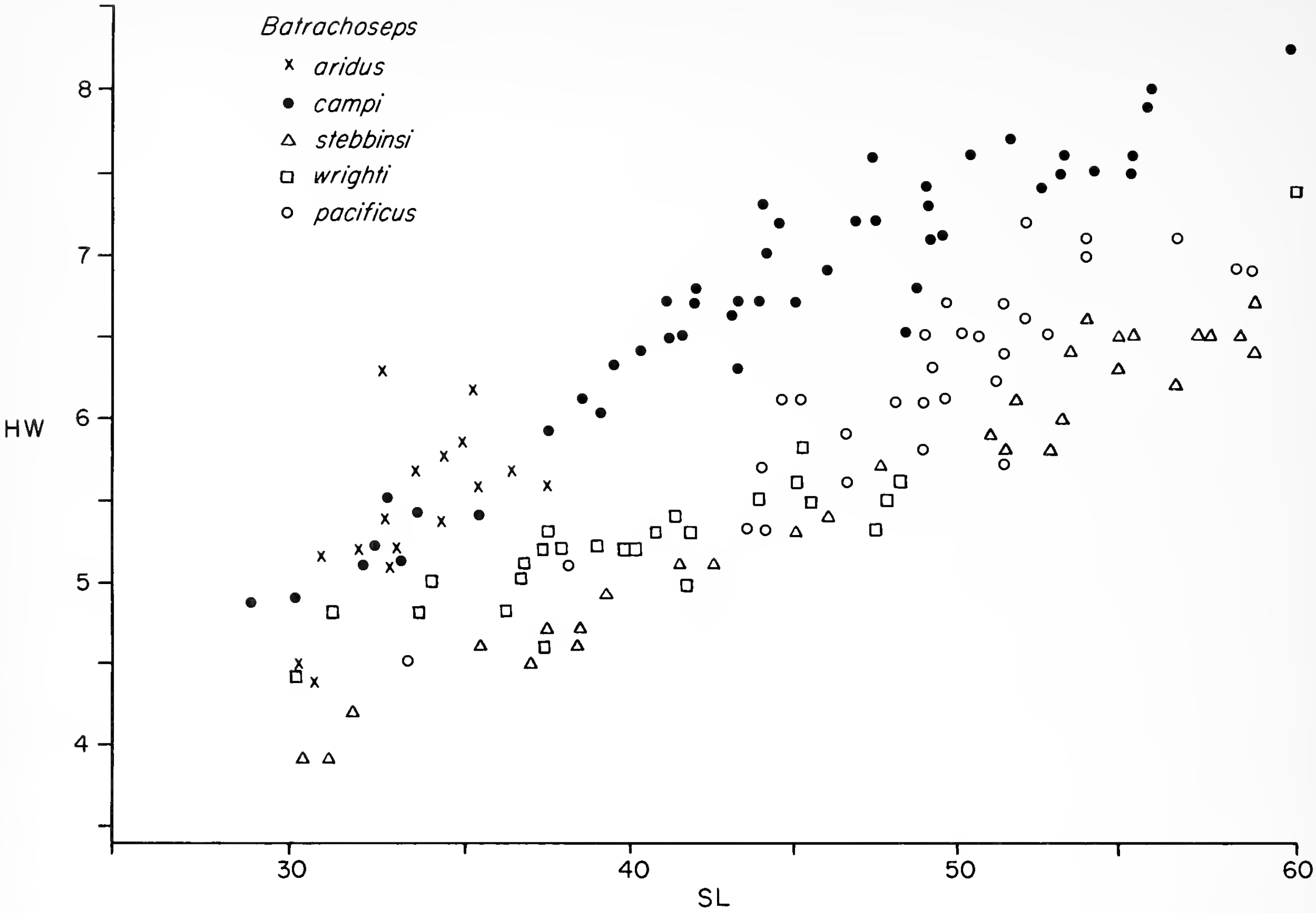


FIGURE 4. Relation of head width to standard length in the five species of *Batrachoseps* having the broadest heads in the genus.

processes are usually mere suggestions of bone growth behind the nares (Fig. 7), but there are two exceptions. In a radiograph of one very large *B. wrighti* (reported by Brame 1964) a small process is clearly evident, and very small processes are evident in a radiograph of one adult *B. aridus*.

The nasolacrimal duct extends anteroventrally from the corner of the eye to the cartilaginous nasal capsule. The opening in the nasal capsule lies in the gap between the facial process of the maxillary and the nasal. Typically, slight evacuations in the lateral margins of the nasals, or more rarely in the anterodorsal margin of the maxillary, mark the route of the duct in species of *Batrachoseps*. In *B. campi* the duct produces slight dorsal concavities in the anterior part of the prefrontals as well.

Frontal bones in *Batrachoseps* contribute importantly to the facial part of the skull, especially by means of a long attenuated process that extends anteriorly below the frontal processes of the premaxillary. In *B. campi* the facial portion of the frontal is relatively less developed than in other species and there is no spinous process. Further, only the tips of the premaxillaries overlap the frontals. In other respects, the frontals in *B. campi* are similar to those in other *Batrachoseps*, with the characteristic posterior divergence of the bones. *B. wrighti* has relatively the widest frontals. Frontals are about one-half the total skull length in *B. campi, B. wrighti* and *B. pacificus*, but on the order of two-thirds the total skull length in *B. stebbinsi, B. aridus*, and the other species.

All species have small parietal bones, with no clear differentiation among the species in terms of relative size. The bones usually fall short of the narrow occipital bridge portion of the skull. In all species a well defined lateral spur is present on the parietal (see Wake 1966), and it is particularly stout in *B. campi*.

Squamosal and quadrate bones are small and have no special features in any single species. Dentaries are slender and similar in structure in all species. Prearticulars have low coronoid processes. All species have columellar processes extending from the opercular plate. These processes are well developed in *B. campi*.

Teeth of *Batrachoseps* typically occur on premaxillary, maxillary, dentary, and vomerine elements, and in addition there is a paired patch of teeth along the parasphenoid. The patches vary greatly within and between species in size and number of teeth.

The hyobranchial apparatus is typical of the genus *Batrachoseps* in all important respects (see Lombard and Wake 1977) including the long, recurved radii, the absence of a lingual cartilage, the basibranchial of relatively uniform width, and the relatively long epibranchial. The genioglossal muscles are slender and elongate. These muscles have a unique arrangement in *Batrachoseps*, originating from the mandible near the jaw articulation and proceeding well forward before extending to the midline

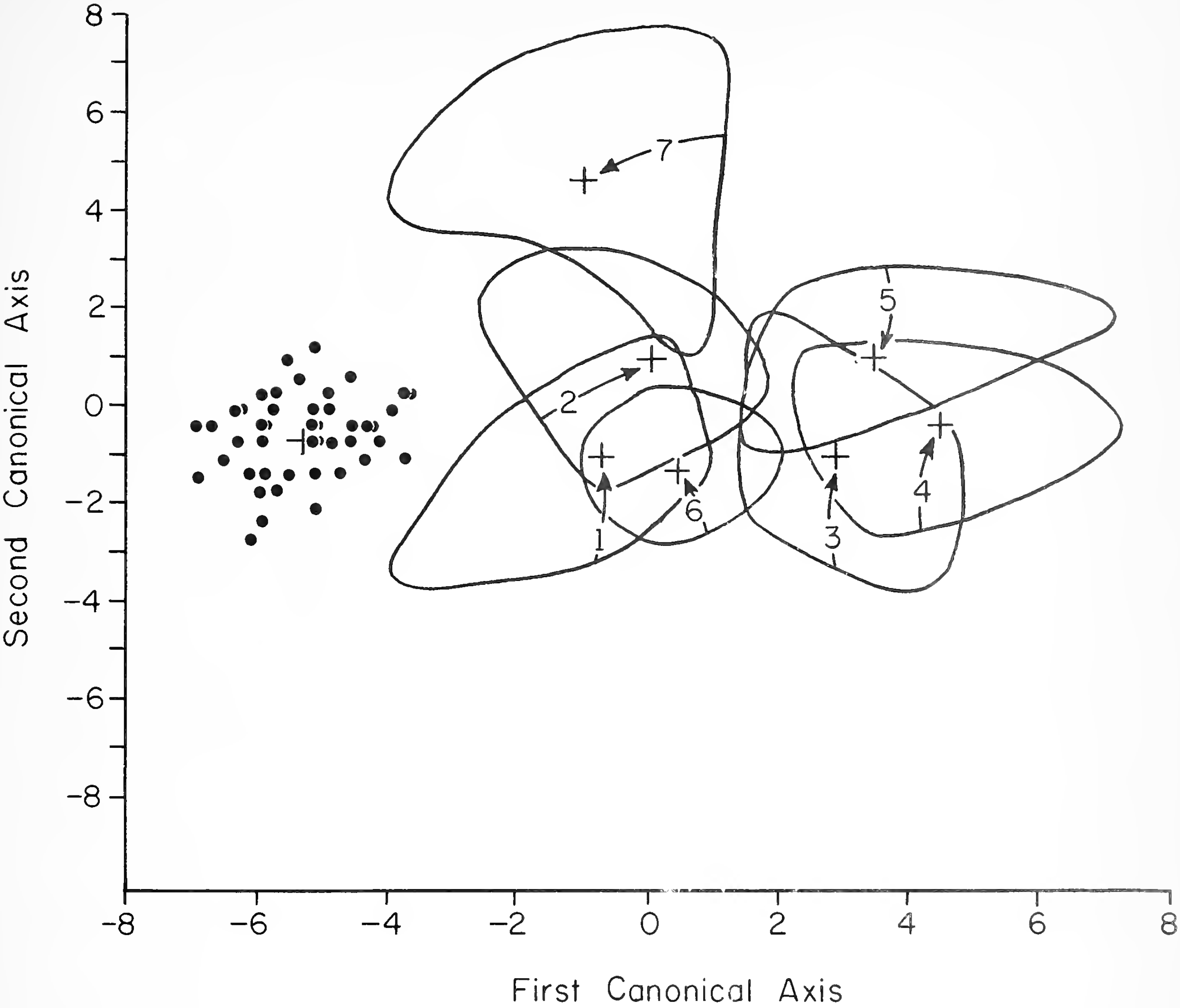


FIGURE 5. Plot of first two canonical variates for adults of eight species of *Batrachoseps*. The discriminant analysis includes 12 morphological variables. The first variate (abscissa) accounts for 69 per cent of the observed interspecific variance. The cross marks the centroid for each species. All individuals for each species are enclosed within the indicated perimeter except for *B. campi*, where all individuals are spotted. 1. *B. aridus*, 2. *B. stebbinsi*, 3. *B. simatus*, 4. *B. attenuatus*, 5. *B. major*, 6. *B. pacificus*, 7. *B. wrighti*.

and dorsally into the tongue (Piatt 1935).

Trunk vertebrae in *Batrachoseps* number from 16 to 23, but any single population has a maximal range of variation of four. *B. wrighti*, the species with the shortest trunk, has a modal number of 17. Some populations of *B. relictus* also have a modal number of 17, but others have modal numbers as high as 21. In *B. campi* there is a strong mode of 18, with a range of 17–19 (mean = 17.9 ± .42 SD). All individuals from Long John Canyon have 18 trunk vertebrae. *B. aridus* has a strong mode of 19, with a range of 19–20 (Brame, 1970). The remaining species all have higher numbers of trunk vertebrae, with both *B. major* and *B. attenuatus* having modes as high as 22, and occasional individuals of these species and *B. relictus* having as many as 23.

Genera of plethodontid salamanders have either two or three caudosacral vertebrae, with the exception of *Batrachoseps*, in which both numbers may occur in a single population (Wake 1966). *B. campi* is typical of the genus, some individuals having two and others, three.

Complete tails are present in 32 of the type series of *B. campi*. In these individuals postsacral vertebrae (including either 2 or 3 caudosacral and all of the caudals) range from 22–34 (mean 28.44 ± 2.18), with numbers increasing from juveniles to adults. This is a very low number for *Batrachoseps*, but accurate comparative data are not available for other species. The main problem in obtaining accurate counts is the high frequency of tail breaks. However, numbers as high as 60 caudal vertebrae occur in some of the species. Relatively few caudal vertebrae might also be expected in the relatively short-tailed *B. aridus*, but our

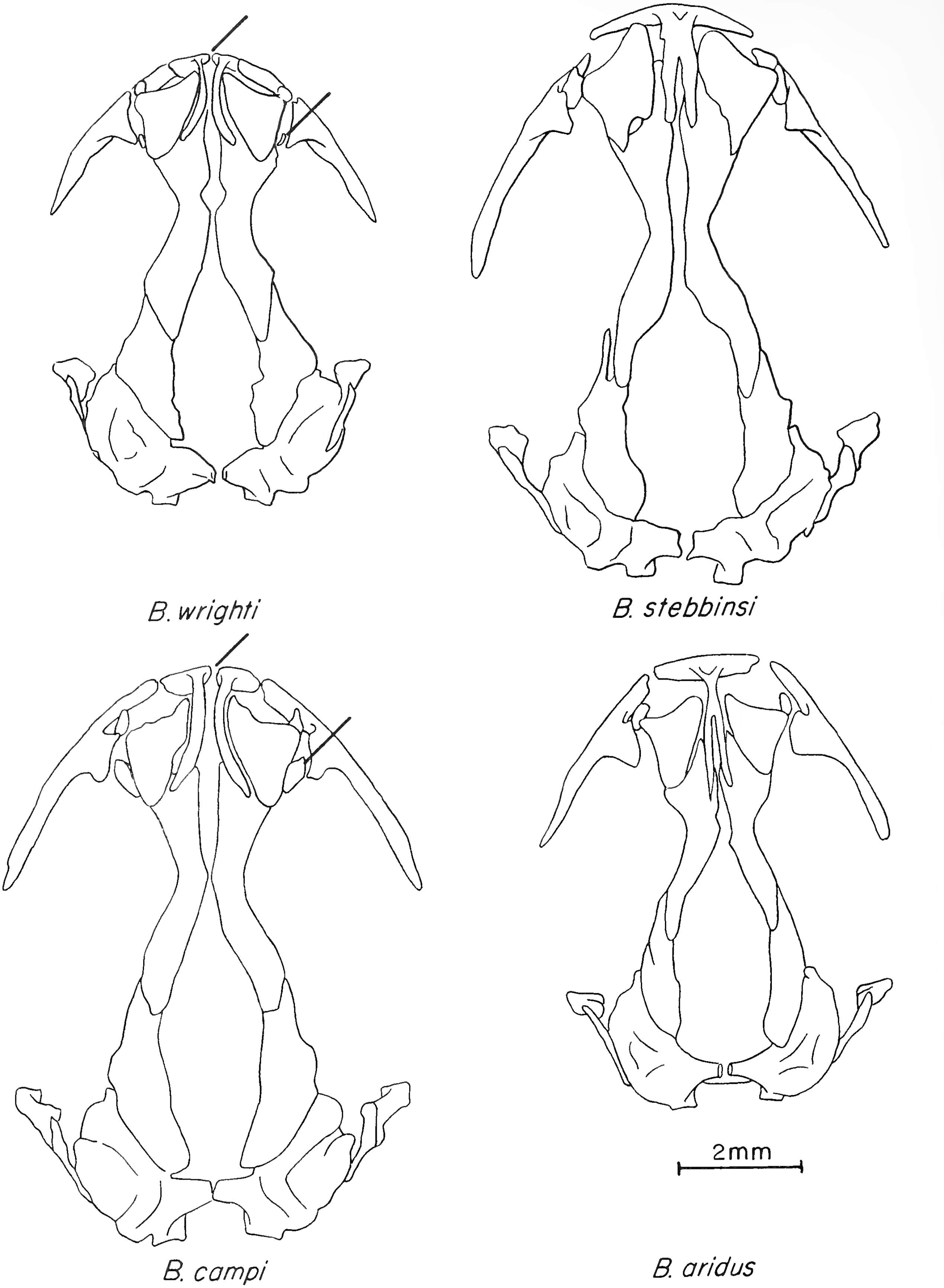


FIGURE 6. Dorsal views of the skulls of four species of *Batrachoseps*. The lines indicate the divided premaxillary bones and the prefrontal bones found only in *B. campi* and *B. wrighti*.

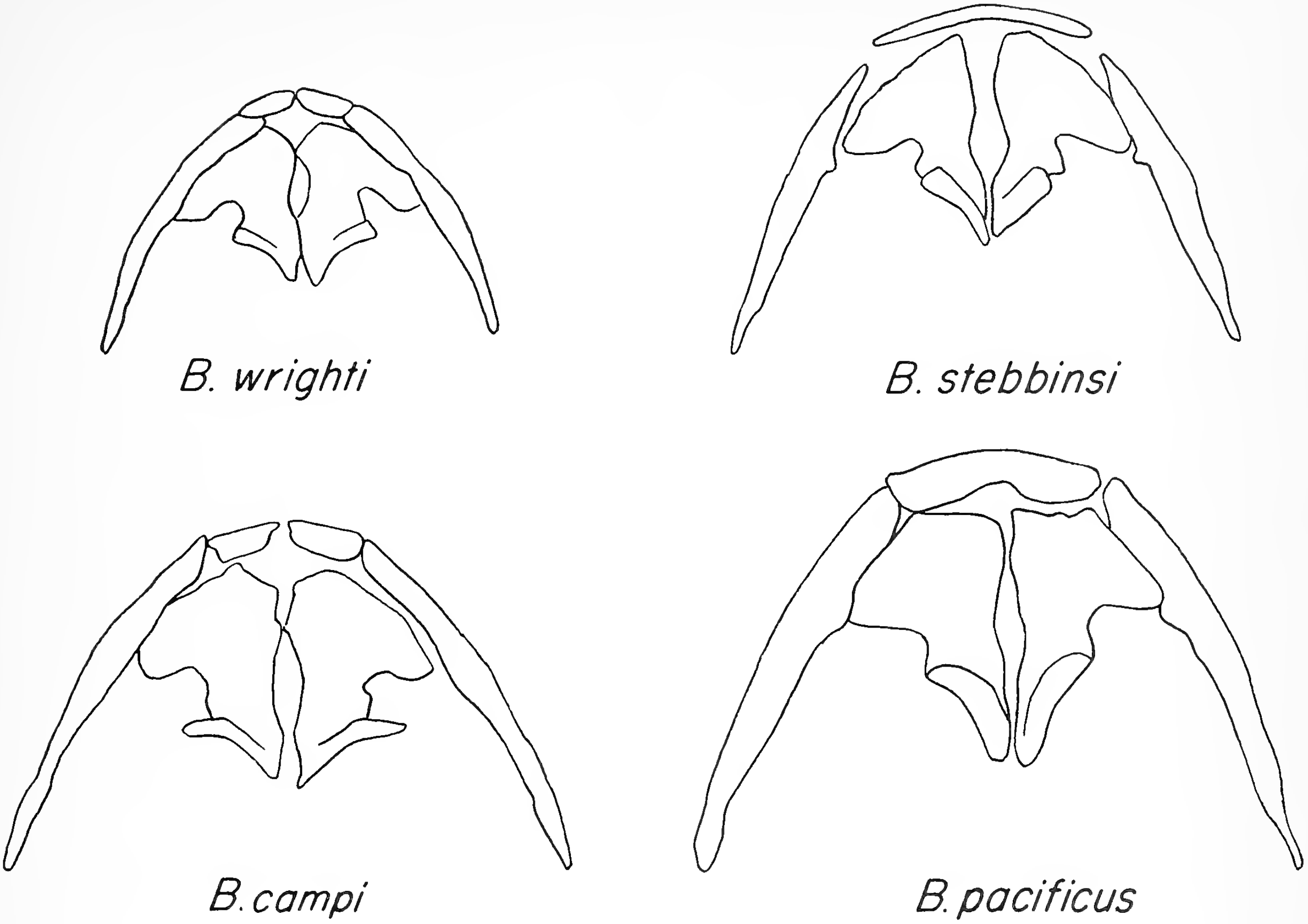
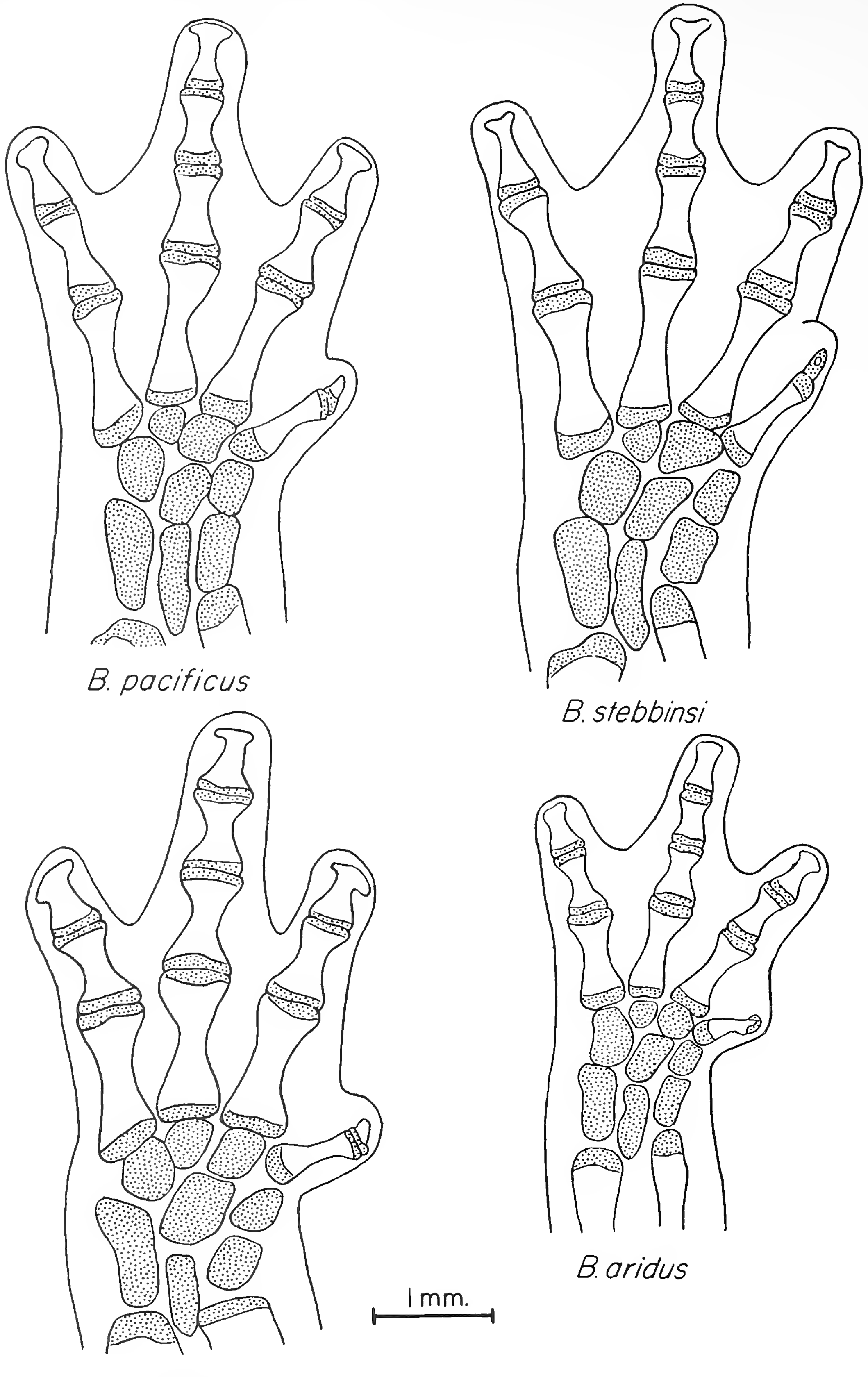


FIGURE 7. Ventral view of the anterior part of the skull of four species of *Batrachoseps*. The bones are the premaxillaries, maxillaries, and vomers. Teeth not indicated. Same scale as Figure 6.

largest cleared specimen (41.0 SL) has 32 (a total of 34 postsacrals) and larger specimens reasonably could be expected to have more. In *B. wrighti,* also relatively short-tailed, as many as 38 caudal vertebrae are present.

The limbs of *B. campi* are stouter than those of most other *Batrachoseps* but are of about the same relative length as those of *B. stebbinsi*. In osteological detail they are very similar to those of the more generalized species of *Batrachoseps* (Fig. 8). The tibial spur is well developed in *B. campi*. This structure is absent in many populations of *B. attenuatus,* but is characteristically present in other species. Wake (1966) reported that all species of *Batrachoseps* except *B. wrighti* and some populations of *B. pacificus* (these particular populations are now referred to *B. major,* following Brame and Murray 1968) have seven rather than the primitive plethodontid number of eight carpal elements as the result of fusion of the ulnare and intermedium cartilages. We have found eight carpals in some *B. major* and in most specimens of *B. wrighti,* but other members of these species have seven. All populations of *Batrachoseps* have eight tarsal elements. *B. campi* has seven carpals and eight tarsals. The usual phalangeal formula in *Batrachoseps* is 1–2–3–2 for both hand and foot, but Wake (1966) and Brame (1970) report 0–2–3–2 rarely in *B. attentuatus*. Brame and Murray (1968) and Brame (1970) also indicate that *B. stebbinsi* and *B. aridus* differ from other species in lacking a phalanx on the first digit of the hand and foot. A small terminal phalanx is present on the first digit of the hand in four of five specimens examined of *B. aridus*, and on the first digit of the foot in two of these specimens. Extremely small phalanges that do not appear on radiographs are present on the first digit of both hands and feet in all nine specimens of cleared *B. stebbinsi* available to us. These are often only dots of mineralized tissue, and in one foot in each of two specimens no sign of a phalanx is seen. Terminal phalanges of the first digit are also greatly reduced in *B. simatus*, and in one foot of one individual (of a total of 13) this phalanx is absent. In *B. campi* the hands and feet are relatively large and stout. The generalized phalangeal formula is present. The first phalanx is well developed and discrete. Phalanges are especially well ossified with relatively little cartilage, especially in large adults (Fig. 8). Expansion of the most terminal phalanx of each digit is characteristic of all species of *Batrachoseps*, including *B. campi*.

EVOLUTIONARY RELATIONSHIPS: Those of us who discovered *B. campi* were impressed immediately with its robustness and its relatively short body and tail. We thought it might be a representative of *Hydromantes* or some other genus, and did not think of assigning the new species to *Batrachoseps* until we noticed that it had but four toes. The species is hardly a typical *Batrachoseps*, as that taxon has been understood, and its discov-



B. pacificus

B. stebbinsi

B. campi

B. aridus

FIGURE 8. Feet of four species of *Batrachoseps*, drawn from cleared and stained specimens with aid of microprojector. Cartilage stippled.

ery forces us to re-evaluate the status of the genus.

In several morphological features *B. campi* approaches hypothesized ancestral states for the entire tribe Bolitoglossini (*Batrachoseps, Hydromantes,* and the tropical salamander groups in the supergenus *Bolitoglossa–Pseudoeurycea, Chiropterotriton, Oedipina, Thorius, Lineatriton, Parvimolge,* and *Bolitoglossa*). The species is more generalized than other *Batrachoseps* in osteology and myology as well as in external form. Features in which it retains ancestral conditions as compared to existing conditions in *Hydromantes* include presence of prefrontals and of genioglossal muscles. It matches *Hydromantes* in having paired premaxillaries. The paired premaxillaries distinguish it from all described species of the supergenus *Bolitoglossa*. Only the absence of a fifth toe (including tarsal, metatarsal and phalanges) and the presence of a fontanelle in the skull roof remove *B. campi* from the presumed ancestral state for the tribe Bolitoglossini (for comparative data see Wake 1966).

Perhaps *B. campi* is a very early derivative of the ancestral stock of all bolitoglossines, representing a lineage that appeared shortly after the differentiation of the *Batrachoseps* stock from a more generalized ancestral group. The superficial similarity of *B. campi* to members of such genera as *Hydromantes, Chiropterotriton,* and *Pseudoeurycea* may reflect the great conservatism inherent in these relatively ancient lineages. Nevertheless *B. campi* can rather easily be accommodated in the genus *Batrachoseps* so long as *B. wrighti* is also included. The close relationship of *B. campi* to other species of *Batrachoseps* rather than to other bolitoglossines is evident, based on the number and nature of derived features that are shared. It is in ancestral features that *B. campi* resembles members of other genera.

The discovery of *B. campi* and knowledge of its structure tend to make the tribe Bolitoglossini a somewhat tighter unit than formerly perceived. However, no new insight is provided into relationships of *Batrachoseps* as a unit relative to *Hydromantes* and the supergenus *Bolitoglossa*. There is no reason to modify the conclusions of Wake (1966) that *Batrachoseps* is cladistically closer to the supergenus *Bolitoglossa* than to *Hydromantes*. The single most important piece of evidence is the derived karyotype of *Batrachoseps* and the supergenus *Bolitoglossa,* both groups having a haploid chromosome number of 13 as opposed to the 14 chromosomes characteristic of *Hydromantes* and all other plethodontids (Kezer 1964; Kezer and Macgregor 1971; Morescalchi 1975).

Certain specialized and presumably derived morphological conditions are shared by *B. campi* with all other members of the genus *Batrachoseps*. Accordingly we conclude that the species is most appropriately associated with *Batrachoseps*. These features include: (1) the hyobranchial apparatus and musculature, specifically a genioglossus muscle that takes its origin near the posterior end of the mandible. This arrangement of the muscle is unique to *Batrachoseps* (Piatt 1935; Wake 1966; Lombard and Wake 1977). Further, in all other features of the apparatus the species is like other *Batrachoseps* rather than like any other genus. (2) A distinct fontanelle is present in the skull roof, bordered by markedly narrowed frontals and parietals. No comparable fontanelle is found in any other salamander. *Thorius* has a smaller fontanelle involving narrowed frontals but its parietals have proportions typical of less specialized genera.

Some derived features occur in *B. campi* and other species of *Batrachoseps* which either are less distinctive than those mentioned above, or are not exclusively present in *Batrachoseps*. These add strength to the case for inclusion of *B. campi* in the genus. The characters include: (1) A strongly developed lateral spur on the parietal bone. This spur is shaped like that in other *Batrachoseps,* but spurs of a somewhat different shape are also present in the supergenus *Bolitoglossa* (Wake 1966). (2) The number of caudosacral vertebrae may be either two or three in a given population. Typically plethodontid species have either two or three vertebrae in this region, and only in *Batrachoseps* does intrapopulational and intraspecific variation occur (Wake 1966). (3) Four digits present on the hind foot. All other plethodontids have five digits on the hind foot, except *Hemidactylium scutatum* and *Eurycea quadridigitata,* both distinctly different from *Batrachoseps* in many features. (4) A haploid chromosome number of 13 (see Appendix).

Within the genus, *B. campi* is the most generalized species in having superficial structure similar to that of other generalized plethodontids and a number of osteological characters present in ancestral states. These latter features include notably the paired premaxillary bones, the prefrontal bones, and the preorbital processes of the vomers. Only in large, presumably old *B. wrighti* do these features appear in combination, and the first two characters are found only in *B. campi* and *B. wrighti.* All three characters are related to degree of morphogenesis (see Wake 1966, for a lengthy discussion of this issue). In plethodontids that have a larval stage, all three features are associated with metamorphosis, making their appearance at about that time. There is no metamorphosis in a technical sense in *Batrachoseps* and other salamanders with direct development, and the changes which ordinarily occur during the relatively short metamorphic period are spread out over the entire life span of these organisms. In most species of *Batrachoseps* the metamorphic features listed above are delayed in appearance to such an extent that the life span of the organism is insufficiently long for them to appear. According to this interpretation, metamorphosis of these structural features occurs early in *B. campi,* late or not at all in *B. wrighti,* and never in other species of *Batrachoseps*.

It can be argued that *B. campi* is primitive in respect to its entire pattern of development (i.e., it is the least paedomorphic), and that one should not "count" three primitive states, but only one. However one counts, *B. campi* seems to qualify as the most primitive species. In addition to its primitive osteological characters, *B. campi* has external proportions that are more similar to those of generalized plethodontids than are those of any of the other species of *Batrachoseps*. Its broad head, long limbs, relatively short trunk, and short tail are all generalized features.

It is unclear what the closest relatives of *B. campi* might be. Osteological and chromosomal comparisons suggest that *B. wrighti* is the closest relative. In addition to the features discussed above, both species have relatively low numbers of trunk vertebrae. Those features which separate *B. campi* and *B. wrighti* from other *Batrachoseps* are more striking than those which separate some other genera of salamanders within the family (Wake 1966). We considered placing *B. wrighti* and *B. campi* in the resurrected genus *Plethopsis* (Bishop 1937; see also Stebbins and Lowe 1949). However, *Plethopsis* would have to be founded on the basis of a suite of primitive characters, and given the difficulties in deciding whether we are dealing with one general metamorphic event or several independently evolving characters we believe that it is advisable to keep the genus intact. In fact, there are reasons for thinking that *B. campi* might be more closely related to some other species than *B. wrighti*. *B. aridus* is much

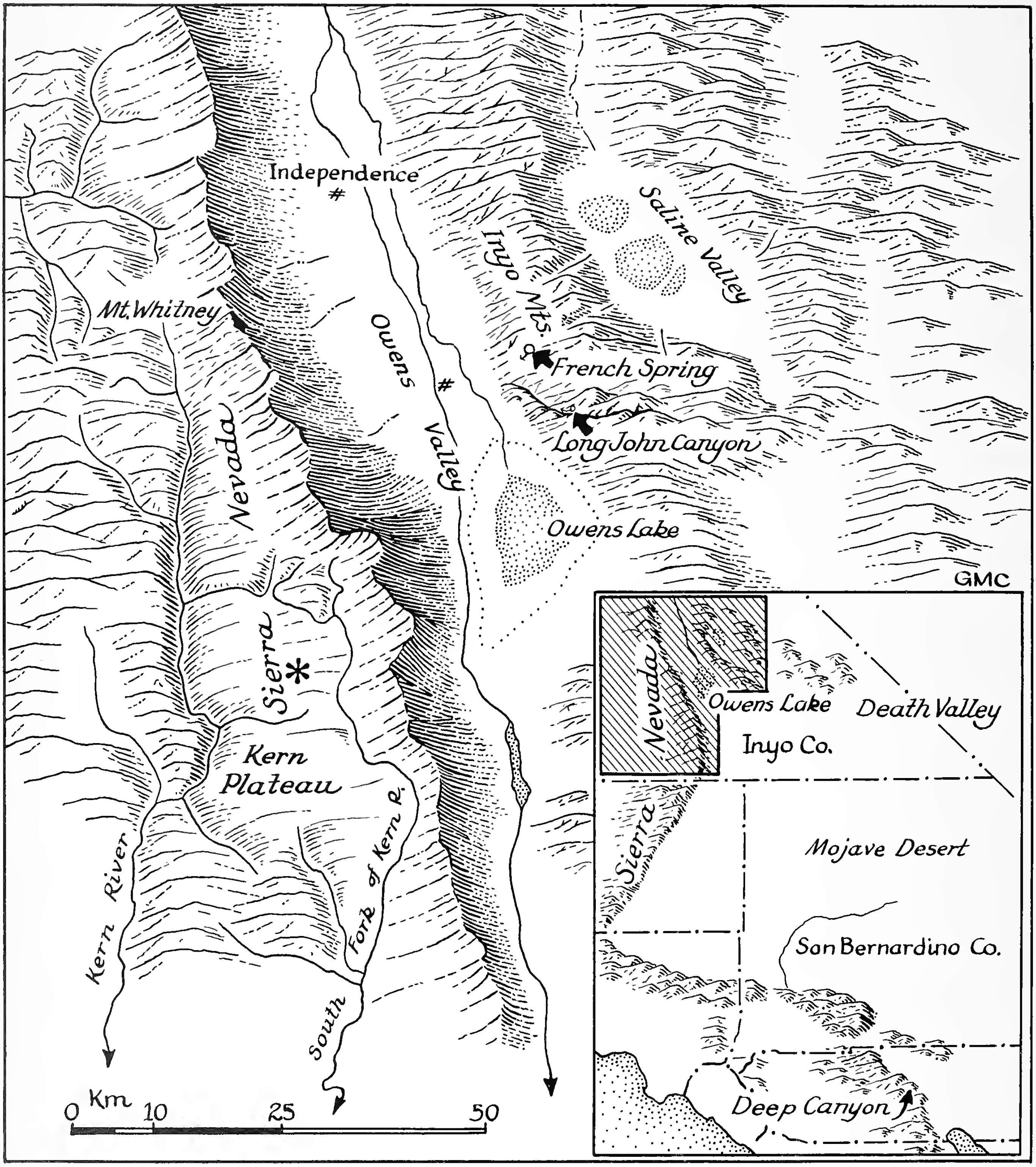


FIGURE 9. Map of eastern California showing the two localities of *Batrachoseps campi*. The closest locality for *B. stebbinsi* is indicated by an asterisk. Deep Canyon, Riverside County, California, is the only other desert locality for plethodontid salamanders *(B. aridus)* and it is indicated on the inset map.

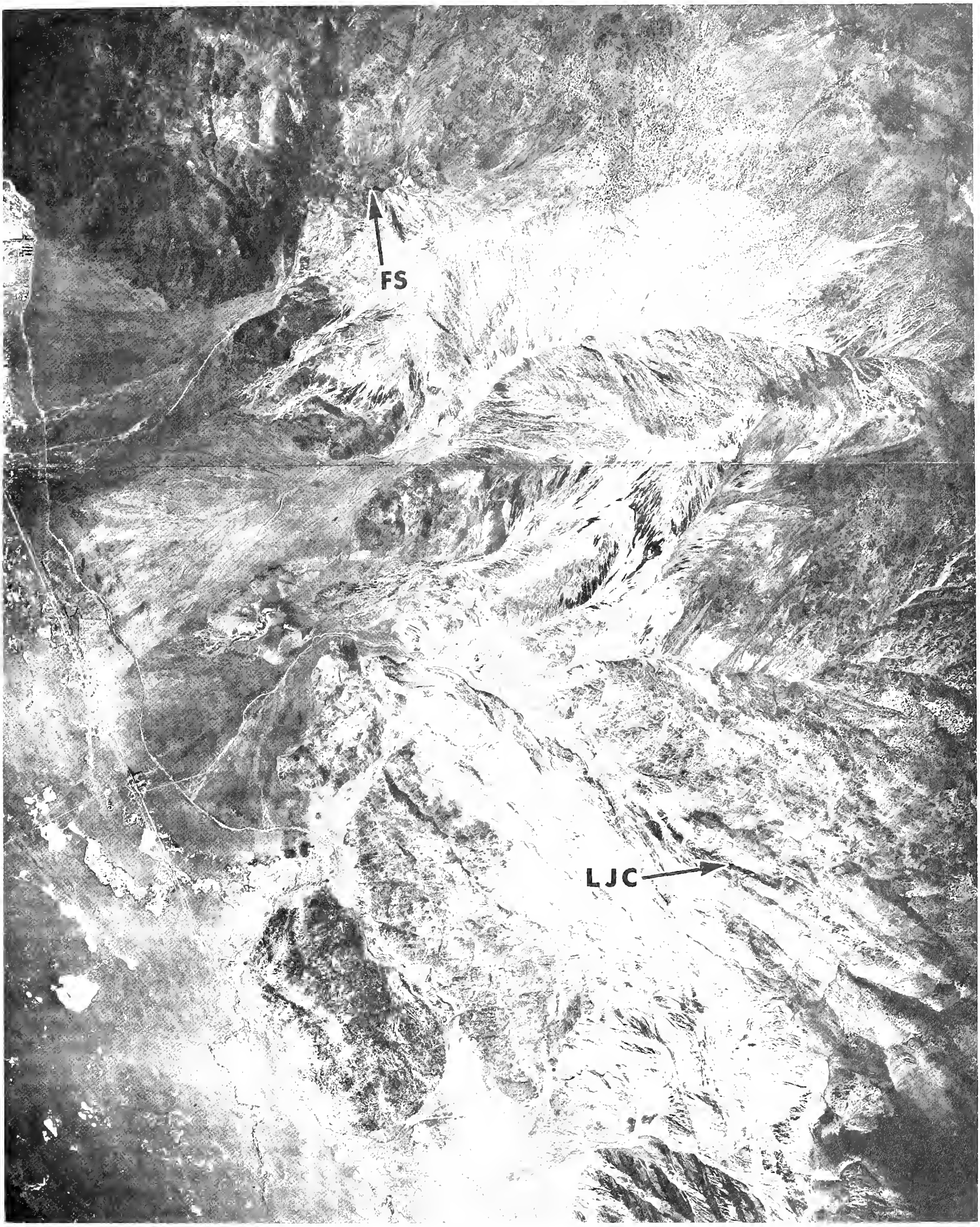


FIGURE 10. Aerial photograph of the two localities for *Batrachoseps campi*. Note the scant vegetation. FS, French Spring; LJC, Long John Canyon. Photo courtesy of the USGS.

smaller than *B. campi*, but in many proportions it is rather similar (Fig. 4). Further, the color patterns in the two species are somewhat similar, and differ from those in all other species. Osteology provides the only certain means of separating these two species on other than size-related grounds. *B. campi* is matched in some aspects of size by *B. pacificus*, but the species are highly distinct osteologically. Further, *B. pacificus* has the characteristic striped dorsal pattern that is seen in all species except *B. aridus* and *B. campi*. Both *B. stebbinsi* and *B. pacificus* have proportions more similar to *B. campi* than any species except *B. aridus*.

The presence of *B. campi* and *B. aridus* in remote and totally isolated desert habitats raises questions concerning historical biogeography of this region. The animals survive in highly restricted microhabitats surrounded by seemingly uninhabitable desert (Figs. 9 and 10). Both species must utilize underground retreats. Possibly they can travel for some distance through crevices and solution channels in limestone formations. Brame (1970) reports limestone at the type locality of *B. aridus*. While limestone outcrops are not obvious in the two localities of *B. campi*, in parts of the southern Inyo Mountains near these localities fossil-bearing marine shales and limestones of Triassic age are found in sections up to 1,800 ft (about 550 m) thick. These rocks are exposed in many sites now and presumably they have been for long periods in the past (Oakeshott 1971). The desert species of *Batrachoseps* are unlikely to be Pleistocene relics, stranded in areas of favorable habitat which they reached during pluvial stages. More likely, these species have been occupying habitats associated with exposures of these ancient rocks for a long period, perhaps since early Tertiary times. They may have maintained themselves in favorable microhabitats through many cycles of heating and cooling, moistening and drying. Had they entered desert habitats during Pleistocene pluvial periods, they would have dispersed from somewhere. There are no extant populations in California that could have served as ancestors for either *B. aridus* or *B. campi*, and it seems unlikely that these ancestors all would have become extinct or given rise to such species as *B. stebbinsi* in the relatively short time since even the beginning of Pleistocene.

Finally we note that salamanders recently have been collected in a number of canyons in parts of the Inyo Mountains other than those mentioned here. These populations are under intense study currently.

PROTECTIVE MEASURES

Long John Canyon and French Spring are within the boundaries of National Resource Lands administered by the Bureau of Land Management. Vehicle travel in the area currently is permitted only on roads and trails established prior to November 1, 1973. Both springs are Public Water Reserves. Water cannot be appropriated, and no camping is allowed within 150 m of the water.

Better protection for these populations would be afforded if Long John Canyon in the area of the spring were closed to vehicles, and the habitat areas in both Long John Canyon and French Spring were withdrawn from potential mining. Due to its small range and limited habitat, *B. campi* qualifies as "rare" and should be afforded protection under state law.

Feral horses and burros have caused massive destruction to the vegetation and soils surrounding desert springs and water courses in the Southwest. Burros are established in the Inyo Mountains and the United States Fish and Wildlife Service and the California Resources Agency should assess their impact and take steps to reduce or eliminate damage. Those springs in the area where horses and burros presently occur should be carefully surveyed for other populations of salamanders.

The California Resources Agency and other agencies should re-evaluate the practice of opening and clearing desert springs, often with explosives, for the enhancement of habitat for upland game and other animals. The manipulation of fragile desert seep, spring, and stream communities for any reason should proceed only after rigorous investigation of the consequences of the anticipated activities.

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APPENDIX

Chromosomes of *Batrachoseps campi*

James Kezer has studied the chromosomes of a single *B. campi* and has graciously provided the following information which he has encouraged us to present as part of the description of this species. For some years Prof. Kezer has been accumulating information concerning the chromosomes of members of the genus *Batrachoseps*, and comparative data derive from this work.

Chromosomes of *B. campi* were obtained from the testes of an adult male. The testes were fixed in three parts absolute ethanol and one part glacial acetic acid. Testes were squashed in 45 per cent acetic acid and spermatocytes were examined for chromosomes. Unstained slides were photographed using phase-contrast optics. Data were derived from anaphase cells of the second meiotic division. Two haploid sets of chromosomes from one such cell (Fig. 11) were the source of quantitative data (Table 2) used to construct an ideogram (Fig. 12).

The haploid chromosome number of *B. campi* is 13. This is the same number found in other species of *Batrachoseps* and in the tropical salamanders of the supergenus *Bolitoglossa* (Kezer and Macgregor 1971; León and Kezer 1978). All other plethodontids that have been examined, including the remaining bolitoglossine genus *Hydromantes*, have a haploid number of 14 chromosomes.

The karyotype of *B. campi* has two chromosomes having centromeres in subterminal regions (numbers 6 and 13, Fig. 12). In *B. attenuatus* and *B. major* centromeres are all in median and submedian regions, but *B. wrighti* has two chromosomes with

FIGURE 11. Late anaphase II chromosome preparation of *Batrachoseps campi,* prepared and photographed by James Kezer. Unstained squash. The chromosomes of this photomicrograph were used in preparing Table 2 and Figure 12.

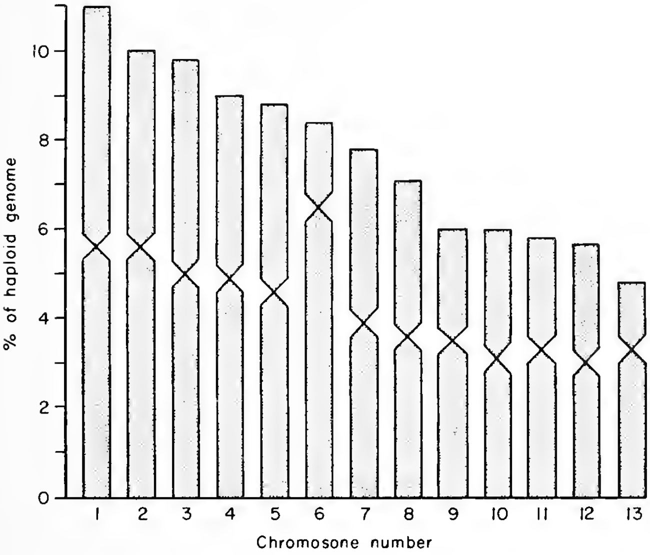

FIGURE 12. Ideogram of haploid chromosome set of *Batrachoseps campi* based on data in Table 2.

subterminal centromeres (see Kezer 1964, Fig. 7A.16). Information is not available for other species of *Batrachoseps.* At present not enough information is available to determine homologies of salamander chromosomes. Should the two subterminal chromosomes of *B. campi* prove to be homologous with those of *B. wrighti,* and should they represent derived conditions, the hypothesized close relationship of the two species would gain additional support.

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In these series, the *Contributions in Science* are comprehensive papers of imperial octavo size whereas the Series are papers of variable lengths of quarto or larger size. Issues in each serial are numbered separately and consecutively, and report on the research and collections of the Natural History Museum, or of research activity of professional colleagues. The Museum's publications are distributed through mailing lists to libraries, universities, and similar institutions throughout the world.

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Edward Ostermeyer
Editor

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NATURAL HISTORY MUSEUM OF LOS ANGELES COUNTY

NOTES FOR A REVISION OF THE ANT GENUS *FORMICA*. 2. REIDENTIFICATIONS FOR SOME SPECIMENS FROM THE T. W. COOK COLLECTION AND NEW DISTRIBUTION DATA (HYMENOPTERA: FORMICIDAE).

By André Francoeur and Roy R. Snelling

Published by the NATURAL HISTORY MUSEUM OF LOS ANGELES COUNTY • 900 EXPOSITION BOULEVARD • LOS ANGELES, CALIFORNIA 90007

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NOTES FOR A REVISION OF THE ANT GENUS *FORMICA*. 2. REIDENTIFICATIONS FOR SOME SPECIMENS FROM THE T.W. COOK COLLECTION AND NEW DISTRIBUTION DATA (HYMENOPTERA: FORMICIDAE).[1]

By André Francoeur[2]
and Roy R. Snelling[3]

ABSTRACT: Specimens of the *Formica neogagates* and *Formica fusca* groups from the T.W. Cook collection are reidentified. New morphological variations are presented for *F. longipilosa*, together with a first description of the male. Some of these data extend the geographical distribution of the less well known species particularly in California.

"The Ants of California" was privately published by Thomas Wrentmore Cook in 1953. This was Cook's only published work on ants and it does no credit to a many-faceted man. The book consists, for the most part, of records and descriptive and biological notes gleaned from previously published work of other authors. These applied, for the most part, to California forms, but no effort was made to correct records based on misidentified specimens. The present paper reveals so many surprising misidentifications and misinterpretations in *Formica* species or species groups, that it becomes impossible to use any data from "The Ants of California" without having the specimens at hand.

Furthermore, the drawings illustrating the book are misleading or inaccurate: the head of *Formica subnuda* (p. 368) and the mesosoma of *F. occidua* (p. 385) are erroneously proportioned; the "female" head of *F. subsericea* (p. 368) is that of a male; the maxillary palpi of *F. sibylla* (p. 392) are too short; the figure of *F. subpolita camponoticeps* (p. 392) is a worker of *F. neorufibarbis*.

Numerous other deficiencies are pointed out by Brown and Wilson (1953).

Cook died in 1962. In 1964 his collection was donated to the Oakland Museum by his widow. The ants were transferred to the Natural History Museum of Los Angeles County in 1971. There were 4,397 pinned ant specimens and an undetermined number in 213 vials (Arnaud and Wale 1973). Almost half of the pinned material consisted of specimens from W. M. Wheeler's collection acquired during a brief stay at Harvard. Most of the remainder were specimens from the collections of Stanford University, still bearing the distinctive "L.S. Jr. U." labels. The Stanford University specimens were collected mostly by W.M. Mann. The specimens in vials were, in large part, collected by Cook. Judging by the number of specimens clearly collected by Cook and by the localities visited, he had a very limited first hand acquaintance with the ants of California.

The present note attempts first of all to clarify some of the erroneous citations in "The Ants of California." We also cite new distributional and morphological data, particularly on several species in the *F. fusca* group described recently by the senior author (Francoeur 1973). A few specimens, cited as various forms of *Formica*, belong to other genera and are noted at the end of this paper.

The following abbreviations are used: LSJU (Leland Stanford Jr. University); TWC (T.W. Cook); WMM (W.M. Mann); WMW (W.M. Wheeler).

FORMICA NEOGAGATES GROUP

NEOGAGATES COMPLEX

Formica lasioides Emery

Formica neogagates lasioides: Cook, 1953, p. 360

Formica neogagates lasioides var. *vetula:* id. p. 361

Formica fusca fusca: id. (in part), p. 371

Formica subpolita var. *camponoticeps:* id. (in part), p. 397

Labelled *neogagates lasioides* var. *vetula:* 3 ☿ from Pacific Grove (WMM), 3 ☿ from Lake Tahoe, 4 ☿ from Quincy (TWC), CALIF.

Labelled *fusca:* 1 ♀, 3 ☿ from Lake Tahoe, CALIF.

Labelled *subpolita camponoticeps:* 1 ♀, 5 ☿ from Glacier Point, Yosemite, CALIF.

Unidentified: 4 ☿ from Eagle Creek (LSJU), 1 ☿ from Oswego (Duncan), 2 ☿ from Rowena (LSJU), ORE.; 6 ☿ from Big Lagoon, Humboldt Co., 5 ☿ from Lake Tahoe, 9 ☿ from Mirror Lake, elev. 4096 ft., CALIF.

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Contrib. Sci. Natur. Hist. Mus. Los Angeles County. 1979. **309:**1–7.

Formica neogagates Emery

Unidentified: 5 ϙ from Ithaca, N.Y.; 13 ϙ from Pullman, WASH. (WMM).

OBTUSIPILOSA COMPLEX

Formica perpilosa Wheeler

Labelled *Formica:* 4 ϙ from Santa Clara Co., CALIF. The label is the same as on other specimens from the Stanford University collection and they are surely from that collection.

FORMICA FUSCA GROUP

CINEREA COMPLEX

Formica canadensis Santschi

Labelled *fusca* var. *argentea:* 1 ϙ from Colorado Springs, COLO. (E.S. Tucker).

Formica pilicornis Emery

Formica cinerea var. *lepida:* Cook (in part), 1953, p. 373

Formica pilicornis: id. (in part), p. 385

Labelled *pilicornis:* 9 ϙ from South San Francisco and 18 ϙ from San Francisco, CALIF. (TWC).

Labelled *cinerea* var. *lepida:* 16 ϙ from Saugus, CALIF.

Unidentified: 6 ϙ from Tejon Pass, CALIF. (TWC).

NEOCLARA COMPLEX

Formica neoclara Emery

Formica cinerea var. *neocinerea:* Cook (in part), 1953, p. 374.

Labelled *fusca* var. between *neoclara* and *argentata:* 3 ϙ from Pullman, WASH. (LSJU).

Labelled *fusca* var. *neoclara:* 4 ϙ from Colorado Springs, COLO. (E.S. Tucker).

Labelled *fusca* var.: 5 ϙ from Sisson, CALIF. (J.C. Bradley).

SUBPOLITA COMPLEX

Formica subpolita Mayr

Formica subpolita: Cook, 1953, p. 396.

Formica subpolita var. *camponoticeps:* id. (in part), p. 397.

Formica fusca var. *marcida:* id. (in part), p. 379.

Formica fusca var. *neorufibarbis:* id. (in part), p. 380.

Labelled *subpolita:* 8 ϙ from Pacific Grove (WMM), 8 ϙ from Corte Madera Creek, 27 ϙ from Greenville, CALIF.

Labelled *subpolita* var. *camponoticeps:* 3 ϙ from Yosemite, 6 ϙ from Yosemite Falls Top, 3 ϙ from Yosemite Village, 1 ♀, 3 ϙ from Old Village, Yosemite Valley, 15 ϙ from Glacier Point, Yosemite, 2 ϙ from Mt. Tamalpais, CALIF.

Labelled *fusca* var. *marcida:* 5 ϙ from Point Joe, near Pacific Grove, CALIF.

Labelled *fusca* var. *neorufibarbis:* 1 ϙ from top of Mount Wilson, CALIF. (J.C. Bradley) together with 1 ϙ of *Liometopum* sp.

LEPIDA COMPLEX

Formica aerata Francoeur

Formica cinerea var. *neocinerea:* Cook, (in part), 1953, p. 374.

Labelled *cinerea* var. *neocinerea:* 3 ϙ from Three Rivers (J.C. Bradley), 3 ϙ from Sacramento (H.S. Smith), 1 ϙ from Stanford University, CALIF. (LSJU).

Labelled *Formica:* 3 ϙ from Stanford Univ., CALIF.

Unidentified: 1 ϙ from Santa Clara Co., CALIF. (Harkins); 3 ϙ from 3.5 mi. south of Kirby, ORE.

Formica lepida Wheeler

Unidentified: 1 ϙ from Smith River Camp, Del Norte Co., CALIF. This is the second record for this species.

Formica longipilosa Francoeur

Figures 1–3

Unidentified: 20 ϙ and 2 ♂ from Ukiah, CALIF. (LSJU). These specimens are the second series known to us. They provide new data on the morphology of the workers. The male is described here for the first time.

WORKER: The series fits the original description (Francoeur 1973, p. 126–127). However, the size averages somewhat smaller: head width 0.96–1.14 mm; head length 1.09–1.31; eye diameter 0.41–0.47; scape length 1.07–1.27; trunk length 1.59–1.84. The dorsal margin of petiole less convex, in one case feebly and narrowly excised.

MALE: First description based on two androtypes (in LACM and senior author's collection). General morphology similar to *F. transmontanis* Francoeur, but averaging smaller. Measurements in mm: head width 1.61–1.35; eye diameter 0.70–0.71; trunk length 3.05–3.20; pronotum width 1.56–1.65. Head distinctly broader than long, occipital margin slightly convex, ocelli small (0.12–0.14 mm); clypeus bulging, faintly carinated, anterior margin convex; mandible rather narrow with only an apical tooth. Petiole low and thick in profile, dorsal margin with large, weak concavity and rounded corners. Genitalia: posterior half of parameres more acute and larger, with long hairs; subgenital plate shining, when ventral surface is seen from above, posterior end not produced as in *transmontanis,* rather straight, with two concavities separated medially by rounded process. Body concolorous brown, antennae paler, legs yellowish brown; most parts with dense and long pubescence, particularly on anterior dorsal half of head, pronotum, petiole and gaster; pilosity distributed as in *transmontanis* but longer and finer especially on head and thorax.

Formica pacifica Francoeur

Unidentified: 5 ϙ from Cannon Beach (LSJU), 3 ϙ from Goble (LSJU), 1 alated ♀ from Umpqua River, Canyonville, ORE.

SUBSERICEA COMPLEX

Formica argentea Wheeler

Formica sibylla: Cook (in part), 1953, p. 393.

Labelled *fusca* var. *argentata* or var. *argentea:* 8 ϙ from Pullman, WASH. (WMM).

Labelled *fusca* var.: 2 ϙ 2 ♂, & 1 ♀ from San Juan Island, WASH. (WMM).

Labelled *sibylla:* 3 ϙ from Lake Tahoe, CALIF.

Unidentified: 1 ϙ from Boyd, 2 ϙ from Linsley, 1 ϙ from Rowena (LSJU), 7 ϙ from Tygh Valley (LSJU), ORE.; 1 ϙ from Hewlett Point, 1 ϙ from Prescott (L.R. Dice), WASH.

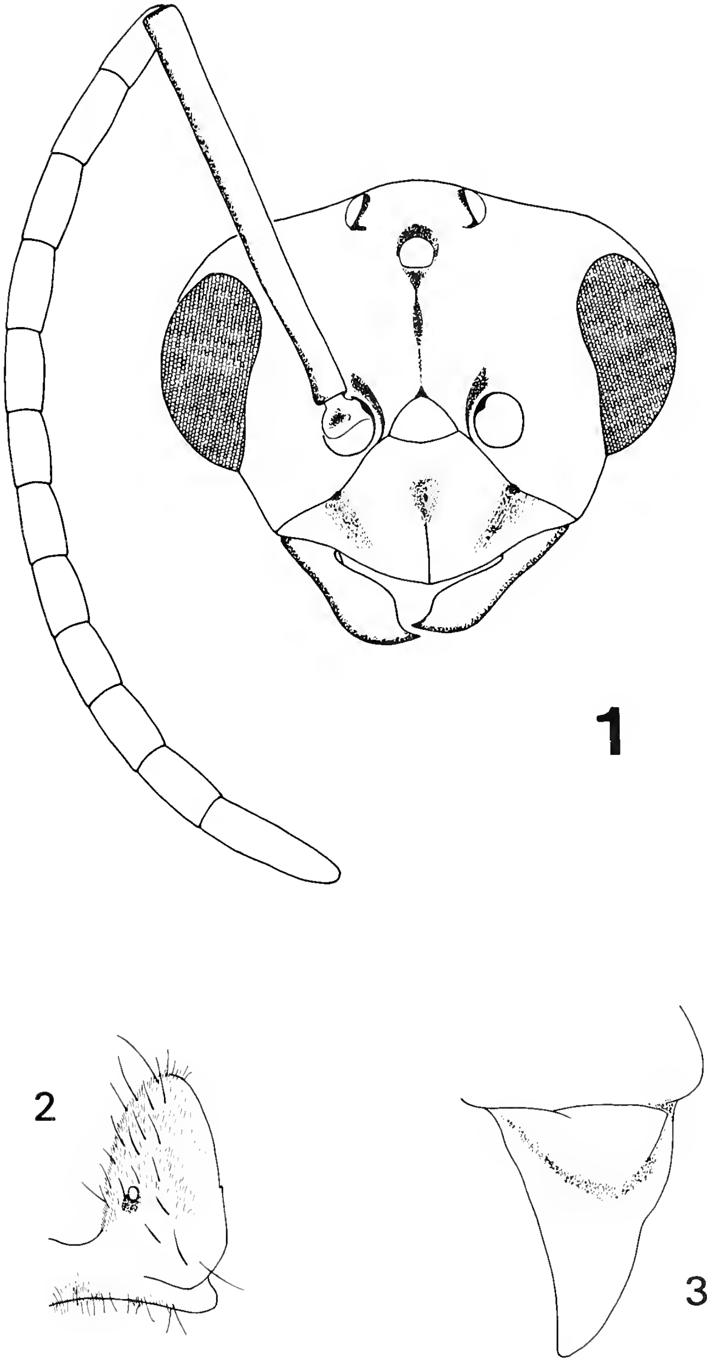
Formica podzolica Francoeur

Formica sibylla: Cook (in part), 1953, p. 393.

Labelled *sibylla:* 18 ϙ from Marysville, CALIF.

Formica subsericea Say

Unidentified: 6 ϙ from Ithaca, N.Y.



Figures 1–3. *Formica longipilosa* male (50X). 1, head, frontal view, without pilosity; 2, petiole, lateral view; 3, paramere, lateral view.

FUSCA COMPLEX

Formica accreta Francoeur

Formica fusca var. *subsericea:* Cook (in part), 1953, p. 384.

Formica sibylla: id., p. 393.

Labelled *fusca* var.: 26 ☿ & 1 ♀ from Quincy, CALIF.

Labelled *fusca* var. *subsericea:* 3 ☿ from Stinson Beach, CALIF. (TWC).

Labelled *sibylla:* 5 ☿ from Mirror Lake, Yosemite Valley, 2 ☿ from Glacier Point, Yosemite, 17 ☿ from Carmel (together with 1 ♂ of *Camponotus* sp.), CALIF.

Unidentified: 4 ☿ from Patrick Creek, CALIF.; 1 ☿ from Oswego (Duncan), 2 ☿ from Eagle Creek (LSJU), 1 ☿ from Columbia (LSJU), ORE.

Formica fusca Linné

Formica neogagates lasioides var. *vetula:* Cook (in part), 1953, p. 360.

Formica fusca fusca: id. (in part), p. 369.

Formica cinerea var. *neocinerea:* id. (in part) p. 373.

Formica fusca var. *argentea:* id. (in part), p. 375.

Formica sibylla: id. (in part), p. 392.

Formica fusca: Francoeur, 1973, p. 189–201.

Specimens classified in the *marcida* form:

Labelled *cinerea* var. *neocinerea:* 3 ☿ from Mt. Tamalpais, CALIF.

Labelled *sibylla:* 6 ☿ & 2 ♀ from Alta Meadow (WMW), 2 ☿, 1 ♀ & 1 ♂ from Lake Tahoe (WMW), CALIF.

Labelled *neogagates lasioides* var. *vetula:* 4 ☿ & 1 ♀ from Alta Meadow, CALIF. (WMW).

Labelled *fusca* var. *neoclara:* 3 ☿ from Lake Tahoe, CALIF. (WMW).

Unidentified: 2 ☿ from Yosemite, CALIF; 1 ☿ from Mt. Hood, ORE. (LSJU).

Specimens classified in the *subaenescens* form:

Labelled *fusca:* 4 ☿ from Lake Tahoe, CALIF. (WMW).

Labelled *fusca* var. *argentea:* 3 ☿ from Colorado Springs, COLO. (E.S. Tucker).

Formica microphthalma Francoeur

Formica sibylla: Cook (in part), 1953, p. 393.

Labelled *sibylla:* 5 ☿ from Lake Tahoe, CALIF. (WMW).

NEORUFIBARBIS COMPLEX

Formica neorufibarbis Emery

Formica subpolita: Cook (in part) 1953, p. 395.

Labelled *rufibarbis* var. *gnava.* 8 ☿, 3 alated ♀ & 1 ♂ from Lake Tahoe, CALIF. (WMW).

Labelled *subpolita:* 18 ☿ & 3 ♀ Blue Lake, CALIF. (J.C. Bradley).

Labelled *subpolita* var. *camponoticeps:* 11 ☿ from Glacier Point, CALIF. (WMW).

The workers of the above series are among the largest for the species.

Labelled *fusca* var.: 2 ☿ from San Juan Isl., WASH.

Unidentified: 1 ☿ from Paradise Valley, 2 ☿ from Mt. Hood, 6 ☿ from Cannon Beach, ORE; 1 ☿ from San Juan Isl., WASH.

RUFIBARBIS COMPLEX

Formica foreliana Wheeler

Labelled *fusca* var. *gnava:* 3 ☿ from Ramsey Canyon, Huachuca Mts. ARIZ. (WMM). These are topotypes.

Formica occidua Wheeler

Formica rufibarbis var. *occidua:* Cook (in part) 1953, p. 391.

Formica rufa obscuripes: id. (in part), p. 406.

Formica rufa propinqua: id. (in part), p. 409.

Formica microgyna californica: id. (in part), p. 413.

Labelled *rufibarbis* var. *occidua:* 1 ☿ from Stanford University, 21 ☿ from Napa (TWC), 6 ☿ from San Rafael, CALIF. (TWC).

Labelled *rufibarbis* var. *gnava:* 3 ☿ from Santa Cruz Isl., CALIF. (R.V. Chamberlain).

Labelled *rufa obscuripes:* 1 ☿ from Marin Co. (TWC), 15 ☿ from Del Monte (TWC), 9 ☿ from Santa Cruz Isl., CALIF. (R.V. Chamberlain).

Labelled *truncicola integroides* var. *propinqua:* 4 from Pismo (Beach), and 3 ☿ from Santa Cruz Isl., CALIF. (R.V. Chamberlain).

Labelled *microgyna californica:* 3 ☿ from Del Monte (TWC), 6 ☿ from Santa Cruz Isl., CALIF.

Unidentified: 3 ☿ from Cazadero (J.C. Bradley), 5 ☿ from Garberville, 3 ☿ from Santa Cruz Isl. (R.V. Chamberlain), 2 ☿ from Santa Clara Co. (Harkins), 1 ☿ from Berkeley, 20 ☿ from Davis, CALIF.

SIBYLLA COMPLEX

Formica sibylla Wheeler

Formica sibylla: Cook (in part), p. 393.

Labelled *sibylla:* 3 ☿ from Happy Isles, Yosemite Valley, 3 ☿ from Alta Meadow, 3 ☿ from Lake Tahoe, CALIF.

Labelled *fusca:* 3 ☿ from Lake Tahoe, CALIF.

Without name: 4 ☿ from Glacier Point, CALIF.

SPECIES ERRONEOUSLY CITED AS FORMICA

Subf. DOLICHODERINAE

Tapinoma sessile (Say)

Formica fusca var. *marcida:* Cook (in part), p. 379.

Labelled *fusca* var. *marcida:* 3 ☿ from Mt. Tallac, Lake Tahoe, CALIF.

Subf. FORMICINAE

Lasius niger (Linné)

Formica neogagates var. *lasioides:* Cook (in part), p. 360.

Labelled *neogagates* var. *lasioides:* 3 ☿ from Lake Tahoe, CALIF.

Lasius pallitarsis (Provancher)

Formica fusca var. *blanda:* Cook (in part), p. 377.

Labelled *fusca* var. *blanda:* 6 ☿ from Alta Meadow, CALIF.

Myrmecocystus mendax Wheeler

Formica subpolita camponticeps: (in part), p. 397.

Labelled *subpolita* var. *camponoticeps:* 6 ☿ from Hidden Springs Canyon, CALIF. (Snelling, 1976).

Myrmecocystus mimicus Wheeler

Formica sibylla: Cook (in part), p. 393.

Labelled *sibylla:* 2 ☿ from Pasadena, CALIF.

In each of the above the specimens cited are the only examples from the cited localities with the identification listed. They are, therefore, the presumed basis for the record in Cook's book.

ACKNOWLEDGMENT

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NATURAL HISTORY MUSEUM OF LOS ANGELES COUNTY

SYSTEMATICS AND DISTRIBUTION OF CERATIOID ANGLERFISHES OF THE FAMILY CAULOPHRYNIDAE WITH THE DESCRIPTION OF A NEW GENUS AND SPECIES FROM THE BANDA SEA

By Theodore W. Pietsch

Published by the NATURAL HISTORY MUSEUM OF LOS ANGELES COUNTY • 900 EXPOSITION BOULEVARD • LOS ANGELES, CALIFORNIA 90007

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Editor

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SYSTEMATICS AND DISTRIBUTION OF CERATIOID ANGLERFISHES OF THE FAMILY CAULOPHRYNIDAE WITH THE DESCRIPTION OF A NEW GENUS AND SPECIES FROM THE BANDA SEA[1]

By Theodore W. Pietsch[2]

ABSTRACT: The ceratioid anglerfish family Caulophrynidae is revised on the basis of all known material. The genus *Caulophryne* is represented by 26 female specimens collected from all three major oceans of the world. Of the six nominal species, three are recognized: *C. pelagica,* with *C. ramulosa* and *C. acinosa* as synonyms; *C. jordani,* with *C. regani* as a synonym; and *C. polynema.* A new caulophrynid genus and species is described from a single female recently collected from the Banda Sea. It differs from *Caulophryne* in having a considerably longer illicium, shorter jaw teeth, and a smaller number of relatively short median-fin rays. The tentative distribution of each species is plotted, evolutionary relationships are discussed, and a key to the genera and species of the family is provided.

This study supports a classification of the Ceratioidei in which the Caulophrynidae is the primitive sister-group of the Melanocetidae, Himantolophidae, Diceratiidae, Centrophrynidae, Oneirodidae, and Thaumatichthyidae. The position of the closely related families Linophrynidae, Gigantactinidae, and Neoceratiidae (and perhaps the Ceratiidae) is unclear. This assemblage is apparently derived either from a caulophrynid-like ancestor, forming a part of a sister-group that is primitive to all other ceratioids, or it is derived from some oneiroidid-like ancestor. In either case, it is concluded that sexual parasitism has evolved independently in at least two separate ceratioid lineages.

The ceratioid family Caulophrynidae includes globose, bathypelagic anglerfishes, easily distinguished from members of allied families by the absence of an escal bulb, the presence of two pectoral radials, extremely long dorsal and anal rays, and neuromasts of the acoustico-lateralis system located at the tips of elongate filaments. The only currently recognized genus of the family was established by Goode and Bean (1896) with the description of *Caulophryne jordani* based on a single female specimen with a parasitically attached male collected off Long Island, New York, by the Fisheries Steamer *ALBATROSS.* Since this original publication, five additional forms have been described, each from a single adolescent or adult female: *C. pelagica* (Brauer 1902); *C. polynema* Regan 1930; *C. ramulosa* and *C. acinosa* Regan and Trewavas 1932; and *C. regani* (Roule and Angel 1932). At the time of Bertelsen's (1951) monograph on the Ceratioidei the family was represented by only nine female specimens, one parasitic male, a male in metamorphosis, and 16 larvae. Not finding sufficient reason for subdividing this material into several speeies, Bertelsen (1951:37) provisionally recognized three subspecies: *C. jordani jordani,* representing a western North Atlantic subspecies; *C. jordani pelagica,* with *C. ramulosa* and *C. acinosa* as synonyms; and *C. jordani polynema,* including *C. regani* as a synonym.

The available material of *Caulophryne* represents three species: *C. pelagica,* represented by six female specimens collected from the eastern and Indo-west Pacific Ocean; *C. jordani,* by 11 females from all three major oceans of the world; and *C. polynema,* known from eight females and one attached male from the eastern Pacific and eastern Atlantic. The separation of these species is based on differences in dorsal and anal fin ray counts, tooth counts, illicium length, and illicial and escal morphology.

Despite a nearly three-fold increase in the number of known metamorphosed female specimens of *Caulophryne* since Bertelsen's (1951) revision, males are represented by only three individuals. Two of these are parasitically attached adults; the third is an unattached metamorphosis stage.

A new caulophrynid genus is also described in this paper and compared with *Caulophryne.* The single known female specimen of this new form is part of the extensive midwater collections made by Bruce H. Robison of the Marine Science Institute, University of California, Santa Barbara, during the 1975 *ALPHA HELIX* Southeast Asian Bioluminescence Expedition.

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METHODS AND MATERIALS

Standard lengths (SL) are used throughout. Measurements were taken from 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 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 both left and right sides. Head length is the distance from the anterior tip of the upper jaw to the posteriormost margin of the preoperculum. Head width is the distance between the tips of the sphenotic spines. 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 symphysial 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 distal surface of the esca, excluding escal appendages. Lengths given for dorsal and anal rays are estimates of actual values since their distal portions are nearly always broken off.

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).

Locality data are presented for all specimens examined. Coordinates for the starting position only of each trawl are included. Most collections were made with an open, 3-meter Isaacs-Kidd midwater trawl (IKMT). Material deposited at the Institut für Seefischerei, Hamburg, was collected with a Combined Midwater Bottom Trawl, having a rectangular mouth and a 1600 mesh circumference (CMBT-1600). This and similar gear are described more fully by Schärfe (1966, 1969). Material from the Institute of Oceanographic Sciences, Surrey, England, was collected with a Rectangular Midwater Trawl, mouth area eight square meters, mesh size five millimeters (RMT 8/5), equipped with an opening and closing device (Clark 1969).

Material used for the osteological investigation (two female

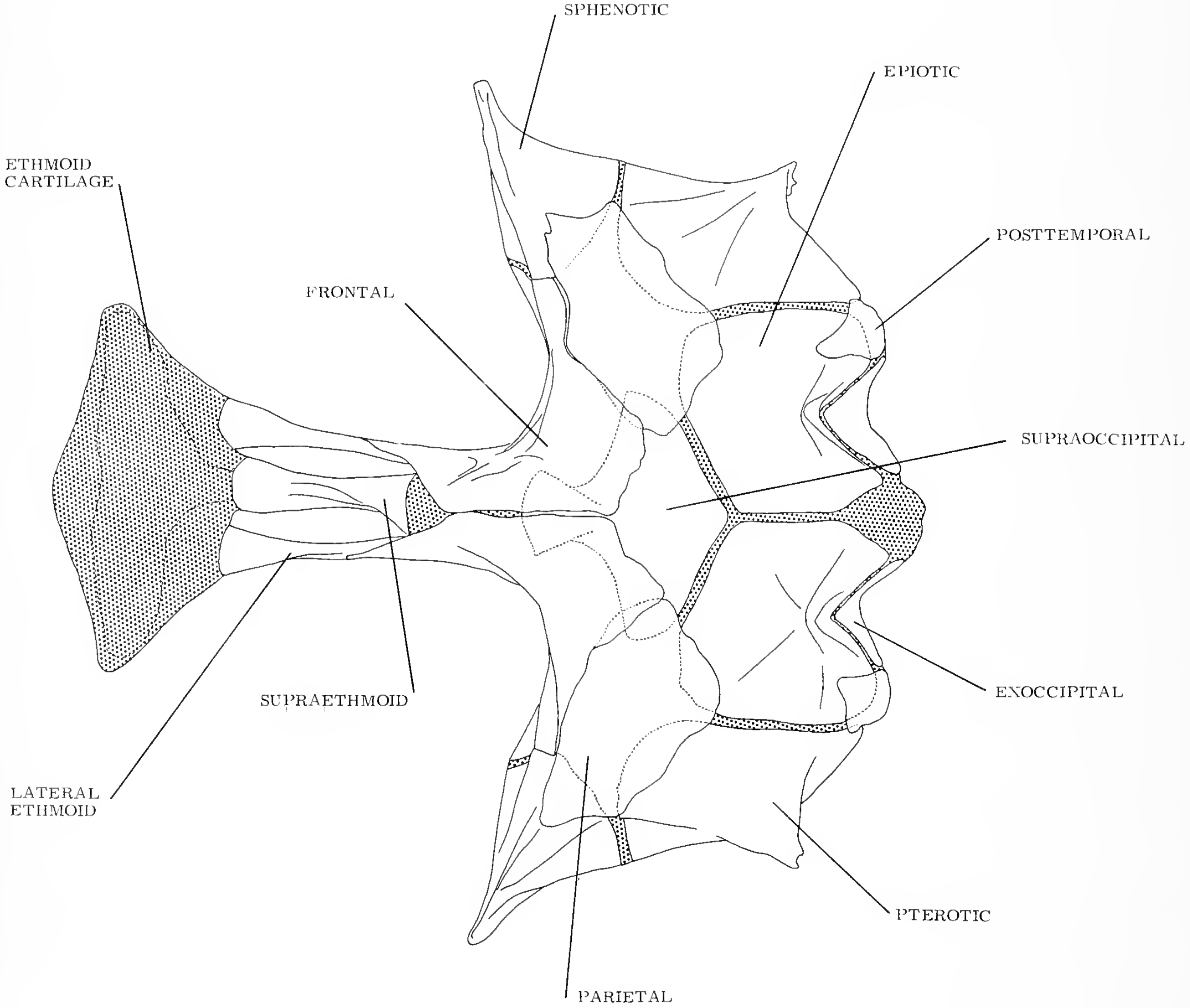

FIGURE 1. Dorsal view of cranium of *Caulophryne jordani*, IOS, 68.0 mm.

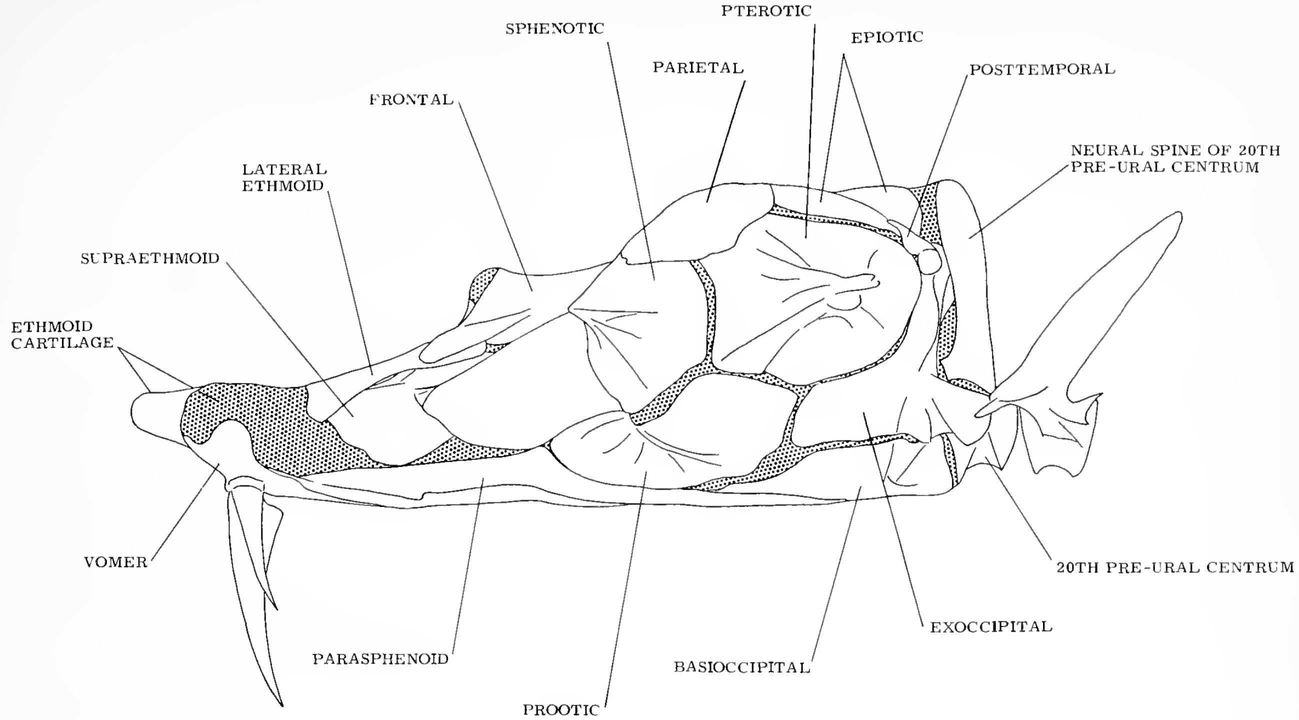

Figure 2. Lateral view of cranium of *Caulophryne jordani,* IOS, 68.0 mm.

Caulophryne jordani, 41.0–68.0 mm) was cleared and stained with alizarin red S following the trypsin digestion technique (Taylor 1967). In many cases dissections were made of uncleared specimens to confirm observations made on cleared and stained specimens and to determine ontogenetic changes. Bone terminology follows Pietsch (1972a) and Nybelin (1963). In osteological drawings cartilage is stippled, and where necessary for clarity, open spaces are rendered in solid black.

Unless otherwise indicated, all diagnoses and descriptions are based on females. For males and larvae see Bertelsen (1951:31–38). Material is deposited in the following museums and Institutions:

BMNH: British Museum (Natural History), London.
IOAN: Institute of Oceanography, Academy of Sciences of the USSR, Moscow.
IOS: Institute of Oceanographic Sciences, Surrey, England (formerly the National Institute of Oceanography).
ISH: Institut für Seefischerei, Hamburg.
LACM: Natural History Museum of Los Angeles County.
MCZ: Museum of Comparative Zoology, Harvard University.
MOM: Musée Oceanographique de Monaco.
ROM: Royal Ontario Museum, Toronto.
USNM: National Museum of Natural History, Washington.
ZMB: Zoologisches Museum der Humboldt-Universität, Berlin.
ZMUC: Zoological Museum, University of Copenhagen.

OSTEOLOGY

Figures 1–13

The osteology of *Caulophryne* was partially described by Regan (1926:16, fig. 7), Regan and Trewavas (1932:42, figs. 56–58), and Bertelsen (1951:31, fig. 8). In the following account, only those comparative aspects that need amending or that have not previously appeared in the literature are discussed.

Cranium (Figs. 1–6): the ethmoid cartilage of *Caulophryne* broadly covers the dorsal surface of the vomer, extending beyond the margins of this bone on all sides. Anteriorly and laterally the head of the vomer turns upward to cup the ethmoid cartilage. The ventral surface of the vomer may bear as many as five, recurved and depressible teeth arranged in a transverse row.

In oneirodids (Pietsch 1974a:8, figs. 1, 4) the symphysial cartilage of the upper jaw butts up against a nearly vertical supraethmoid bone. In contrast, backward movement of the upper jaw of *Caulophryne* is limited by the lateral extensions of the vomer; an elongate, narrow groove is formed between the parallel lateral ethmoids and the obliquely placed supraethmoid providing space within which the small symphysial cartilage (see below) can slide. The anterior part of the pterygiophore (basal bone) of the illicium does not lie in this narrow groove as stated by Regan (1926:16).

The frontals are considerably shorter than those of oneirodids (Pietsch 1974a, figs. 1, 2). They meet on the midline for most of their length. Anteriorly, they contribute to the extremely narrow orbital region, overlapping the posterior ends of the lateral ethmoids; posteriorly they become greatly expanded laterally.

The parietals of *Caulophryne* occupy a more anterior position than in oneirodids, and are far removed from the posttemporals. Each is expanded laterally in an oblique position, overlapping four other bones: the sphenotic laterally, the pterotic and epiotic posteriorly, and the supraoccipital medially. Anteromedially, each parietal is slightly overlapped by the respective frontal bone.

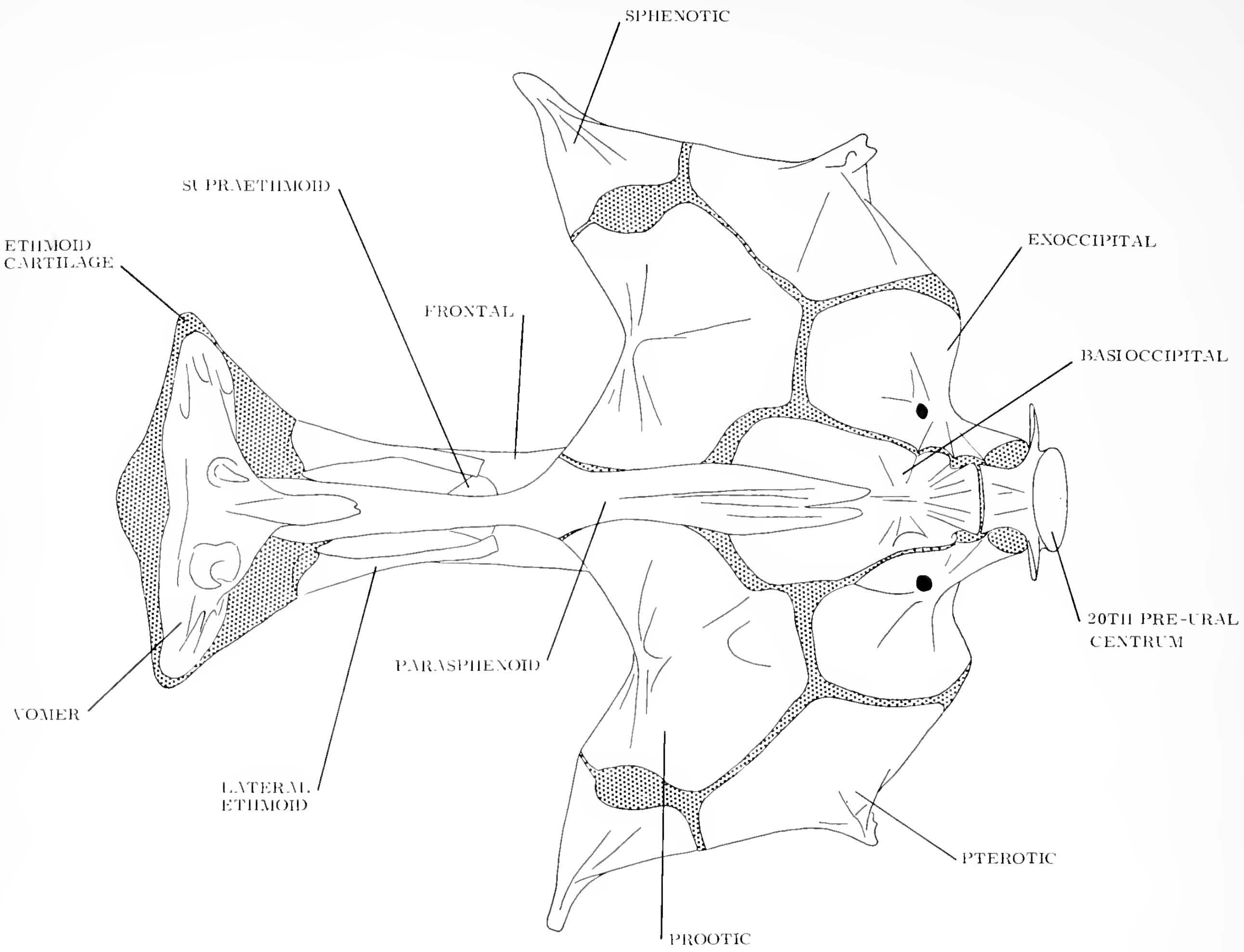

FIGURE 3. Ventral view of cranium of *Caulophryne jordani*, IOS, 68.0 mm.

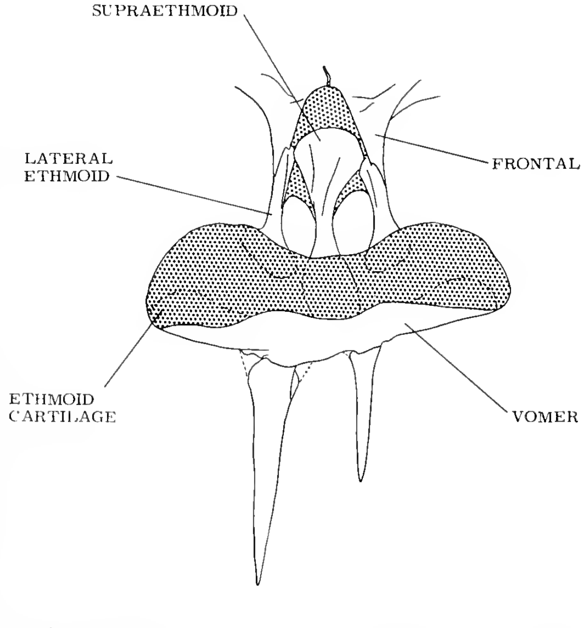

FIGURE 4. Anterior view of anterior half of cranium of *Caulophryne jordani*, IOS, 68.0 mm.

The pterosphenoid is absent (Pietsch 1972a:29).

Each sphenotic is a large, anterolaterally directed, cone-shaped element, the apex of which forms an elongate, blunt projection. On its ventral margin, each frontal, with the respective prootic bone, forms an oval-shaped cartilaginous area within which the anterior head of the double-headed hyomandibular articulates. The pterotic is also cone-shaped, but posterolaterally directed with a much larger base. A facet for the articulation of the posterior head of the hyomandibular bone is located ventrally at the apex of each pterotic.

In oneirodids (Pietsch 1974a:7, figs. 1–3) the prootics are separated anteriorly by the anteroventral process of the supraoccipital. In *Caulophryne* the supraoccipital maintains a dorsal position, largely overlapped anteriorly by the frontals, so that the prootics meet on the midline contributing to the formation of the posterior surface of the orbit.

Mandibular arch (Figs. 7, 8): Each premaxillary has a short articular process lying slightly behind and below an ascending process of similar size. Lying on the midline at the posterior tips of the ascending and articular processes of the premaxillae is a small, rounded symphysial cartilage loosely held by short ligaments and connective tissue. A postmaxillary process of the premaxillary is absent. The curved elongate portion of each premaxillary bears 12 recurved, depressible teeth of mixed sizes.

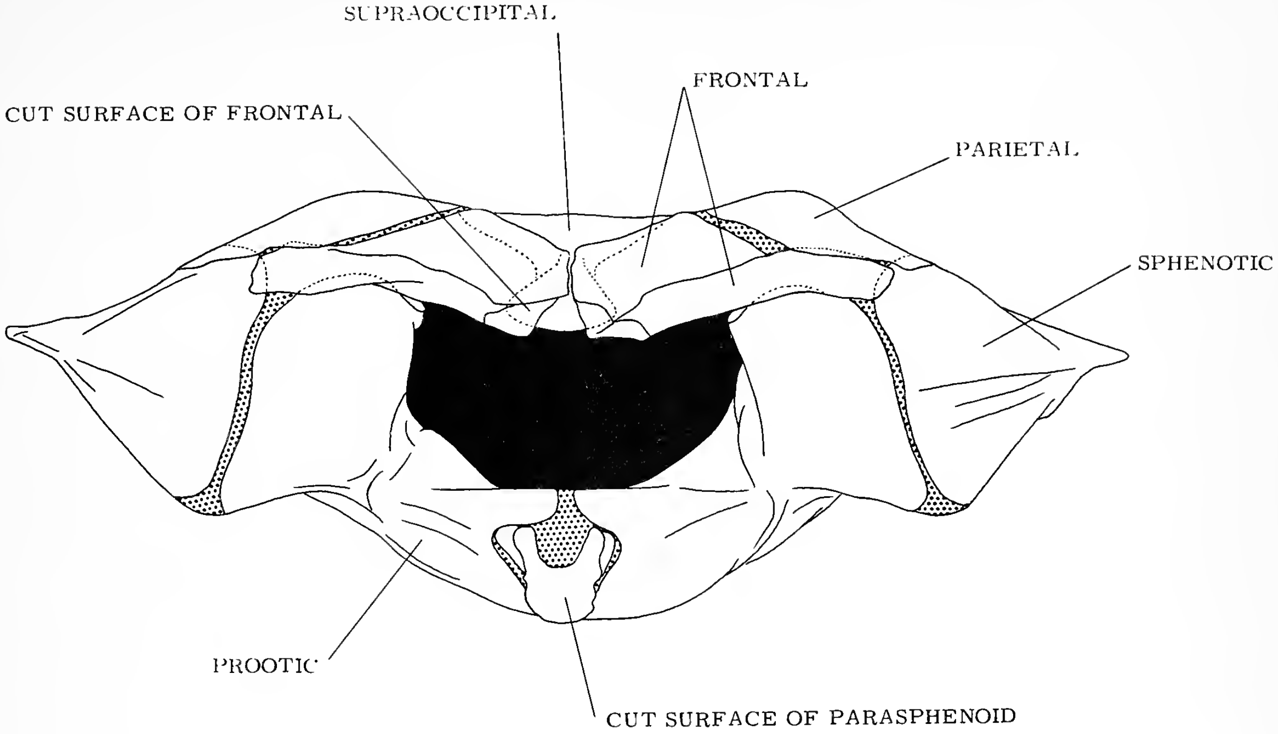

Figure 5. Anterior view of posterior half of cranium of *Caulophryne jordani*, IOS, 68.0 mm.

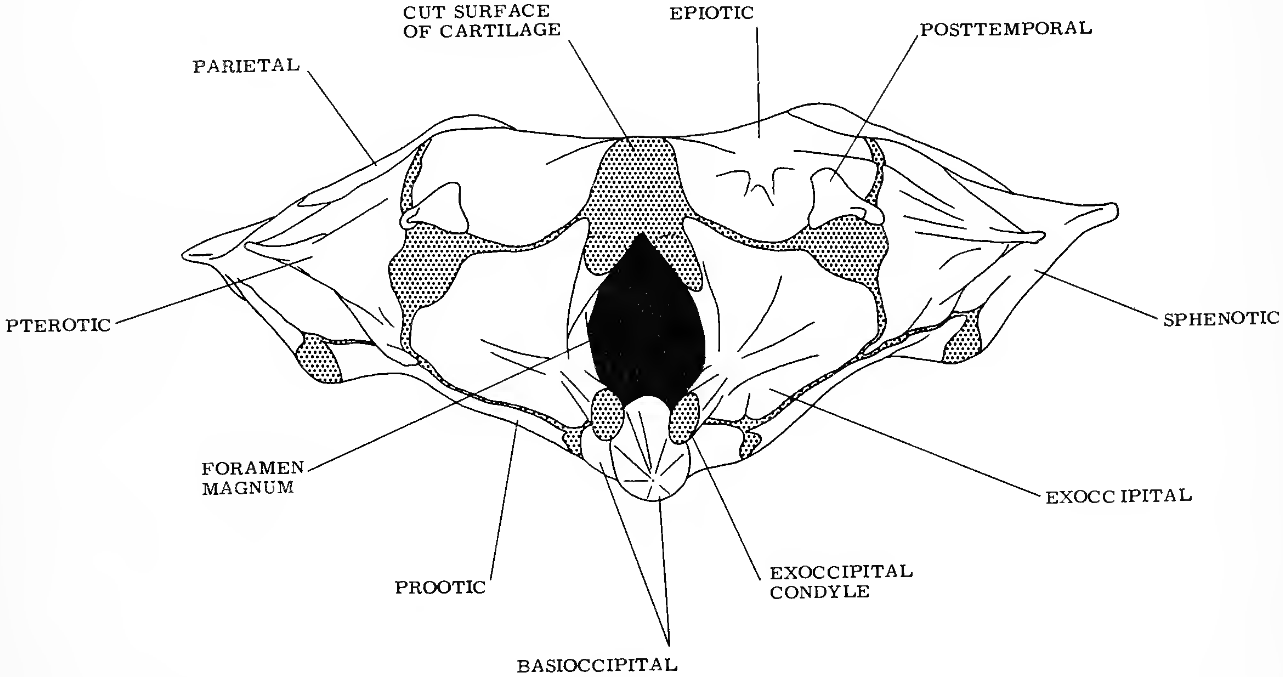

Figure 6. Posterior view of cranium of *Caulophryne jordani*, IOS, 68.0 mm.

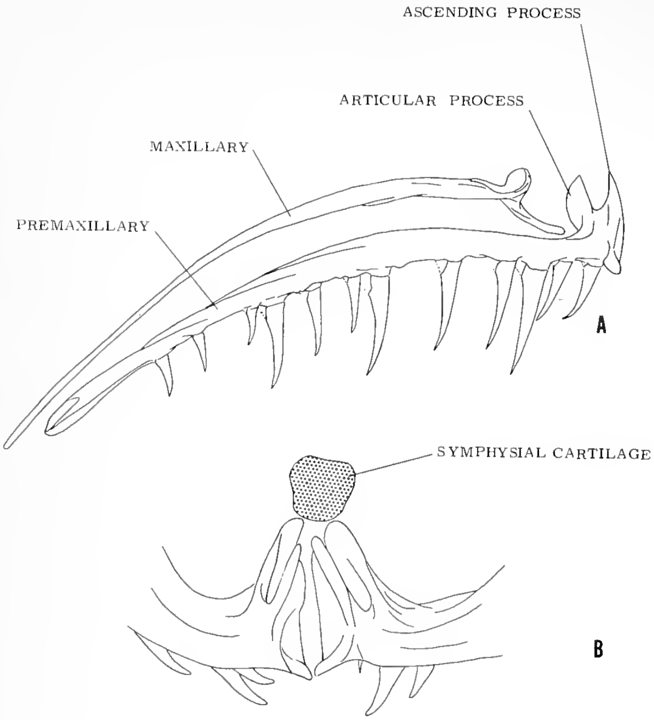

FIGURE 7. Upper jaw of *Caulophryne jordani:* A. IOS, 68.0 mm, lateral view of maxillary and premaxillary, right side; B. LACM 6844–3, 41.0 mm, lateral view of symphysis of premaxillaries showing symphysial cartilage.

The articular head of the maxillary consists of a slightly concave dorsal process which receives the anterior head of the double-headed palatine bone (see below), and a ventromedial projection which passes beneath, and provides support for, the premaxillary.

On each side, the posterior ends of the premaxillary and maxillary are united by a short ligament that passes posteriorly to attach to the ascending process of the articular. The anterior-maxillomandibular ligament (labial cartilage of Le Danois 1964; Pietsch 1972a:31), so well developed in oneirodids (Pietsch 1974a:9), is absent.

Anteriorly the dentaries curve to meet on the midline where they form a strong symphysial spine. The anterior half of each dentary bears nine to ten recurved, depressible teeth of mixed sizes.

Palatine arch (Fig. 8): The palatine arch is elongate and slender throughout. The anterior end of the palatine is T-shaped, consisting of a posterior head which is attached to the ethmoid cartilage, and an anterior head, which is loosely held within a shallow cavity of the dorsal process of the respective maxillary bone by connective tissue and by the palatomaxillary ligament. A narrow mesopterygoid is present but makes no contact with the metapterygoid.

Hyoid Arch (Figs. 8, 9): The suspensorium of *Caulophryne* is unusually narrow and elongate, and strongly directed obliquely backwards (compare with a typical oneirodid; Pietsch 1974a, fig. 8). The posterior head of the double-headed hyomandibular is the larger and longer of the two heads, forming a broad articulation with the pterotic. The anterior head of the hyomandibular articulates within a cartilaginous area formed between the sphenotic and prootic bones (the pterotic does not border on the articular area of the anterior head of the hyomandibular as it does in oneirodids; Pietsch 1974a:10, figs. 2, 3).

The greater length of the suspensorium, relative to other ceratioids (see above), is due largely to the extremely narrow, elongate quadrate. A large cleft is formed between the anterior and posterior portions of the quadrate within which lies the narrow ventral end of the symplectic. The interhyal is large compared to that of oneirodids (Pietsch 1974a, fig. 8).

The epihyal and especially the ceratohyal are narrow and elongate compared to those of oneirodids (Pietsch 1974a, fig. 9). In all but the most specialized lophiiforms (e.g., *Gigantactis, Neoceratias*) examined by me (Pietsch 1974a, Appendix B), the ceratohyal is notched anterodorsally to receive the posterior extension of the elongate, dorsal hypohyal (Rosen and Patterson 1969:439, fig. 57; Pietsch 1972a, fig. 14; 1974a, figs. 9, 10). In *Caulophryne* the anterodorsal notch is absent; the dorsal hypohyal is short and does not extend back over the dorsal surface of the ceratohyal. At midlength each ceratohyal forms a dorsal process that is securely attached to the anterolateral surface of ceratobranchial I by ligamentous connective tissue. A narrow ligament also extends anteriorly from the dorsal process of the ceratohyal to insert on the cartilage of the hypohyals.

The left ceratohyal of the 68.0 mm specimen (Fig. 9A) appears to be abnormally developed in having a deeply excavated posteroventral margin; together with the anteroventral corner of the epihyal, it supports only five branchiostegal rays: one anterior element (without an expanded head) on the inner side of the anterior, depressed portion of the ceratohyal, and four posterior elements (with expanded heads) on the outer surface of the elevated portion of the ceratohyal. The right ceratohyal (Fig. 9B) appears to be normally developed bearing six branchiostegals. Only one of these, however, is located anteromedially; five (all with expanded heads) are in a posterolateral position. Examination (by dissection) of all additional available material of *Caulophryne* showed the normal complement of six branchiostegal rays, two anteromedial elements, and four posterolateral elements. Previous to this, no lophiiform examined by me has had more than four posterior, laterally articulated branchiostegals; this number is considered diagnostic for the Paracanthopterygii as well as the Acanthopterygii (Greenwood, et al. 1966:353; Rosen and Patterson 1969:439).

Opercular bones (Fig. 8): The reduced operculum is bifurcated proximally forming two, extremely slender, and nearly parallel forks. The lower fork, more than three times the length of the upper, supports the suboperculum distally. The suboperculum is small, weakly-ossified (thought to be absent by Regan and Trewavas 1932:43, fig. 56), and deeply notched on its posterior margin. The large, posteriorly-curved preoperculum strengthens the entire length of the long hyoid arch extending dorsally along the posterior margin of the hyomandibular well past the point of the articulation of the operculum.

Branchial arches (Fig. 10): Pharyngobranchials I and IV are absent; those of the second and third arches are extremely well developed, bearing four to six recurved depressible fangs. Epibranchial I and ceratobranchial V are reduced, lying free in the connective tissue matrix. No ossified or cartilaginous remnants of hypobranchials or basibranchials could be found.

Vertebrae and caudal skeleton (Fig. 11): In the two cleared and stained specimens examined there are 20 vertebral centra (including the half-centrum to which is fused the hypural plate; Pietsch

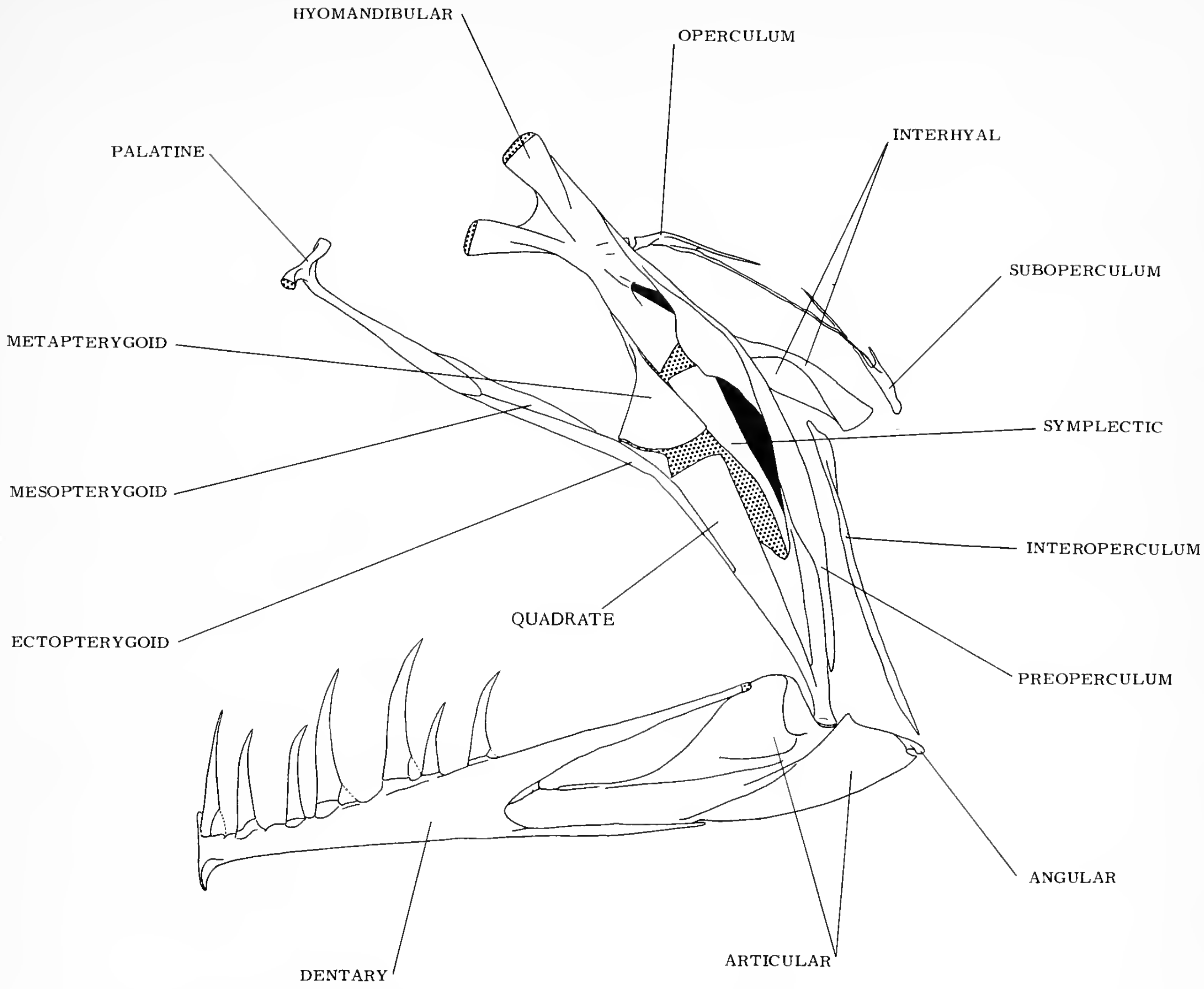

FIGURE 8. Lateral view of left side of lower jaw and suspensorium of *Caulophryne jordani*, IOS, 68.0 mm, with opercular bones in place.

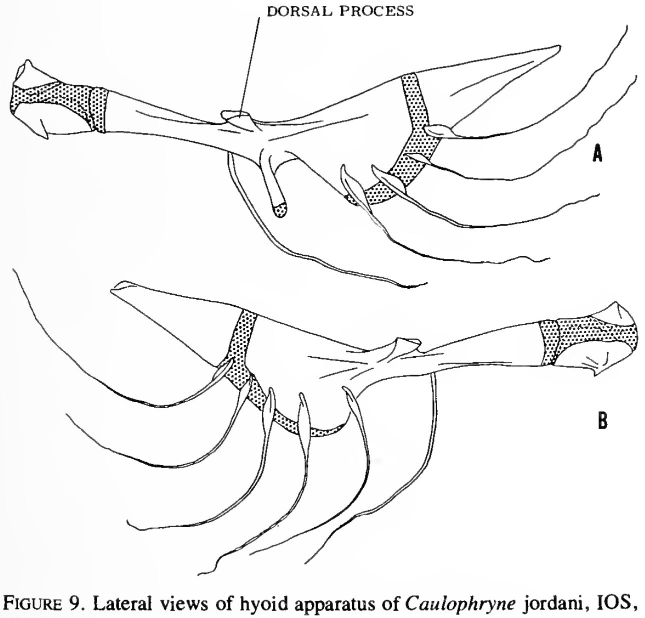

FIGURE 9. Lateral views of hyoid apparatus of *Caulophryne* jordani, IOS, 68.0 mm: A. Left side; B. Right side. Interhyal not shown.

1972a:38) of which ten or 11 are caudal vertebrae (those centra bearing complete haemal arches). There is a single, reduced epural (Pietsch 1972a:38). The hypural plate, deeply notched posteriorly in the larger cleared and stained specimen, but entire in the smaller specimen, bears the overlapping bases of eight principal caudal rays, the uppermost of which is exceptionally large. The central four caudal rays are bifurcated distally.

Median fins and illicial apparatus (Figs. 11, 12): The rays of the median fins are unusually long compared to other ceratioids, measuring, in extreme cases, more than twice the standard length. These rays are all biserial, segmented and unbranched, supported by elongate radials. In the 68.0 mm specimen there are 19 dorsal rays supported by 14 radials. The anteriormost radial supports the first dorsal ray and lies above the neural spine of the 12th pre-ural centrum. The posteriormost radial (which appears to be the product of two fused radials) supports the 14th and 15th dorsal rays and lies above the neural spine of the sixth pre-ural centrum. In the anal fin there are 17 rays supported by 14 closely associated radials. The anteriormost radial supports the first anal ray and lies below the haemal spine of the eighth pre-ural centrum. The posteriormost radial supports the 14th anal ray and lies below the haemal spine of the fourth pre-ural centrum.

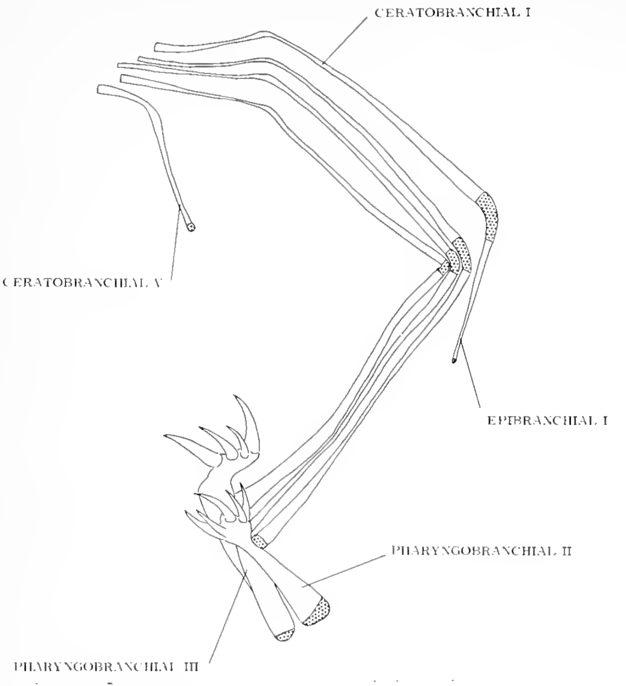

FIGURE 10. Branchial arches of *Caulophryne jordani*, IOS, 68.0 mm. The ventral part of the branchial basket is shown in dorsal view, the dorsal part (epibranchials and pharyngobranchials) is folded back and shown in ventral view.

The pterygiophore of the illicium, excluding its downturned, cartilaginous posterior portion, is approximately 16 percent of standard length. The remnant of the second cephalic ray is a minute, toothlike ossification that lies on the pterygiophore just behind the articulation of the illicial bone. The length of the illicial bone varies slightly among *Caulophryne* species and becomes longer proportionately with growth (Fig. 16).

Pectoral girdle, pectoral fin, and pelvic bones (Fig. 13): The posttemporals of *Caulophryne* are small compared to those of other ceratioids. In oneirodids each posttemporal meets the respective parietal and overlaps the pterotic, epiotic and exoccipital (Pietsch 1974a:14, figs. 1–3, 5, 6). The reduced posttemporal of *Caulophryne* overlaps only the pterotic and epiotic being far removed from both the parietal (see above) and the exoccipital.

The supracleithrum of *Caulophryne* is unusually large covering most of the lateral surface of the upper portion of the cleithrum. The lower portion of the cleithrum is reduced to a slender, thread of bone.

The scapula consists of a rounded ossification bounded on three sides by cartilage. The posterior margin of the ossified part of the scapula supports the uppermost pectoral radial. The coracoid consists of an expanded dorsal portion which meets the cartilage of the scapula, an anteroventral process which is connected by a ligament to the reduced lower portion of the cleithrum, and an extremely large posteroventral process which meets the slen-

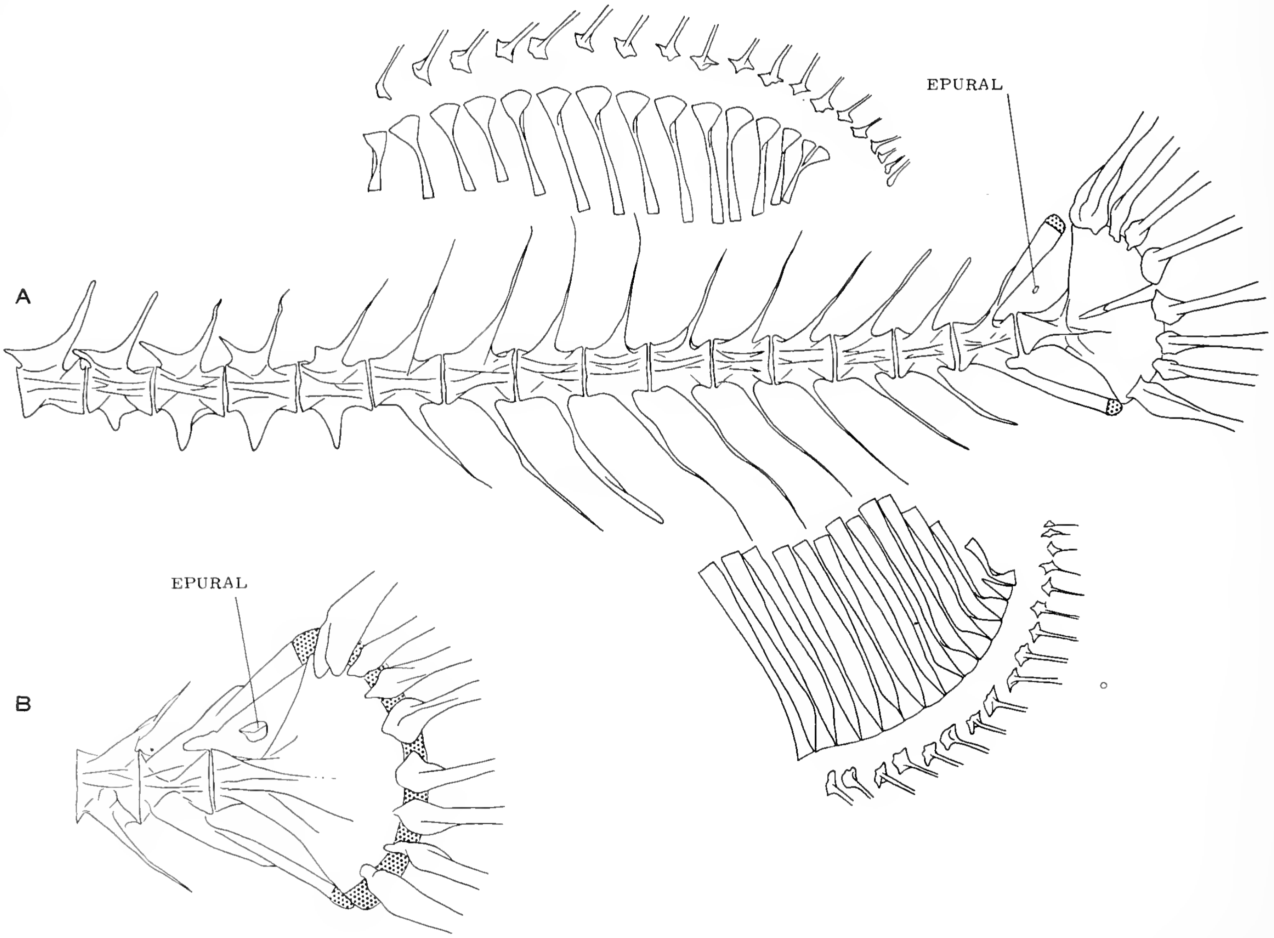

FIGURE 11. Vertebrae, caudal skeleton, and median fins of *Caulophryne jordani:* A. IOS, 68.0 mm; B. LACM 6844–3, 41.0 mm.

der postcleithrum distally.

There are two separate, well-ossified radials in fully metamorphosed specimens of *Caulophryne,* a small upper radial that bears no pectoral fin rays, and a much larger, distally expanded, lower radial that bears all the rays of the pectoral fin. The lower radial, however, is probably the product of two or more fused radials. A cleared and stained metamorphosing female (10.0 mm) clearly shows a deep, posterior cleft in the lowermost radial indicating at least three centers of ossification in the pectoral lobe (Fig. 13B). Fusion of pectoral radials appears to be common among ceratioids (Pietsch 1972a:41, fig. 23; Bertelsen and Struhsaker 1977).

Caulophryne is unique among ceratioids in the retention of pelvic fins in larval stages. Metamorphosis involves the loss of the pelvic fin rays but a pelvic bone is retained. The slender pelvic bones of *Caulophryne* lie free in the connective tissue matrix, far removed from the cleithrum. Unlike other ceratioids, these elements do not have cartilaginous distal tips.

Skin spines: Thorough microscopic examination of the skin of cleared and stained specimens failed to show the presence of embedded dermal spines.

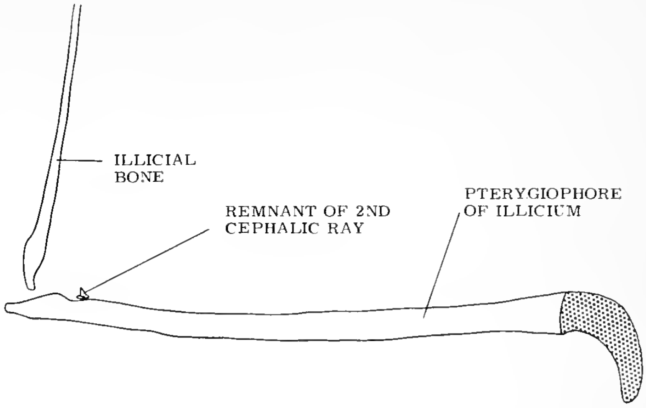

FIGURE 12. Illicial apparatus of *Caulophryne jordani,* IOS, 68.0 mm.

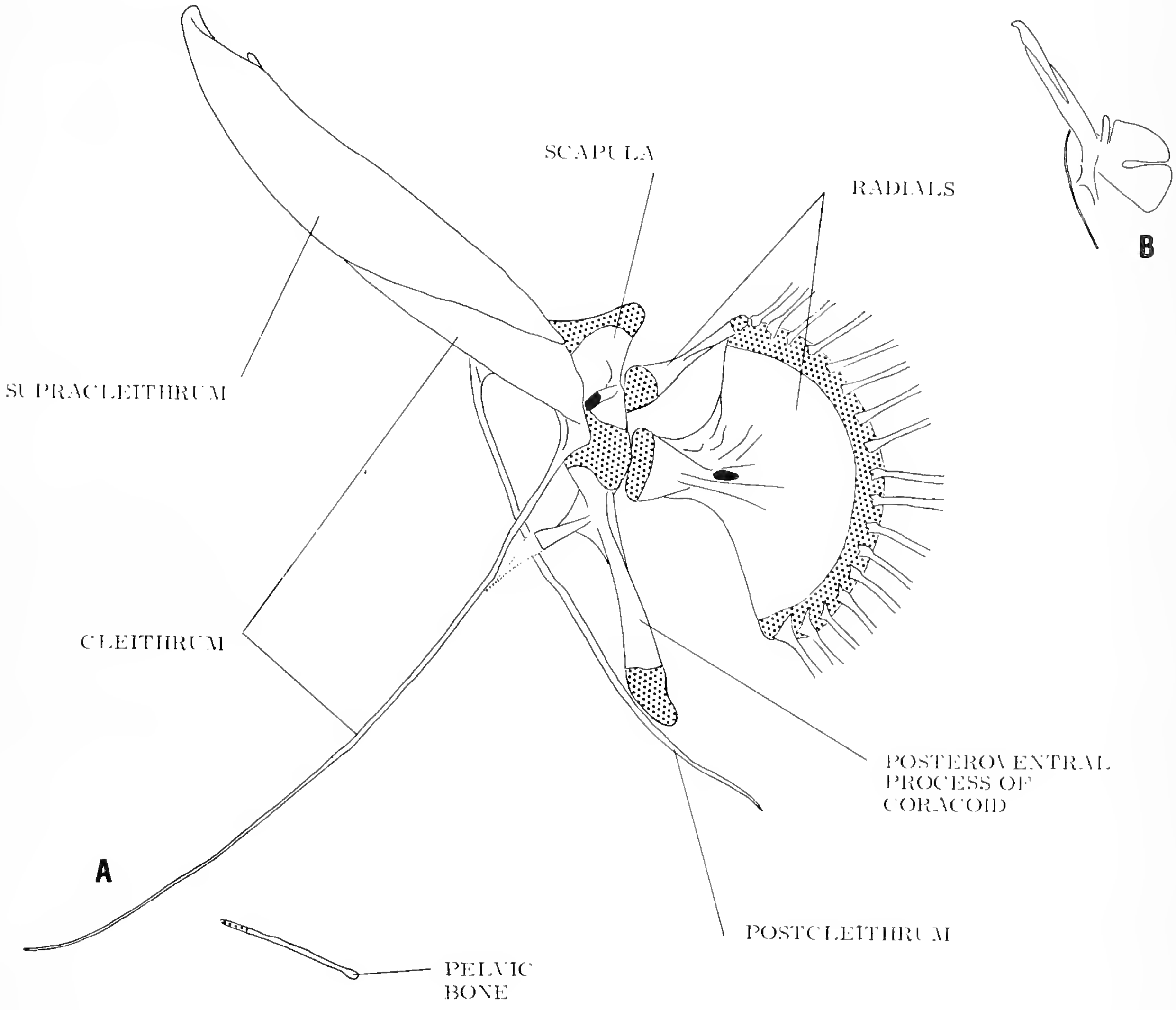

FIGURE 13. Lateral view of pectoral girdle, pectoral fin, and pelvic bone of *Caulophryne:* A. *C. jordani,* IOS, 68.0 mm; B. *C.* sp., IOAN, 10.0 mm.

SYSTEMATICS
Family Caulophrynidae Regan

Type genus *Caulophryne* Goode and Bean 1896.

Caulophrynidae Regan 1912:285, 288. Regan 1926:4, 16, 22. Regan 1930:195. Regan and Trewavas 1932:6, 14, 24, 25, 26, 42, 100. Roule and Angel 1933:55. Fowler 1936:1145, 1346. Belloc 1949:958. Bertelsen 1951:29, 31. Grey 1956:232. Monod 1960:684. Le Danois 1964:13, 14. Kobayashi, et al. 1968:8. Fitch and Lavenberg 1968:125, Fig. 69. Ueno 1971:102. Pietsch 1972a:18, 43, 45. Maul 1973:666. Pietsch 1976:783, 788, 791, 792.

DIAGNOSIS: The metamorphosed females of the family Caulophrynidae are distinguished from those of all other ceratioid families by having two pectoral radials, extremely elongate dorsal and anal rays, eight caudal rays, neuromasts of the acoustico-lateralis system located at the tips of extremely elongate filaments, larval pelvic fins, and the absence of an escal bulb. In addition, female caulophrynids share the following combination of characters: jaws equal anteriorly; supraethmoid present; parietals present, displaced anteriorly; pterosphenoid absent; anterior-maxillomandibular ligament absent (labial cartilage of Le Danois 1964; Pietsch 1972a:31); hyomandibular with a double head; 2 hypohyals; 6 (rarely 5) branchiostegal rays; operculum bifurcate, both forks reduced; suboperculum notched posteriorly, anterior spine or projection absent; pharyngobranchial I absent; epibranchial and ceratobranchial teeth absent; hypobranchials and basibranchials absent; a single, reduced epural; posterior margin of hypural plate notched in some specimens; only an ossified remnant of second cephalic ray present; posttemporal reduced; lower portion of cleithrum reduced; posteroventral process of coracoid well-developed; pelvic fins present in larvae; pelvic bones of metamorphosed females rod-like, not expanded distally; esca without denticles; skin spines absent.

DESCRIPTION: Body relatively short, globular (Figs. 14, 20); oral valve well-developed, lining inside of both upper and lower jaws; two nostrils on each side at the end of a single short tube; eye small and subcutaneous, appearing through a circular, translucent area of integument; gill opening oval in shape, situated just posteroventral to pectoral lobe; all four epibranchials closely bound together by connective tissue; posterior third of ceratobranchial I bound to ceratobranchial II; no opening behind fourth arch; gill filaments present on anterior-most tip of ceratobranchial I and full length of ceratobranchials II through IV; pseudobranch absent; pattern of placement of acoustico-lateralis system as described for other ceratioids (Pietsch 1969, 1972b, 1974a, b); neuromasts situated at the tips of elongate filaments; ovaries paired; two, short pyloric caeca.

Illicium becoming proportionately longer with growth (Fig. 16); anterior end of pterygiophore of illicium exposed, emerging on snout, its posterior end concealed under skin; esca unpigmented and translucent, simple, without elaborate appendages *(Robia),* or consisting of several branched appendages or numerous filaments *(Caulophryne);* escal bulb and central lumen absent; entire length of illicium covered with translucent filaments in some forms of *Caulophryne.*

Teeth slender, recurved and depressible, those in lower jaw less numerous, but slightly longer than those in upper jaw; number of teeth in lower jaw 14–34, in upper jaw 20–45; total number of teeth on vomer 1–5; pharyngobranchials II and III heavily toothed.

Color in preservative dark brown to black over entire surface of body (except for esca, and in some forms, the illicium) and oral cavity; viscera unpigmented.

D. 6–22; A. 5–19; P. 15–18 (Table 1); pelvics with 3–4 rays in larvae and metamorphosis stages, absent in adolescents and adults; C. 8 (2 unbranched – 4 branched – 2 unbranched).

The following measurements, expressed in percent of SL, are summarized for the females (20.0–142.0 mm) of all species: head length 27.2–41.7; head depth 32.7–45.4; head width 21.9–30.6; lower jaw 31.3–48.1; premaxillary 28.9–44.4; longest tooth in lower jaw 5.1–9.5; longest dorsal ray 63.4–155.3; longest anal ray 39.0–151.1; illicium 16.0–268.3.

Robia NEW GENUS

Type species: *Robia legula* new species.

DIAGNOSIS: The genus *Robia* is distinguished from *Caulophryne* (the only other member of its family) in having a considerably longer illicium (268.3 percent of SL), shorter jaw teeth,

Key to the Genera and Species of the Caulophrynidae

The following key will differentiate adolescent and adult female specimens only. Characters that allow specific identification of males (known from only three specimens, two of which are parasitically attached to females) and larvae (16 specimens; Bertelsen 1951:35, figs. 8, 11) are unknown.

1A. Illicium long, 268 percent of SL in a 41 mm specimen; D.6, A.5 .... *Robia legula* new genus and species (single known specimen, 41.0 mm).
1B. Illicium short, less than SL; D. 14–22, A. 12–19.......... *Caulophryne* 2
2A. Illicium with translucent filaments along entire length (Figs. 19, 21); length of illicium less than 35 percent SL (Fig. 16); D. 16–22, A. 14–19 (Table 1) 3
2B. Illicium without filaments (Fig. 17); length of illicium greater than 35 percent of SL (Fig. 16); D. 14–17, A. 12–16 (Table 1) .... *C. pelagica* (Brauer 1902).
3A. Upper jaw with more than 35 teeth in specimens larger than 40 mm, 30 or more in specimens larger than 20 mm (Fig. 18); illicium with more than 50 filaments along entire length in specimens larger than 32 mm (Fig. 21); D. 20–22 (rarely 19), A. 18–19 (rarely 17) (Table 1) .... *C. polynema* Regan 1930.
3B. Upper jaw usually with less than 35 teeth in specimens larger than 40 mm, less than 30 in specimens larger than 20 mm (Fig. 18); illicium with less than 15 filaments along length (Fig. 19); D. 16–18 (rarely 19), A. 14–17 (rarely 18) (Table 1) .... *C. jordani* Goode and Bean 1896.

TABLE 1
Frequencies of fin-ray counts for species of Caulophrynidae

Species	Dorsal										Anal									Pectoral			
	6	14	15	16	17	18	19	20	21	22	5	12	13	14	15	16	17	18	19	15	16	17	18
Robia legula	1										1											2	
Caulophryne pelagica		3	1		2							3	1		1	1				3	2	3	2
Caulophryne jordani				5	2	3	1							3	3	4		1			5	10	3
Caulophryne polynema							1	1	4	2							1	4	3	1	5	6	4
Total	1	3	1	5	4	3	2	1	4	2	1	3	1	3	4	5	1	5	3	4	12	21	9

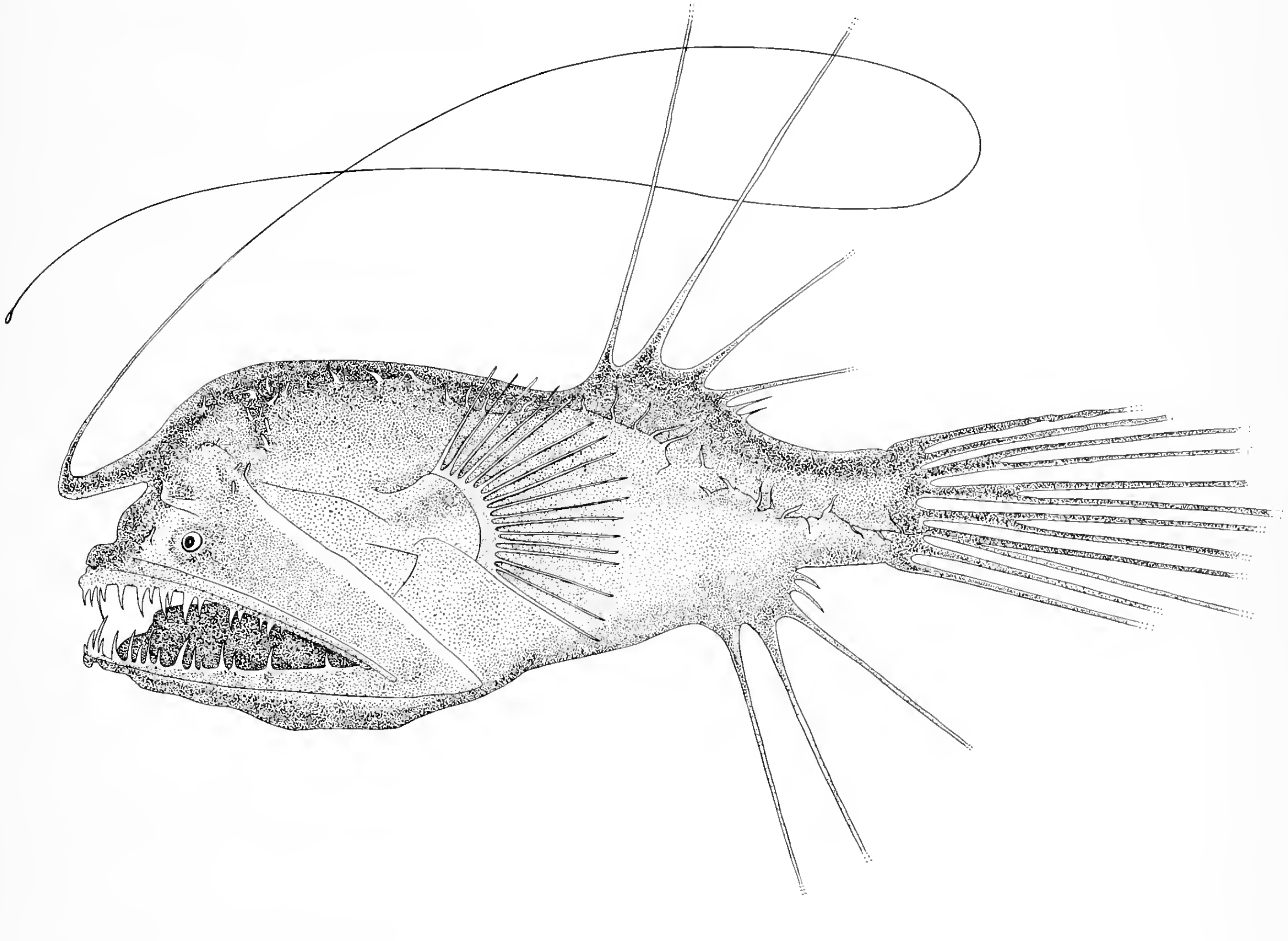

FIGURE 14. *Robia legula*, Holotype, LACM 36024–1, 41.0 mm. Drawn by Caryl Maloof.

and a smaller number of relatively short median fin rays (D.6, less than 65 percent of SL; A.5, less than 40 percent of SL).

ETYMOLOGY: The name *Robia*, to be treated as a noun of feminine gender, is given in honor of Bruce H. Robison (better known to his friends as "Robie") in recognition of his contributions to our knowledge of midwater fishes.

Robia legula NEW SPECIES

Figures 14, 15, 24

HOLOTYPE: LACM 36024–1, 41.0 mm; *ALPHA HELIX* Southeast Asian Bioluminescence Expedition Station 81, Banda Sea, 4° 56.5′S, 129° 59.5′E, RMT-8 with closing device, 1000–1500 m, 0416 – 0616 hr, 28 April 1975.

DESCRIPTION: Illicium without filaments, darkly pigmented along entire length except near esca; esca translucent, with two short lateral appendages and a slightly more opaque distal tip bearing three short appendages (Fig. 15).

Total number of teeth in lower jaw 31, in upper jaw 33; vomerine teeth 4; D. 6; A. 5; P. 17 (Table 1).

Measurements in percent of SL: head length 39.0; head depth 39.0; head width 23.4; lower jaw 47.6; premaxillary 37.8; longest tooth in lower jaw 5.1; longest dorsal ray 63.4; longest anal ray 39.0; illicium 268.3.

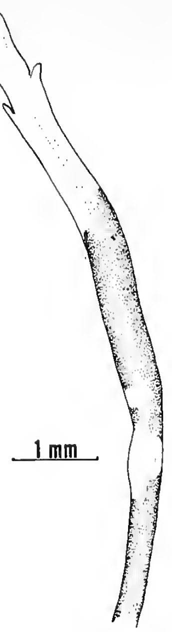

FIGURE 15. Esca of *Robia legula*, Holotype, LACM 36024-1, 41.0 mm.

Rest of characters as for genus and family.

DISTRIBUTION: *Robia legula* is known from a single specimen collected from the Banda Sea (4° 56.5′S, 129° 59.5′E) with an opening-closing trawl between 1000 and 1500 m.

ETYMOLOGY: The name *legula* is derived from the Latin *legula*, meaning collector or gatherer, alluding to the extraordinary collecting abilities of this anglerfish and its collector.

Caulophryne Goode and Bean 1896

Caulophryne Goode and Bean 1896:496, fig. 409 (type species *Caulophryne jordani* Goode and Bean 1896, by original designation and monotypy).

Melanocetus Brauer 1902:295 (in part; type species *Melanocetus johnsoni* Günther 1864, by monotypy). Brauer 1906:321, pl. 15, fig. 5 (after Brauer 1902).

Ceratocaulophryne Roule and Angel 1932:500 (type species *Ceratocaulophryne regani* Roule and Angel 1932, by monotypy). Roule and Angel 1933:55 pl. 3, figs. 26, 26A (after Roule and Angel 1932; expanded description).

DIAGNOSIS: The genus *Caulophryne* is distinguished from *Robia* (the only other member of its family) in having a considerably shorter illicium (less than 50 percent of SL), longer jaw teeth, and a greater number of relatively long median fin rays (D. 14–22, greater than 70 percent of SL; A. 12–19, greater than 60 percent of SL).

Caulophryne pelagica (Brauer 1902)

Figures 16–18, 24

Melanocetus pelagicus Brauer 1902:295 (original description, single specimen). Brauer 1906:321, plate 15, fig. 5 (after Brauer 1902). Regan 1926:22 ("probably a synonym of *C. jordani*").

Caulophryne pelagicus Regan 1912:288 (new combination; listed).

Caulophryne jordani Regan 1926:22 (in part; specimen later described as *C. ramulosa* sp. n. by Regan and Trewavas 1932). Kobayashi, et al. 1968:8–12, figs. 1, 2, tables 1, 2 (additional specimen; description).

Caulophryne ramulosa Regan and Trewavas 1932:100, 101, pl. 7, fig. 160 (original description; single specimen, previously recorded by Regan 1926, as *C. jordani;* in key) Bertelsen 1951:36, 37, tables 2, 3 (description; a synonym of *C. jordani pelagica*).

Caulophryne acinosa Regan and Trewavas 1932:100, 101, pl. 8, fig. 161 (original description; single specimen; in key). Bertelsen 1951:36, 37, tables 2, 3 (description; a synonym of *C. jordani pelagica*).

Caulophryne pelagica Regan and Trewavas 1932:100, 102, fig. 162 (new orthography; in key; description after Brauer 1902, 1906, esca figured). Bertelsen 1951:36, 37, fig. 9, table 3 (figure after Brauer 1906; a subspecies of *C. jordani*).

Caulophryne jordani pelagica Bertelsen 1951:33, 37, fig. 9, table 3 (in key; description, comparison with all known material; includes *C. ramulosa* and *C. acinosa*). Grey 1956:233 (synonymy; after Bertelsen 1951). Kobayashi, et al. 1968:9 (new specimen most similar to).

MATERIAL: Six known females, 11.0 – 92.0 mm.

Holotype of *Melanocetus pelagicus:* ZMB 17711, 11.0 mm; *VALDIVIA* Station 228, Indian Ocean, 2° 38′S, 65° 59′E, 0–2500 m, bottom depth 3460 m.

Holotype of *Caulophryne ramulosa:* ZMUC P9245, 57.0 mm; *DANA* Station 1209(1), Gulf of Panama, 7° 15′N, 78° 54′W, 3500 m wire, 1845 hr, 17 January 1922.

Holotype of *Caulophryne acinosa:* ZMUC P9244, 19.0 mm; *DANA* Station 3920(2), Indian Ocean, 1° 06′S, 62° 25′E, 3500 m wire, bottom depth 4630 m, 1830 hr, 9 December 1929.

NONTYPE MATERIAL: LACM 30619-6, 65.0 mm; *VELERO* IV Station 9903, 29° 30′N, 118° 54′W, 3-m IKMT, 0–834 m, 2315–0515 hr, 7 August 1964. LACM 36023-1, 13.0 mm; *ALPHA HELIX* Southeast Asian Bioluminescence Expedition Station 143, 0° 14.5′S, 128° 46.7′E, RMT-8, 1250–1500 m, 1715–1930 hr, 20 May 1975.

Fisheries Museum, Faculty of Fisheries, Hokkaido University F-1639, 92.0 mm; No. 3 Shichisei Maru, 42° 40′N, 144° 40′E, 0–500 m, 0800–1200 hr, 26 April 1967.

DIAGNOSIS: In addition to differences in escal morphology (Figs. 17, 19, 21), *C. pelagica* may be distinguished from *C. jordani* and *C. polynema* in having a slightly longer illicium (Fig. 16), fewer dorsal fin rays (Table 1), and by the absence of illicial filaments (Figs. 17, 19, 21). It is further separated from *C. jordani* by having a greater number of upper jaw teeth (Fig. 18). *Caulophryne pelagica* probably also has longer median fin rays than its congeners, but this character is difficult to quantify accurately because the distal ends of the rays are nearly always broken off.

DESCRIPTION: Illicium without filaments, darkly pigmented along entire length except near esca; esca consisting of five or six elongate, filamentous appendages: two, more lateral in position, bearing none to several side branches, and three or four, more distal, bearing numerous side branches; opaque areas absent (Regan and Trewavas 1932:101, 102, figs. 160–162; Fig. 17).

Total number of teeth in lower jaw 24–34, in upper jaw 28–40 (Fig. 18); vomerine teeth 2–3; D. 14–17; A. 12–16, P. 15–18 (Fig. 18, Table 1).

Measurements in percent of SL; longest tooth in lower jaw 5.8–6.8; longest dorsal ray 105–228; longest anal ray 132–174; illicium 31.6–43.9 (Fig. 16).

Rest of characters as for genus and family.

DISTRIBUTION: *Caulophryne pelagica* is represented by two specimens collected in the Indian Ocean, a third record from the Halmahera Sea, East Indies (13.0 mm, collected with a closing trawl between 1250–1500 m), a fourth from off Guadalupe Island, Mexico, a fifth off Japan, and a sixth specimen from the

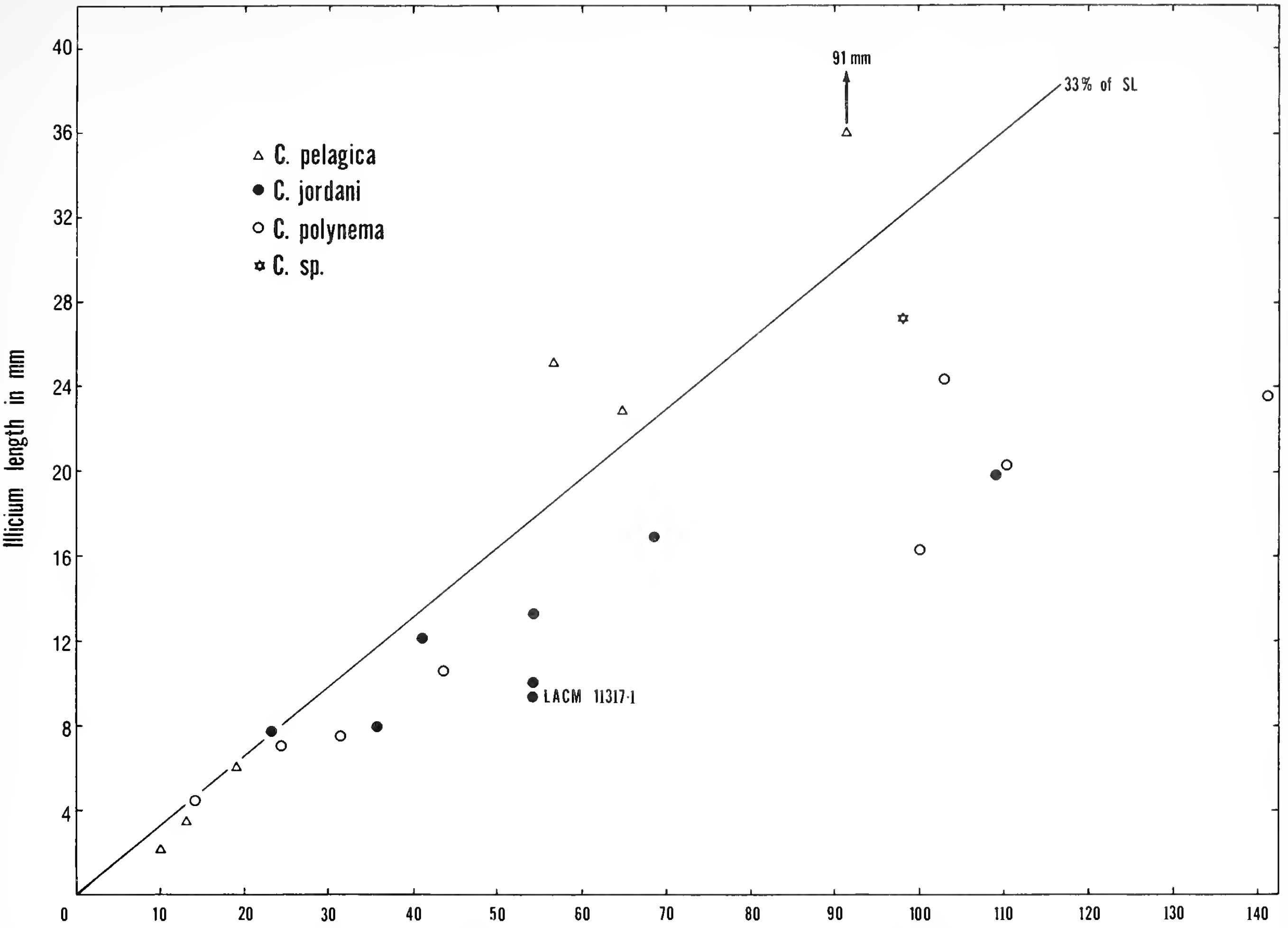

FIGURE 16. Illicial length versus standard length for *Caulophryne* species.

Gulf of Panama (Fig. 24).

COMMENTS: The results of this investigation confirm Bertelsen's (1951:36) opinion that *C. ramulosa* and *C. acinosa* are junior synonyms of *C. pelagica*. The illicia of the holotypes of all three are "well-preserved and constructed in a very similar fashion." Further, all three nominal forms agree in having a slightly longer illicium and fewer median fin rays than other species.

Caulophryne jordani Goode and Bean 1896

Figures 1–13, 16, 18, 19, 24

Caulophryne jordani Goode and Bean 1896:26*, 496, 541, fig. 409 (original description; single specimen; erroneous name in list of plates, index, figure caption). Jordan and Evermann 1898:2735 (description after Goode and Bean 1896). Jordan and Evermann 1900, fig. 957 (figure after Goode and Bean 1896). Gill 1909:586, fig. 24 (brief description and figure after Goode and Bean 1896). Regan 1912:288 (description after Goode and Bean 1896). Beebe 1926:422 (additional specimen). Regan 1926:4, 22, figs. 7, 16 (cranial osteology; expanded description). Beebe 1929:19 (additional specimen). Regan 1930:191, 193 (comparison with *C. polynema*). Regan and Trewavas 1932:6, 100, 101, fig. 159 (in key; brief description after Goode and Bean 1896; illicium figured).

← FIGURE 17. Esca of *Caulophryne pelagica*, LACM 30619–3, 65.0 mm.

Roule and Angel 1933:57 (comparison with *C. regani*). Bertelsen 1951:33–38, figs. 8–11, tables 2, 3 (description, comparison with all known material; three subspecies). Lavenberg and Ebeling 1967:195; fig. 5 (vertical distribution). Kobayashi, et al. 1968:8–12, figs. 1, 2, tables 1, 2 (additional specimen here referred to *C. pelagica;* description). Fitch and Lavenberg 1968:125–127, fig. 69 (distinguishing characters; natural history). Ueno 1971:102 (listed). Pietsch 1972a:29, 35, 36, 38, 41–43, 45, fig. 24(3) (osteology; otolith described, figured). Pietsch 1976:783 (reproduction).

Ceratocaulophryne regani Roule and Angel 1932:500 (original description; single specimen). Roule and Angel 1933:55–57, pl. 3, figs. 26, 26a (expanded description: figures of holotype, lateral, dorsal views). Belloc 1949:17 (listed). Bertelsen 1951:36, table 3 (a synonym of *C. jordani polynema*). Kobayashi, et al. 1968:8 (after Bertelsen 1951).

Caulophryne regani Fowler 1936:1347 (new combination; in key; description after Roule and Angel 1932, 1933).

Caulophryne jordani polynema Bertelsen 1951:33, 37 table 3 (in part; includes *C. regani* here referred to *C. jordani*). Grey 1956:233 (after Bertelsen 1951). Maul 1973:666 (after Bertelsen 1951).

Caulophryne jordani jordani Bertelsen 1951:33, 37, table 3 (in key; one of three subspecies; description, comparison with all known material). Grey 1956:232 (synonymy; after Bertelsen 1951).

MATERIAL: Eleven known females, 23.0–109.0 mm.

Holotype of *Caulophryne jordani:* USNM 39265, 26.0 mm; *ALBATROSS,* off Long Island, New York, 39° 27′N, 71° 15′W, 0–2335 m, 19 September 1887.

Holotype of *Ceratocaulophryne regani:* MOM Galerie: Level 3, Window 55, 38.0 mm; *HIRONDELLE II* Station 3279, west of the Azores, 38° 55′N, 34° 07′W, 0–3000 m, 23 August 1912.

NONTYPE MATERIAL: LACM 11317–1, 54.0 mm; *USNS ELTANIN* Station 1825, 39° 58′S, 160° 34′E, 3-m IKMT, 0–1625 m, 0218–0613 hr, 5 December 1966. LACM 33924–1, 54.0 mm; *VELERO IV* Station 17668, 32° 42′N, 118° 13′W; 3-m IKMT, 0–750 m, 0947–1505 hr, 28 June 1972. LACM 6844–3, 41.0 mm; *VELERO IV* Station 7325, 33° 36′N, 118° 24′ W, 3-m IKMT, 0–640 m, 1129–1420 hr, 9 March 1961 (cleared and stained).

IOS uncatalogued, 68.0 mm; *DISCOVERY II* Station 7480, 39° 55.2′N, 20° 07.4′W, RMT, 1250–1510 m, 0921–1321 hr, 7 November 1970 (cleared and stained). IOS uncatalogued, 36.0 mm; *DISCOVERY II* Station 8281–43, 31° 44′N, 63° 58′W, RMT-8, 1235–1260 m, 1358–1658 hr, 20 March 1973.

USNM 148469, ca. 75 mm; *ALBATROSS* Station 2530, 40° 53′N, 66° 24′W, 14 June 1885. USNM 216461, 54.0 mm; *OCEAN ACRE* Cruise 10, Station 21N, 31° 27′N, 64° 49′W, 3-m IKMT, 0–880, 1955–0135 hr, 6 June 1970.

ROM 27250, 109 mm; *BRANDAL* Tow 3, 50° 30′N, 49° 30′W, Engel Trawl, 0–1070 m, 0710–1000 hr, 12 July 1968.

MCZ 51279, 23.0 mm; *ANTON BRUUN* Cruise 6, Station 339B, APB 7231, 04° 14′S, 65° 02′E, 3-m IKMT, 0–275 m, bottom depth 3900 m, 0715–1610 hr, 30 May 1964.

DIAGNOSIS: In addition to differences in escal morphology (Figs. 17, 19, 21), *C. jordani* is distinguished from *C. pelagica* and *C. polynema* in having fewer upper jaw teeth (Fig. 18). The dorsal fin of *C. jordani* has a greater number of rays than that of *C. pelagica,* and fewer rays than that of *C. polynema* (Table 1). It is further distinguished from *C. pelagica* in having a slightly shorter, filamentous illicium; illicial filaments are absent in *C. pelagica,* but considerably more numerous in *C. polynema* (Figs. 17, 19, 21).

DESCRIPTION: Illicium pigmented except near esca, with 5 to 14 elongate (up to 87 percent of illicium length), translucent filaments along entire length, all but distal-most arising from posterior margin; esca with a posterolateral appendage bearing numerous short filaments and having a palmate (usually bilobed), opaque, distal tip; two distal appendages: the posterior-most slender, bearing numerous filaments, the anterior-most short and stout, opaque along posterior margin, and bearing numerous filaments (separation into two distal appendages not as evident in specimens less than 40.0 mm); and an elongate, filamentous, anterolateral appendage (illicial and escal filaments lost in holotype. see Regan and Trewavas 1932:101, fig. 159; Fig. 19).

Total number of teeth in lower jaw 16–26, in upper jaw 20–39; vomerine teeth 2–5; D. 16–19, A. 14–18, P. 16–18 (Fig. 18, Table 1).

Measurements in percent of SL: longest tooth in lower jaw 6.1–9.3; longest dorsal ray 78–115; longest anal ray 82–110; illicium 17.6–33.9 (Fig. 16).

Rest of characters as for genus and family.

DISTRIBUTION: *Caulophryne jordani* is known from all three major oceans of the world: seven records from the North Atlantic, one from the Indian Ocean, one from the Southern Ocean at approximately 40°S, 160°E, and two from off southern California. The two IOS specimens from the north Atlantic (36.0 and 68.0 mm) were collected with a closing trawl between 1235 and 1260 m, and 1250 and 1510 m, respectively (Fig. 24).

COMMENTS: The illicial apparatus of the holotype of *C. jordani* is somewhat damaged as indicated by a drawing provided by Regan and Trewavas (1932, fig. 159), and as noted by Bertelsen (1951:36). Filaments normally found along the length of the illicium and arising from the esca are absent. The posterolateral escal appendage and two distal appendages, however, remain intact. In these and all other characters the additional material (with a minor exception, see below) here assigned to *C. jordani* compares very well with the holotype.

Bertelsen (1951:37) believed that *Ceratocaulophryne regani* and *Caulophryne polynema* might be synonyms on the basis of similarity in illicial morphology, "position of the fins, and relative dimensions." This conclusion. however, is not supported by data provided by Jørgen Nielsen of the Zoological Museum, University of Copenhagen. In illicial and escal morphology, jaw tooth counts, and in dorsal and anal fin ray counts (16 and 16, not 15 and 14, respectively, as given by Roule and Angel 1933), the holotype of *C. regani* compares well with the material here recognized as *C. jordani. Ceratocaulophryne regani* is removed from the synonymy of *C. polynema* and placed within that of *C. jordani.*

The 54.0 mm specimen of *C. jordani* from the Southern Ocean (LACM 11317–1) differs from other individuals of this species in having a higher number of jaw teeth (Fig. 18).

Caulophryne polynema Regan 1930

Figures 16, 18, 20, 21, 24

Caulophryne polynema Regan 1930:191–195, figs. 1–3 (original description; single female specimen with parasitically attached male). Parr 1930:131, fig. 4 (figure after Regan 1930). Regan and Trewavas 1932:100, 101 (in key; description after Regan 1930). Fowler 1936:1347 (in key; description after Regan 1930). Bertelsen 1951:36, 37, fig. 12, table 3 (figure after Regan 1930; a subspecies of *C. jordani*). Pietsch 1976:789 (reproduction).

Caulophryne jordani polynema Bertelsen 1951:33, 37, fig. 12, table 3 (in key; description, comparison with all known material; includes

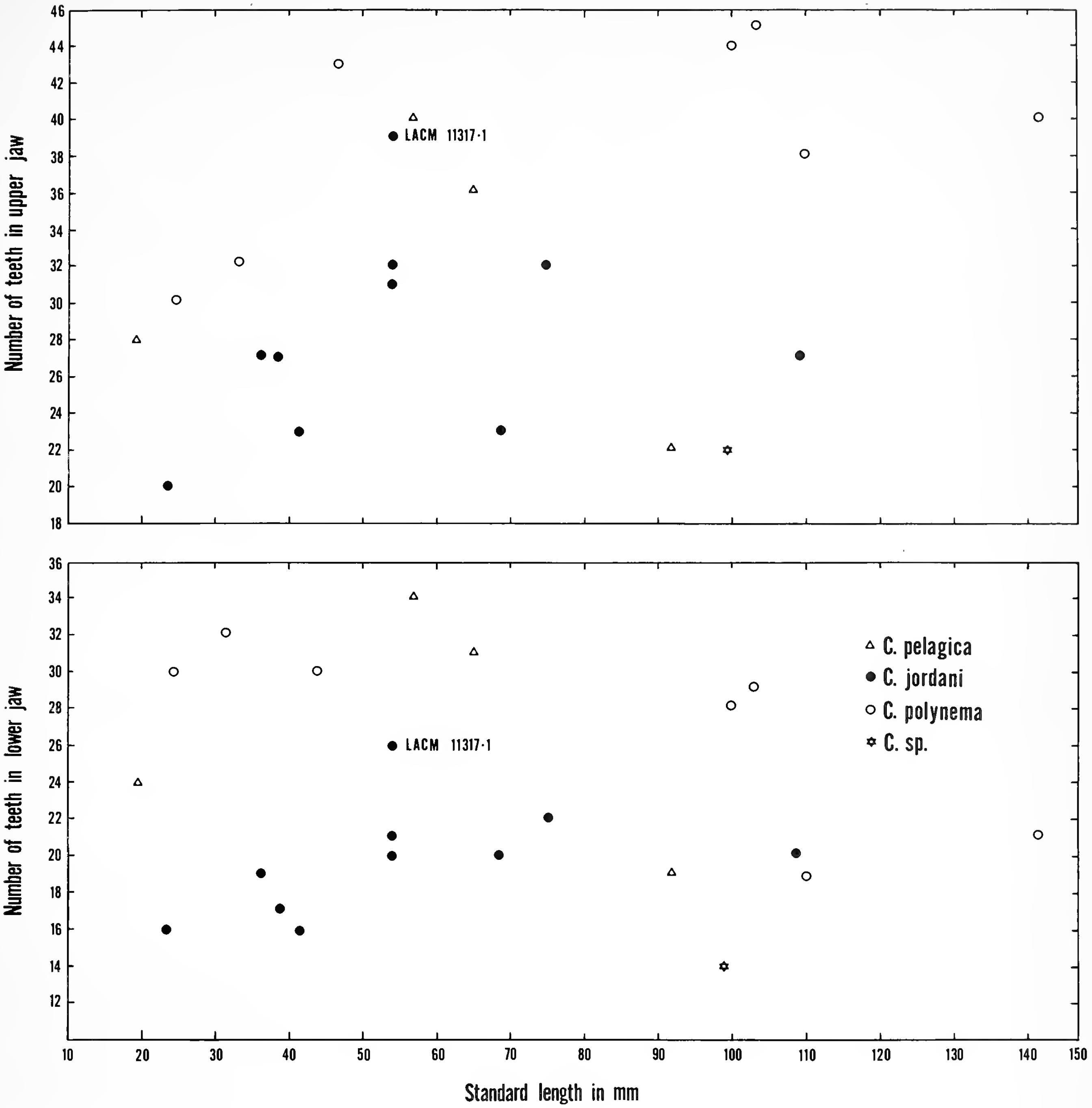

FIGURE 18. Number of teeth in upper and lower jaws versus standard length for *Caulophryne* species.

Ceratocaulophryne regani Roule and Angel 1932). Grey 1956:233 (synonymy; after Bertelsen 1951).

MATERIAL: Nine known females, 14.0–142.0 mm.

Holotype of *Caulophryne polynema:* BMNH 1930.2.7.1, 142 mm; "long line, in deep water," off Funchal Bay, Madeira; 1 February 1929.

NONTYPE MATERIAL: LACM 33923–1, 103 mm; *VELERO IV* Station 14962, 33° 10′N, 118° 31′W, 3-m IKMT, 1000 m wire, 0455–0943 hr, 10 February 1971. LACM 30619–3, 32.0 mm; *VELERO IV* Station 9903, 29° 30′N, 118° 54′W, 3-m IKMT, 0–834 m, 2315–0515 hr, 7 August 1964. LACM 32772–1, 24.5 mm; *TERITU* Cruise Vanilla Fudge, Station 69.11.4, 22° 00′N, 158° 00′W, 3-m IKMT, 0–1150 m, 1225–1635 hr, 12 November 1969. LACM 35897–1, 14.0 mm; *TERITU* Station 74.5.7, 21° 20–30′N, 158° 20–30′W, 4-m IKMT, 0–1000 m, 1405–1650 hr, 25 May 1974.

IOS uncatalogued, 110 mm; *DISCOVERY II* Station 8275, 32° 01.4′N, 50° 33.5′W, RMT, 0–1000 m, 2339–0150 hr, 5 March

FIGURE 19. Esca of *Caulophryne jordani*, LACM 33924-1, 54.0 mm.

1973. IOS uncatalogued, 100 mm; *DISCOVERY II* Station 7856-50, 30° 03.7′N, 23° 00.2′W, RMT, 1000-1250 m, 0917-1317 hr, 5 April 1972. IOS uncatalogued, 11.5 mm; *DISCOVERY II* Station 7089-8, 17° 45′N, 25° 17′W, RMT, 900-1010 m; 0320-0659 hr; 13 November 1969.

ISH 3000/71, 44.0 mm; *WALTHER HERWIG* Station 510/71; 27° 18′N, 19° 44′W; CMBT-1600, 0-2000 m; 1752-2151 hr; 20 April 1971.

DIAGNOSIS: In addition to differences in escal morphology (Figs. 17, 19, 21), *C. polynema* is distinguished from *C. pelagica* and *C. jordani* in having a greater number of dorsal fin rays (Table 1) and a highly filamentous illicium (Figs. 17, 19, 21). It is further separated from *C. pelagica* in having a slightly shorter illicium (Fig. 16), and from *C. jordani* in having more upper jaw teeth (Fig. 18).

DESCRIPTION: Illicium lightly pigmented along anterior margin (fully pigmented in 44.0 mm specimen), and bearing numerous, elongate (up to 71 percent of illicium length), translucent filaments, most of which arise from posterior margin; more than 50 filaments in specimens larger than 32 mm, reduced to approximately 10 in smaller specimens; esca consisting of a posterolateral appendage with a palmate (usually bilobed), opaque, distal tip, and a tapering terminal appendage with an opaque distal tip; escal appendages highly filamentous in specimens larger than 44 mm, number and length of filaments reduced in smaller specimens (most escal filaments lost in holotype, see Regan, 1930:193, fig. 2; Fig. 21).

Total number of teeth in lower jaw 19-32, in upper jaw 30-45; vomerine teeth 1-3; D. 19-22, A. 17-19, P. 15-18 (Fig. 18, Table 1).

Measurements in percent of SL: longest tooth in lower jaw 5.6-9.5; longest dorsal ray 70-155; longest anal ray 60-151; illicium 16.0-32.1 (Fig. 16).

Rest of characters as for genus and family.

DISTRIBUTION: Five specimens of *C. polynema* have been collected from the eastern north Atlantic Ocean as far west as approximately 50° W. Four additional records are known from the eastern north Pacific: two from Hawaii and two from off southern California. The 100 mm IOS specimen from the eastern north Atlantic was captured with a closing trawl between 1000 and 1250 m (Fig. 24).

COMMENTS: *Caulophryne polynema* was separated by Regan and Trewavas (1932:100) from the other species because of its higher number of dorsal and anal-fin rays. Bertelsen (1951:36) however, noted that the high number of fin rays in caulophrynids (compared to other ceratioids) has such a large individual variation (D. 14 to 22, A. 12 to 19) that "we can scarcely attach much weight to this character." The greater amount of material available now indicates that despite this variation within the genus, fin-ray counts are of significant taxonomic importance. *Caulophryne polynema* can nearly always be separated from its congeners by its greater number of dorsal and anal-fin rays (see Key, Table 1).

Caulophryne species

Figures 16, 18, 22, 23

LACM 36025-1, female, 98.0 mm with parasitic male, 12.0 mm; *ALPHA HELIX* Southeast Asian Bioluminescence Expedition Station 37, Midwater Trawl 22, 4° 56′S, 129° 26′E, RMT-8, 0-2000 m, 0320-0530 hr, 12 April 1975.

DESCRIPTION OF FEMALE: Illicium unpigmented with approximately 30 elongate (up to 25 percent of illicium length), translucent filaments along entire length, those on proximal half of illicium arising from posterior margin; esca, a tapering appendage bearing numerous simple filaments and four highly branched lateral appendages: three, more proximal in position, one, more distal; opaque areas absent (Fig. 22).

Gonads well developed (right ovary, 22 mm long or 22.4 percent of SL, containing numerous eggs approximately 0.3 mm in diameter).

Total number of teeth in lower jaw 14, in upper jaw 22;

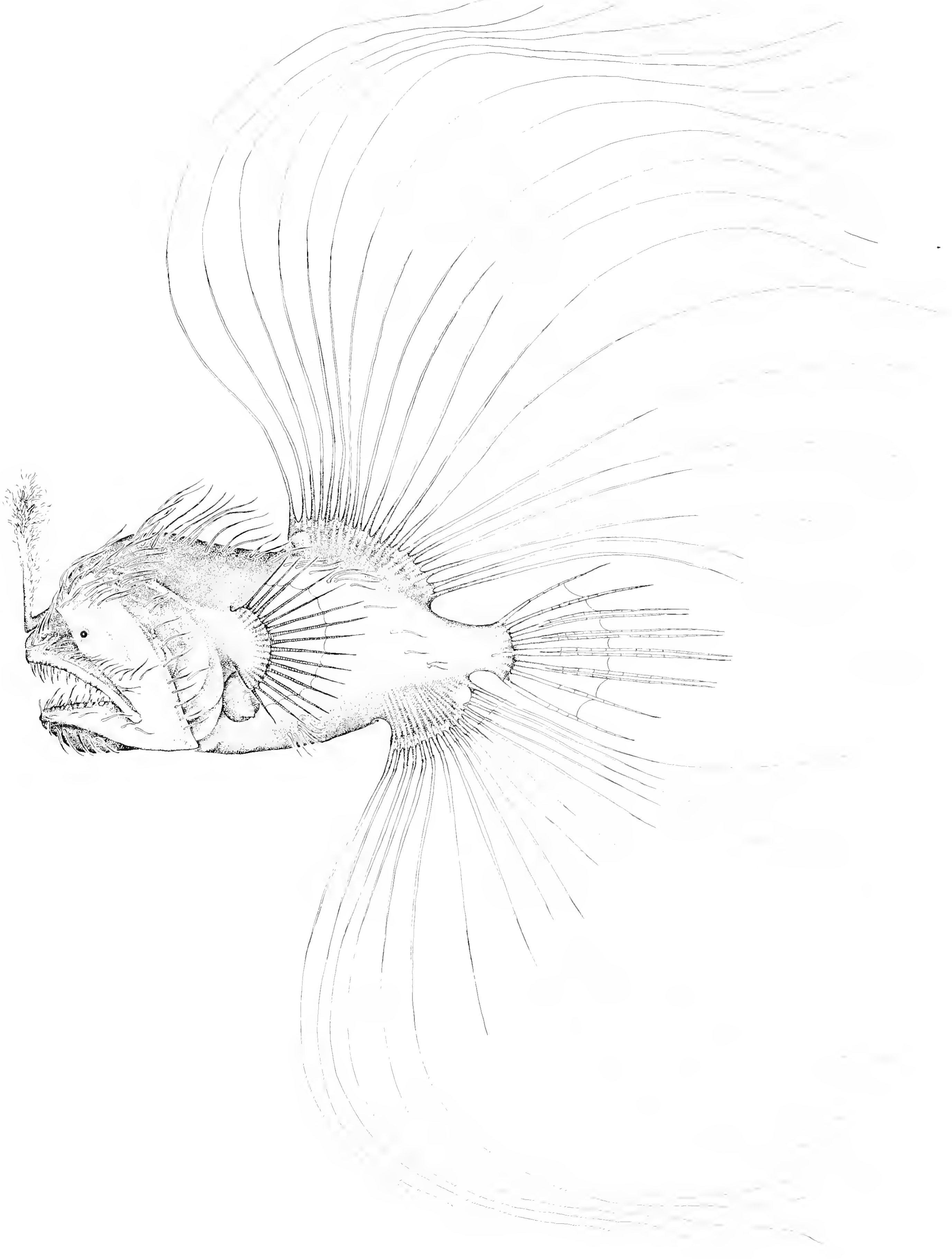

FIGURE 20. *Caulophryne polynema*, LACM 33923–1, 103 mm. Drawn by Elizabeth Anne Hoxie.

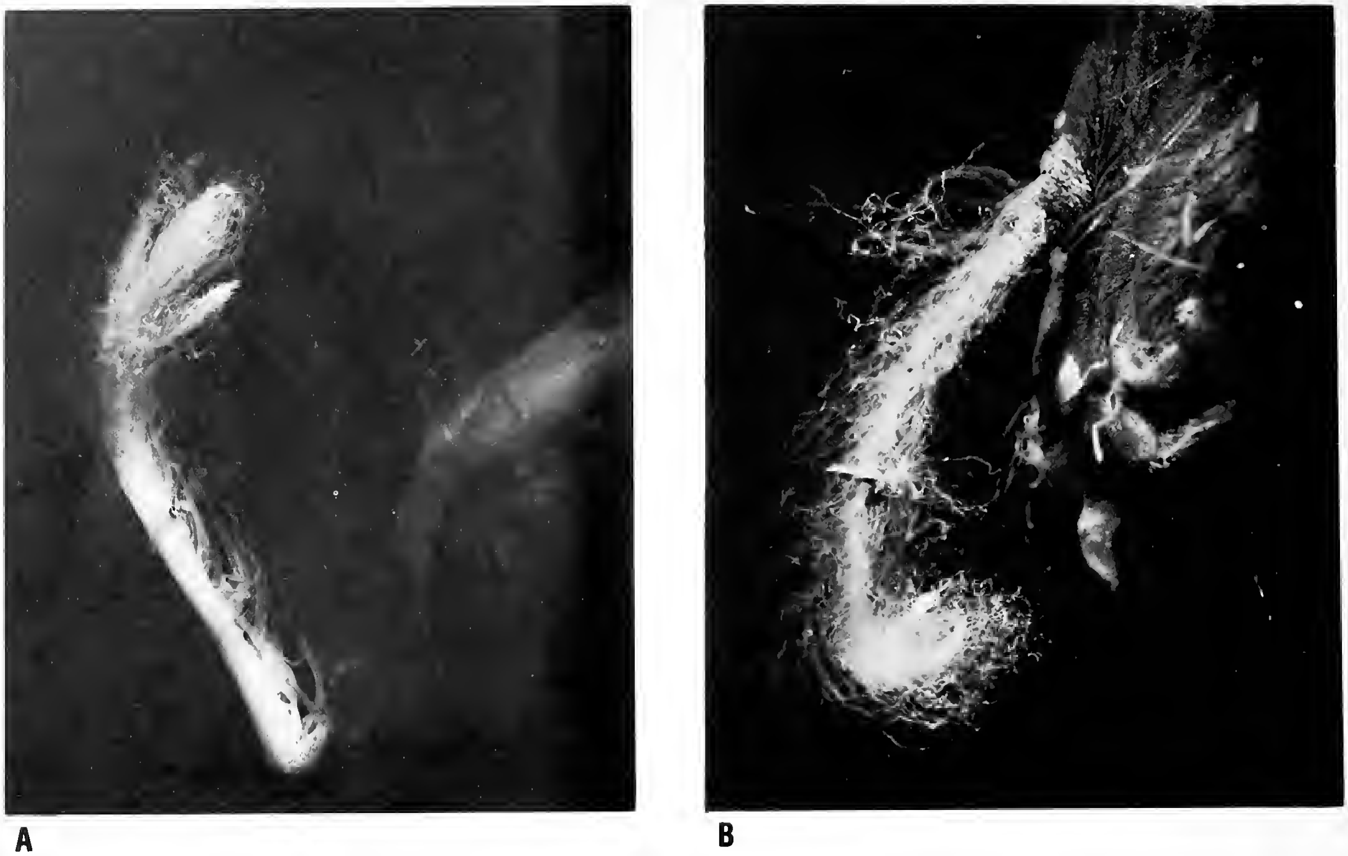

FIGURE 21. Escae of *Caulophryne polynema:* A. IOS, 100 mm; B. IOS, 110 mm. Courtesy of G. Brovard and E. Bertelsen.

vomerine teeth 1; D. 17, A. 15, P. 16–16 (Fig. 18, Table 1).

Measurements in percent of SL: longest tooth in lower jaw 9.2; longest dorsal ray 95+; longest anal ray 95+; illicium 27.6 (Fig. 16).

Rest of characters as for genus and family.

DESCRIPTION OF MALE: Upper and lower denticulars (Bertelsen 1951:21) embedded in an unpigmented, conical papilla on belly of female; passageway from outside into pharynx and out through gill openings retained (Pietsch 1976:790); eyes well developed; nostrils degenerate; gills developed; testes large (2.3 mm long, 19.2 percent of SL); dorsal, anal and pectoral-fin ray counts undetermined; pelvics absent; characteristic gelatinous envelope of larvae absent; entire head and body lightly pigmented (Fig. 23).

COMMENTS: This female and attached male cannot reasonably be placed within the material of any of the three recognized species of *Caulophryne*. The female has the elongate, branched escal appendages characteristic of *C. pelagica* but also the illicial filaments found only in *C. jordani* and *C. polynema* (compare Figs. 17, 19, 21, 22). The illicium appears to be slightly longer than that of *C. jordani* and *C. polynema,* but shorter than that of *C. pelagica* (Fig. 16). Jaw tooth counts are at the bottom of the range of variation for females of all species combined (Fig. 18). Finally, fin-ray counts compare best with *C. jordani* (Table 1).

The attached male (Fig. 23) represents the second example of sexual parasitism in the Caulophrynidae. It does not differ in any significant way from the previously described specimen (Bertelsen 1951:37, fig. 12).

Caulophryne setosus Goode and Bean 1896
NOMEN NUDUM

Caulophryne setosus Goode and Bean 1896:26*, 541, fig. 409.

COMMENTS: This name appears in a figure caption, and is entered in the list of plates and index of Goode and Bean's (1896) original description of *Caulophryne jordani,* without application to a description or type. This error was caught by Jordan and Evermann (1898:2735): "plate named *C. setosus,* by slip in proof reading." The name *setosus* also appears in the catalog of fishes of the National Museum of Natural History (S.J. Karnella, personal communication).

Caulophryne racemosa Monod 1960
NOMEN NUDUM

Caulophryne racemosa Monod 1960:687, fig. 80.

COMMENTS: This name appears in a figure illustrating stages of specialization of lophiiform pectoral radials. There is no application to a description or type. No doubt, Monod (1960) meant to refer to *C. ramulosa*. His figure was taken from Regan and Trewavas' (1932, fig. 58) illustration of the pectoral radials of the holotype of this nominal species.

DISCUSSION

The discovery of yet another new ceratioid genus brings the total number of genera based on females to 34. Although new forms continue to be described, it is unlikely that the total number of ceratioid species will increase significantly (Bertelsen 1951:28). In the last ten years 19 forms have been resurrected from synonymy or described as new (Pietsch 1969, 1972b, 1973, 1974a, b, 1975, 1978; Bertelsen 1973; Nolan and Rosenblatt 1975). During this same time, 28 nominal forms have fallen into synonymy, thus actually decreasing the number of recognized forms.

More so than any other ceratioid group, the caulophrynids exhibit a confusing mosaic of primitive and derived character states. Utilizing the variation found within the entire order Lophiiformes as representing the ancestral character pool for the Caulophrynidae, the following character states that describe *Caulophryne* are considered primitive:

1. frontal bones short, posterior in position, meeting on midline in front of supraoccipital (this is the condition of the frontals in lophioids and antennarioids; and, in addition to caulophrynids among ceratioids, the Neoceratiidae).
2. illicial trough absent (a narrow depression, usually running the full length of the cranium, is present in most ceratioids to receive the pterygiophore of the illicium; it is absent in caulophrynids and neoceratiids as well as in lophioids and antennarioids).
3. dorsal ceratohyal process present (this process is present in lophioids and antennarioids, but absent in all other ceratioids).
4. single epural present (no trace of an epural is found in any other ceratioid; lophioids and antennarioids, except for brachionichthyids, have one epural).
5. high number of median-fin rays (although *Caulophryne* exhibits a slight increase over the already high number of median-fin rays characteristic of lophioids and antennarioids, this probably represents a primitive condition over the greatly reduced median-fin ray counts of most other ceratioids; exceptions include some gigantactinids, neoceratiids, and melanocetids).
6. median-fin rays exceptionally long (like those of larval and young lophioids and antennarioids, but unlike any other ceratioid).
7. sexual dimorphism in the illicial apparatus of larval stages possibly absent (the 16 known caulophrynid larvae all have a well developed outer illicial rudiment, a structure normally found only in female ceratioids; the sex of these larvae cannot be determined from examining the gonads, but since it seems unlikely that only one sex is represented, Bertelsen (1951:31) suggested that the sexual dimorphism characteristic of other larval ceratioids, but absent in lophioids and antennarioids, might be absent in caulophrynids as well).
8. escal bulb absent (the esca of caulophrynids is not a bulbous, bacteria-containing organ as in other ceratioids but a tuft of filaments like that of many lophioids and antennarioids; in addition, Bertelsen (1951:31) stated that the illicium of caulophrynid larvae "is not globular or club-shaped as in most other female ceratioid larvae, but more finger-like as in certain antennarioid larvae."
9. posteroventral coracoid process present (this process is also found in antennarioids; among ceratioids it is present in ceratiids, in the oneirodid genera *Spiniphryne* and *Oneirodes*, and present, but cartilaginous in gigantactinids).
10. pectoral fins exceptionally large, especially in larvae and young (like those of larval and young lophioids and antennarioids, as well as larval gigantactinids among ceratioids; Bertelsen 1951:35, 148, figs. 11, 99, 104).
11. pelvic fins retained in larval stages (pelvic fins, well developed in all lophioids and antennarioids, are not present in larvae or adults of any other ceratioid).

Caulophrynids are considered derived in having the following character states:

1. parietals anterior in position, far removed from posttemporals and expanded laterally.
2. pterosphenoid absent (also absent in linophrynids and gigantactinids).
3. anterior maxillomandibular ligament absent (also absent in linophrynids, gigantactinids and neoceratiids).
4. dorsal hypohyal reduced (absent in *Gigantactis*).
5. hyoid apparatus narrow and elongate (similar in linophrynids, gigantactinids, and neoceratiids).

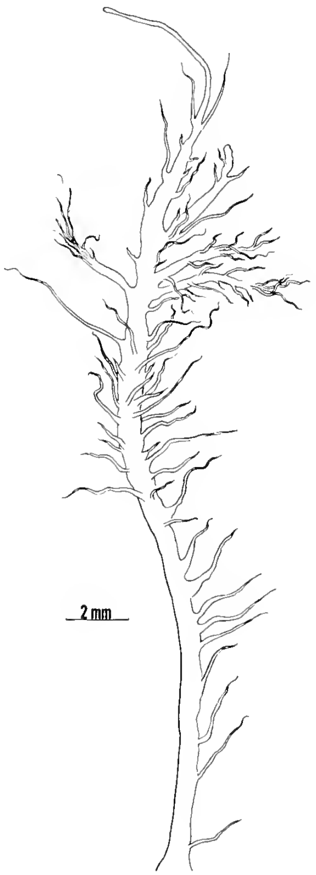

FIGURE 22. Esca of Caulophryne sp., LACM 36025–1, 98.0 mm.

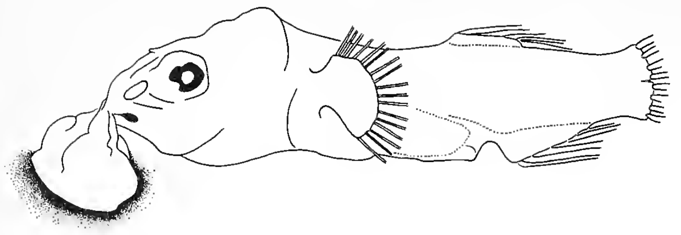

FIGURE 23. *Caulophryne* sp., parasitic male, LACM 36025-1, 12.0 mm.

6. opercular bones reduced (as are those of linophrynids, gigantactinids, and neoceratiids).
7. hypobranchials and basibranchials absent (all hypobranchials are absent in linophrynids and gigantactinids; hypobranchial II is absent, but a small hypobranchial III is present in neoceratiids; all basibranchials are absent in ceratiids, linophrynids, gigantactinids and neoceratiids).
8. caudal rays 8 (ceratiids also show a reduction in the number of caudal rays to 8; all other ceratioids have 9; neoceratiids occasionally have 10, Bertelsen 1951:159, table 36).
9. posttemporals reduced, overlapping pterotics and epiotics, but far removed from parietals and exoccipitals (similarly reduced in gigantactinids).
10. lower portion of cleithrum reduced to a slender thread of bone (similarly reduced in *Gigantactis*).
11. pectoral radial number reduced by fusion to 2 (all other adult ceratioids have 3 or more radials).
12. neuromasts of acoustico-lateralis system located at the tips of elongate filaments (this specialization is unique to caulophrynids; Regan and Trewavas 1932:23, 24, fig. 16C).
13. illicial filaments present in some species (also present in some species of *Gigantactis*).
14. males known to become sexually parasitic (Pietsch 1976:788; reproductive mode shared by ceratiids, linophrynids, neoceratiids, and the oneirodid genus *Leptacanthichthys*).

Due to the presence of a number of the primitive character states listed above (7, 8, 11), Bertelsen (1951:28) placed the Caulophrynidae "first in the suborder." At the same time, he argued that the Linophrynidae showed "such a highly specialized condition that they must be placed last." Since members of both these families are characterized by having parasitic males, Bertelsen's classification requires that this mode of reproduction evolved more than once. For unstated reasons, Greenwood, et al. (1966:397) implied a much closer relationship between the caulophrynids and linophrynids. Likewise, at the 1975 Annual Meeting of the American Society of Ichthyologists and Herpetologists in Williamsburg, Virginia, I reported finding numerous, derived character states shared by these two families as well as with the Gigantactinidae and Neoceratiidae. Ignoring all primitive character states at that time, I presented a phylogeny that argued for a monophyletic origin of sexual parasitism within a lineage derived from some oneirodid-like ancestor (Fig. 25; see also Pietsch 1976:791). This more detailed study of the Caulophrynidae has revealed a considerable number of additional resemblances (albeit, primitive states) to less derived lophiiforms (lophioids and antennarioids) that can hardly be ignored. That these primitive character states suddenly reappeared in a lineage that arose from an ancestor derived in all, is highly improbable; the importance of recognizing and utilizing primitive character states in phylogenetic analysis is apparent.

A return to Bertelsen's (1951) classification is proposed in

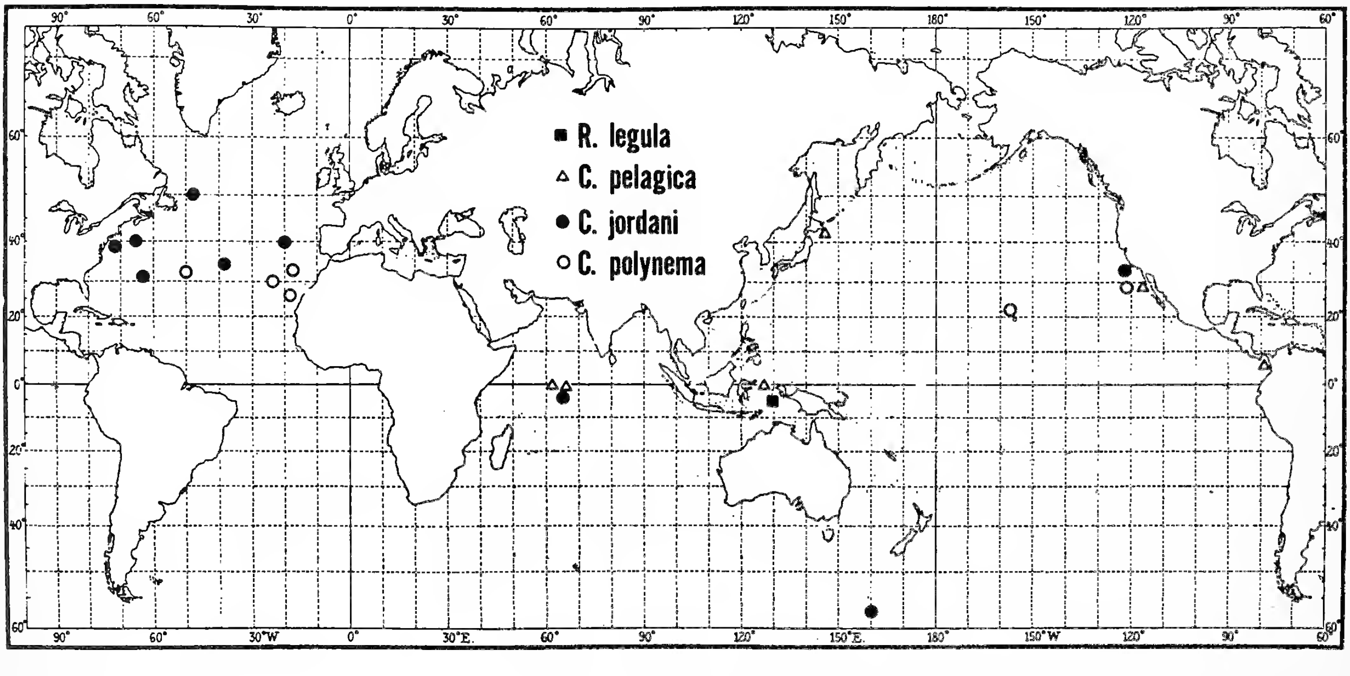

FIGURE 24. Known distribution of species of Caulophrynidae. A single symbol may represent more than one capture.

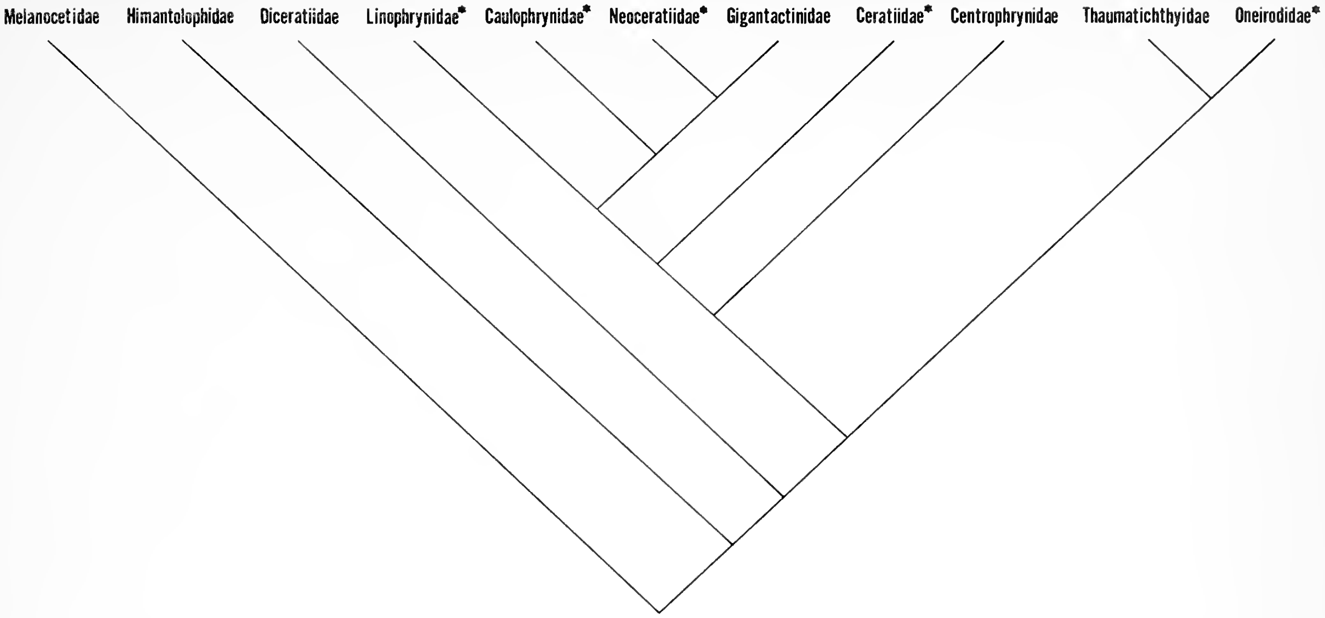

FIGURE 25. Phylogenetic relationships of families of Ceratioidei based on shared derived character states. Starred families contain species known to have parasitic males.

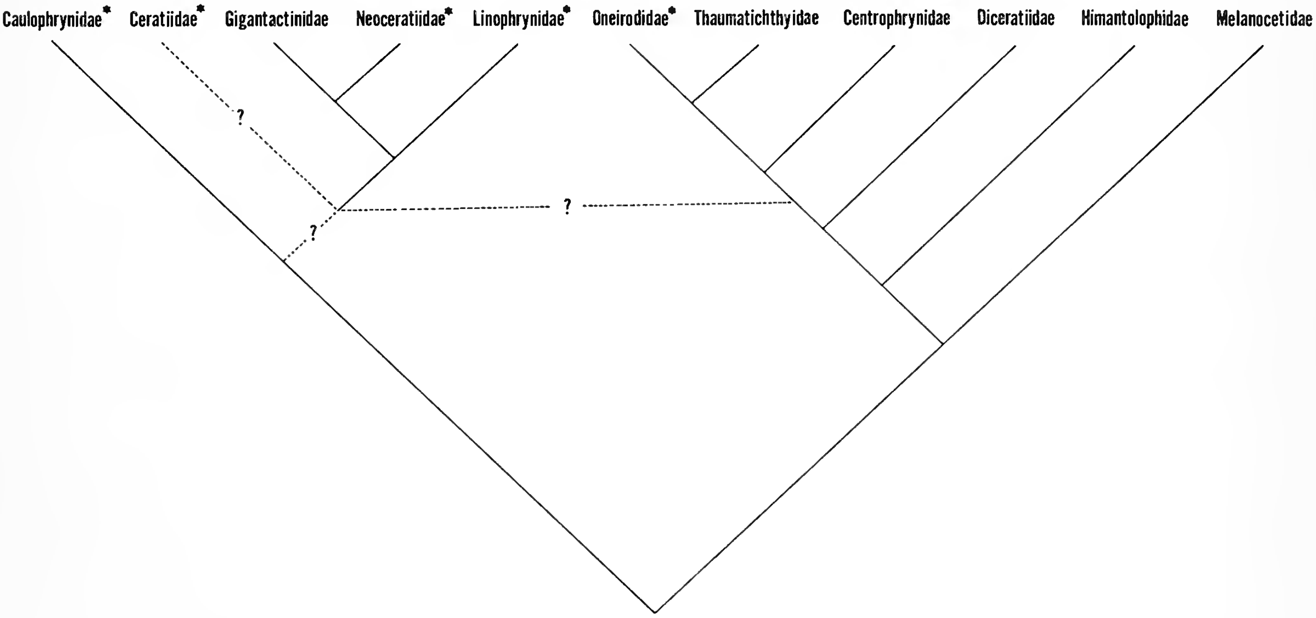

FIGURE 26. Phylogenetic relationships of families of Ceratioidei based on shared primitive as well as derived character states. Starred families contain species known to have parasitic males.

which the Caulophrynidae forms the primitive sister-group of the Melanocetidae, Himantolophidae, Diceratiidae, Centrophrynidae, Oneirodidae and Thaumatichthyidae (Fig. 26). The phylogenetic position of the closely related families Linophrynidae, Gigantactinidae and Neoceratiidae (and perhaps the Ceratiidae) is unclear. All share numerous derived character states among themselves and with the Caulophrynidae; but, most of these are either reduction states or loss of parts, conditions that are found in deepsea groups in general that could well be convergent in origin. This seems to leave two alternatives: either this assemblage is derived from a caulophrynid-like ancestor, thus forming part of a sister-group that is primitive to all other ceratioids, or it is derived from some oneirodid-like ancestor. Clarification of these problems must await further comparative studies; but, regardless of the phylogenetic position of the Linophrynidae and its allies, this interpretation, while recognizing the basal position of the Caulophrynidae, indicates a return to Bertelsen's (1951) view that sexual parasitism has evolved independently in at least two separate ceratioid lineages.

Three characters are available for interpreting intrafamiliar relationships:

1. median-fin ray counts. Within *Caulophryne* there is a trend toward an increase in the number of dorsal and anal-fin rays over the already high number of rays characteristic of lophioids and antennarioids. *Robia*, on the other hand, has a greatly reduced number of median-fin rays. The extremes of these opposite trends are both considered derived character states.
2. illicium length. Elongation of the illicium is a trend found in several other ceratioid groups (Pietsch 1972b, 1974a, b, 1975). The short illicia of *Caulophryne* species is a primitive condition; the extremely elongate illicium of *Robia* is derived.
3. illicial filaments. Within other ceratioid groups there is a trend toward an increase in morphological complexity of the illicial apparatus (Pietsch 1972b, 1974a, 1975). Filaments present along the length of the illicium of *C. jordani* and *C. polynema* (absent in all other ceratioids except for some species of *Gigantactis*) is considered a derived state.

This character analysis indicates that *Robia*, with its greatly reduced median-fin ray counts and extremely elongate illicium, is the more derived of the two caulophrynid genera. *Caulophryne pelagica* has a longer illicium than its congeners, but is considered the least derived member of the genus, having the lowest median-fin ray counts and lacking illicial filaments. *Caulophryne jordani* and *C. polynema* appear to be more closely related to each other than either is to *C. pelagica;* both exhibit an increase in the number of median-fin rays and share the presence of illicial filaments. *Caulophryne polynema* is the most derived member of the group having the highest median-fin ray counts and the most complex illicial structure.

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THE FAMILY BLEPHARICERIDAE IN COSTA RICA (DIPTERA)

By Charles L. Hogue

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CONTENTS

The *Science Bulletin* and *Contributions in Science* of the Natural History Museum of Los Angeles County were merged into a single imperial octavo serial, retaining the name *Contributions in Science* and beginning with Number 301.

This serial has been newly formatted for maximum use of typography and illustrations per page, and sized for maximum use of paper. All photography has been produced utilizing a 200-line screen for detail.

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Contributions in Science are articles in the earth and life sciences, presenting results of original research in Natural History. *Science Bulletin* (Numbers 1–30; 28 June 1965 to 10 April 1978) and *Contributions in Science* (Numbers 1–300; 23 January 1957 to 16 June 1978) were merged into a single imperial octavo serial beginning with Number 301.

THE FAMILY BLEPHARICERIDAE IN COSTA RICA (DIPTERA)[1]

By Charles L. Hogue[2]

ABSTRACT: Five species of net-winged midges of the family Blephariceridae are recorded for Costa Rica. All belong to the genus *Paltostoma;* one was previously known (*delectata* Alexander) but the remaining are described here as new species *(costaricensis, diriageni, exserta* and *zwicki).* The paper includes also a diagnosis and biologic notes on the genus.

The Blephariceridae or "net-winged" midges are notable in the extreme adaptations they exhibit for life in torrential water. Six mid-ventral suckers permit the larvae to hold fast and travel from place to place on smooth rock surfaces in the fastest currents, in waterfalls and cataracts; the pupae are attached permanently to the substratum by ventrolateral adhesive pads. The adults are capable of emergence while totally submersed. This takes place through an explosive egress of the body from the pupal case and unfolding of the appendages, followed by immediate flight. Such rapid escape is made possible by prior development and expansion of the wings and legs within the pupal case. The process requires compression and folding of the complete wing and causes numerous creases to form in its membrane, giving it the reticulate appearance from which the family receives its common name.

Although occurring widely in the Neotropical Region, the Blephariceridae are seldom collected. Consequently, our knowledge of species distributions is fragmentary and the family's regional taxonomy is in a rudimentary state (Hogue 1971). Five genera are presently recognized (including the very primitive *Edwardsina,* with species also in Australia), all apparently having austral origins. Of these, evidently only *Paltostoma* has extended northward through Central America, penetrating Mexico along the Sierra Madre Occidental to latitude 21° N (unpublished record). The genus also occurs on several Caribbean islands.

The Costa Rican fauna includes 5 species. The first known was *delectata,* described by Alexander in 1953 from 2 males, and which, until my recent collecting, remained the sole regional representatives of the family. This paper adds 4 additional species and provides descriptions and illustrations by which all may be recognized. Because little collecting has been accomplished and speciation seems to have occurred between populations that are only narrowly separated geographically, there remain strong possibilities for discovery of still other forms.

The descriptions of the adults are based largely on pharate specimens dissected from their pupal cases. Therefore, measurements of legs and wings, as well as color pattern characters, are not determinable. Quantitative data are given in millimeters and represent means calculated from small samples, hence ranges are omitted. Terminology follows that of Hogue 1973 and 1978.

Paltostoma Schiner

Paltostoma presently contains 13 named species, including those newly described in this paper. Material of several more exists in collections and, surely, more will be discovered when streams are sampled in the vast Andean Mountain system. The genus is characterized as follows:

DESCRIPTIONS

Adult

COLORATION: Generally well sclerotized; velvety brown with sharply defined, silvery ("frosty") or opalescent reflections which vary in position depending on the angle of viewing.

SIZE: Small to medium-sized Blephariceridae; wing length 4.5–9 mm.

HEAD: Small. Normal type. Suprafrons very broad, flat; frontal carina absent. Parietal sclerite very narrow. Ocelli sessile, separate, on slightly elevated boss. Eyes disjunct; undifferentiated into upper and lower divisions; ommatidia all of approximately equal size.

MOUTHPARTS: *Male.* — Proboscis very long (PL/HW 2.5). Labium jointed near base. Labrum rigid, slender; apex attenuate. Margin of hypopharynx entire, a few spicules apically. Maxillary lobes very long, approximately half the length of labium. Labellar lobes small, length slightly greater than width of labium. Palpus very short, segments 1–3 fused, 4–5 absent; sensory pit

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of segment 3 terminal. Mandibles absent. *Female*. — Proboscis moderately long (PL/HW 1.4). Labium jointed at about mid-length. Labrum rigid, broad, apex acute. Lateral margin of hypopharynx serrate, apex with lateral hair-like projections. Maxillary lobes short, slightly less than half the length of labrum. Labellar lobes very short, length less than width of labium. Palpus very short, segments 1–3 distinct, 4–5 absent; sensory pit of segment 3 terminal. Mandibles present.

ANTENNA: Length 1.5–1.8 head width, that of male slightly longer proportionately (1.8–1.9); 15-segmented. Scape globular, pedicel canopiform[3], flagellomeres cylindriform, length of latter about 2.0 width; flagellar segments 1–5 each with a small group of placoid sensilla dorsally.

WING: Venation (Fig. 14) reduced: R_2, R_3, M_3, and basal sector of M_{3+4} absent; 1A reduced; R_{2-5} long; branch of R_4 and R_5 near apex of wing. Dorsal macrotrichia on vein R_5 only, a few also ventrally at apex of this vein. Wing shape broad (L/W 2.9), anal lobe moderately developed.

LEGS: Tibial spur formula 0–0–1 in both sexes, hind tibial spur large, minutely spiculate on inner surface. Tarsal segment 5 longer than 4, a group of spiniform setae ventrobasally. Tarsal claws each with a single, large sub-basal tooth.

ABDOMEN: Short, strongly tapered posteriorly.

MALE GENITALIA: Segments VIII and IX unmodified. IXth tergite lobes triangular, a strong ventral armature produced from the lateral margin of each lobe, its arms converging anteriorly. Basistyle elongate, longer than dististyle. Outer dististyle broad, rectangular, variously incised and setose. Inner dististyle undivided, a long, curved, irregular finger. Phallosome vesica triangular; apodeme longer than vesica, a vertical, oval flange. Parameres undeveloped as separate, distinct tubular structures, their morphological position assumed by a broad, apically reflexed plate ("ventral plate"[4] of Stuckenberg 1958:101, see Fig. 9). Penis filaments 3, all simple, very long, straight rods, without special apical modifications. Tegmen narrow, anchor-shaped; base small, forming a shallow subanal pouch; apex broadly spatulate; margin recurved. Lateral portion of ventral bridge (Fig. 8) forming a complex curved plate weakly continuous with the ventral bridge proper.

FEMALE GENITALIA: VIIIth sternite lobe elongate, median fold deep, wide, Oviscapt elongate, apical lobes extended latero-posteriorly, a ventral, transverse Ω-shaped apodeme present in inner piece. Spermathecae ovoid; ducts very long, exit from body of spermatheca laterally, their proximal sections coiled 1 to several times around body before leading to gonotreme. Sensilla of cercus all chaetiform, apical tubular sensilla absent; a short, subapical, ventral finger-like lobe extending posteriorly from the cercus.

CHAETOTAXY: Body without long hairs. Setal groups minimal and inconspicuous. Occipital bristles of head short, scattered and not differentiated into upper and lower series. Postgenal bristles very few (1–3).

Larva

Intercalary convexities undeveloped. Head capsule with deep lateral incisions. Antenna short, 2-segmented. Dorsal pseudopods and sclerotized major plates and processes absent. Dorsal integument densely striate. Ventral gill filaments stellate in arrangement, 9–10 (usually 10) in number. Primary trunk sensilla recognizable as follows: **ic** (on anterior margin of division, rather than at level of intercalary portion), short, chaetiform; very small **it** (in normal positions on divisions II–VI); moderately long chaetiform sensilla **st** (P, I–V), **psu** (M–T), **tp** (II–V), **ss** (P–T, in line) and **pd** (I–VI). Secondary sensilla in two fields on dorsum: small, scattered capitate to conoid types generally and similarly shaped but much larger types in linear series antero- and posterolaterally on each division, the latter often flattened and tending to close interlobular spaces dorsally. Terminal setae reduced in size and number to 1–2.

Pupa

Elliptical to oval in outline, cross-section hemi-oval, flat. Lateral margins underfolded. Dorsal cuticle of all sclerites except cephalic and alar densely set with long spines; those middorsally flanked basally with 2 or more very short spinelets (spines often lacking in specimens suffering from rough handling or stream abrasion). Respiratory processes erect, disjunct at base; individual plates (lamellae) rigid, triangular, with acute apices; inner plates smaller and weaker than outer. Antennal cases short, extending to a level less than apex of the mouthpart cases. Ventral adhesive pads four in number.

DISTRIBUTION: Restricted to Neotropical Region between latitudes 25° S and 21° N, Pacific Cordillera and Caribbean Islands. See the map (Fig. 40) for the distribution of species in Costa Rica.

Paltostoma costaricensis NEW SPECIES

Figures 1–2, 5–9, 25, 27–29, 37, 40

DIAGNOSIS

This species may be distinguished by the following combination of characteristics of the male genitalia: long penis filaments with gradually widened bases. Broadly rounded, improminent IXth tergite lobe; arms of ventral armatures of the lobes contiguous and fused anteriorly. Outer dististyle incised apicoventrally, the dissected portion forming a thumblike projection.

It is also decidedly smaller than any other Costa Rican *Paltostoma*. Although comparable measurements for most structures are not available because of the lack of fully developed specimens of both sexes of all the species, the fact is readily apparent from general inspection. Head widths and lengths of wing vein R_5, characters which could be compared among all species, indicate that *costaricensis* is approximately 20% smaller than either *zwicki* or *delectata* and 40% smaller than *diriageni* and *exserta*.

DESCRIPTIONS

Male (Figs. 1, 5–9)

A composite description, based on four pharate specimens dissected from their pupal cases:

COLORATION: Not determinable, probably similar to that of female (see below).

SIZE: A small *Paltostoma*. Measurements as follows (from 3 pharate specimens): Wing and leg dimensions not determinable. Head width 0.66. Clypeus-labrum length combined 1.76. Palpal segments 1–3 combined 0.20.

HEAD (Fig. 1): Palpal segment proportions indeterminable, fusion of segments 1–3 complete, no perceptible constrictions or joints. Antennal segment proportions 1.3, 1.6, **1.00**, 1.0, 1.1,

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[3] Shape like a typical Egyptian canopic jar.

[4] This homology is questionable, however. Comparative anatomical studies are needed; the term is used here for convenience only.

1.1, 1.1, 1.1, 1.1, 1.1, 1.1, 1.1, 1.1, 1.1, 1.4. Ultimate segment 1.3 length of penultimate.

LEGS: Segment proportions not available.

WING: Venation and trichia typical for genus.

GENITALIA (Figs. 5–9): IXth tergite lobe improminent, apex broadly rounded; arms of ventral armature contiguous anteriorly. Outer dististyle incised apicoventrally, the dissected ventromedian portion forming a thumb-like projection. Inner dististyle simple, smoothly curved and tapered, slightly capitate. Tegmen elongate, narrow, with two parallel straplike sclerotizations; basal portion narrow, articulating with the contiguous arms of the ventral armature of the IXth tergite lobes. Phallosome totally lacking parameres; penis filaments evenly tapered, only slightly widened basad.

Female (Figs. 2, 25)

Based primarily on specimen from Golfito; head structures from Rincón series:

COLORATION: *Head.* — All sclerites medium-brown, darker towards vertex and posteriorly, with extensive velvety texture and silvery opalescent reflections; ocellar triangle dark-brown. Mouthparts and antenna dull medium-brown, the latter darker. *Thorax.* — Generally medium-brown. Scutum, scutellum, anterior pronotum and ventral portions of episternum and meron darker; extensive silvery opalescent reflections as on head; remaining sclerites and membranous portions dull yellow-brown. Disc of scutum with dark-brown, parallel, median vittae separated from a more posterior, broad, V-shaped, dark-brown vitta bordering the transverse suture. *Legs.* — Generally dull medium-brown, lighter basad, darker abruptly distad (before apices of tibiae), including tarsi and claws. *Wing.* — Membrane hyaline; veins brownish-black. *Haltere.* — Stem light-brown basad, darkening distad; knob velvety gray-brown. *Abdomen.* — Color characteristics not available.

SIZE: Measurements as follows (from 5 pharate and one mature specimen): Body length not determinable. Wing length 6.8, width 2.3. Head width 0.84. Clypeus length 0.39. Labrum length 0.67. Palpal segments 2–3: 0.16, 0.22. Leg segment lengths as below (from Golfito specimen):

	fore	mid	hind
femur	4.4	5.7	7.1
tibia	5.4	5.5	6.3
tarsus 1	1.89	2.00	2.06
2	0.79	0.86	0.43
3	0.41	0.44	0.24
4	0.26	0.28	0.21
5	0.28	0.26	0.25

HEAD (Fig. 2): Palpus very short, segments 1–3 distinct, proportions 2–3: 1.0, 1.4. Antennal segment proportions: 1.0, 1.5, 1.00, 1.1, 1.1, 1.1, 1.1, 1.1, 1.1, 1.1, 1.1, 1.1, 1.0, 1.1, 1.8; ultimate segment 1.6 length of penultimate.

LEGS: Progressive segment proportions as below:

foreleg	1.0	1.2	0.4	0.4	0.5	0.6	1.1
midleg	1.0	1.0	0.4	0.4	0.5	0.6	0.9
hindleg	1.0	0.9	0.3	0.2	0.6	0.9	1.2

WING: Venation and trichia typical for genus.

GENITALIA (Fig. 25): Oviscapt broad, ratio length/width = 1.3. Setae of VIIIth sternite lobe short, 10–14 in number.

Pupa (Fig. 37)

SIZE: Small. Measurements (N=10): male, length 2.9, width 1.7; female, length 4.3, width 2.5.

STRUCTURE: Outline elongate-oval, L/W 1.7, strongly convex, cross section hemispherical, peripheral margin rounded. Cephalic sclerite strongly underfolded (to level of tips of palpus case). Cuticular spines proportionately long, longest lateral spines about as long or slightly longer than mid-dorsal length of scutellar sclerite; numerous spines in mesoposterior region of scutum; parabasal spinelets, when present, one on each side of the major spine and mostly of equal length. Lamellae of respiratory processes divergent, no. 1 much so, projecting anteriorly beyond body margin; subequal in length; outer pair heavier than inner and triangular; inner pair 0.6–0.7 width of outer at their bases, no. 2 the smallest; apex of no. 3 slightly attenuate and tortuate, curving around inner margin of no. 2.

Larva (Figs. 27–29)

SIZE: Small. Measurements (N=10): Body length 5.0; head capsule width 1.26.

CHAETOTAXY (trunk segments only): Secondary dorsal sensilla all small and coniform; those of antero- and posterolateral linear series larger and coniform to clavate, the latter more poorly developed dorsomesad.

STRUCTURE: Pseudopods short, L/W about 2.3, arising from ventrolateral depression. Posterolateral lobe of anal division poorly developed, apex directed caudad. Lateral margin of anal division entire, a cluster of secondary coniform sensilla with large alveoli situated on a slight boss anterior to posterolateral lobe. Posterior extreme of anal segment not excessively pigmented nor sclerotized, the margin a smoothly rounded arc continuous with lateral margin. Ventral integument mesal to base of pseudopod strigose over only a small area immediately mesal to insertion of pseudopod.

MATERIAL AND TYPE LOCALITY:

Types. COSTA RICA, *Puntarenas Province,* 1.8 miles W Rincón, Linguita Creek, 11 March 1971, C.L. Hogue and J.P. Donahue: HOLOTYPE ♂ (pharate, dissected from and mounted entire on slide series No. CLH 73–16a–e: LACM); ALLOTYPE ♀ (pharate, dissected from and mounted entire on slide series No. CLH 73–156a–e: LACM); 6♂, 5♀ PARATYPES (pharate adults mounted entire on slide series).

Additional. COSTA RICA, *Alajuela Province,* 0.7 miles W Grecia, Río Vigía, 18 June 1972, C.L. Hogue (1 larva: LACM). *Puntarenas Province,* Golfito, 15 August 1957, A.S. Menke (1♀: LACM). Las Cruces, (rock quarry) 6 miles S San Vito de Jabá, Río Jabá, 22 March 1967, R.W. McDiarmid, RWM 21 (2 pupae, 14 larvae: LACM). 27 June 1972, C.L. Hogue (2 pupae, 21 larvae: LACM). 1.8 miles W Rincón, Linguita Creek, 3 July 1963, C.L. Hogue (2 larvae: LACM). 11 March 1971, C.L. Hogue and J.P. Donahue (32 pupae and pupal skins, 24 larvae: LACM).

ETYMOLOGY: The species is named for Costa Rica, its country of origin.

Paltostoma delectata Alexander

Figures 12–14, 30–33, 40

Paltostoma delectata Alexander 1958:47. Type locality: Costa Rica, San José Province, Rio Buena Vista, Rivas. Deposited in private collection of C.P. Alexander, Amherst, Massachusetts.

Paltostoma delectata, Hogue 1971:8.7.

DESCRIPTIONS

Male (Figs. 12–14)

From the original description and the single paratopotype:

COLORATION: *Head.* — Front dull-orange, silvery pruinose, mouthparts pale-brown; remainder of head chestnut-brown, variegated with silvery on the anterior vertex. *Antenna.* — Not determinable. *Thorax.* — Scutum chestnut-brown, including four broad confluent prescutal stripes, leaving broad silvery areas on the posterior pronotum and at the prolongations of the [parapsidal?] ''suture.'' Lateral sclerites yellow. *Legs.* — ''. . . coxae and trochanters yellow; forefemora chiefly black, more brightened basally and with a very obscure yellow to scarcely evident subterminal yellow ring; remaining femora yellow, the extreme tips brownish black; foretibiae and tarsi black, the remaining tarsi obscure brownish yellow. . . .'' *Wing.* — Membrane hyaline; vein brownish black to black. *Haltere.* — Stem yellow, knob blackened. *Abdomen.* — First tergite yellow, the remainder brown, their extreme bases paler and more or less pruinose. Sternites more extensively yellow, silvery pruinose beneath, the sides infuscated. *Genitalia.* — Dark-brown.

SIZE: Measurements as follows (from paratopotype): Body length 3.5. Wing length 4.9, width 1.9. Head width 0.80. Clypeus-labrum length combined 1.55. Palpal segments 2–3, lengths not available. Leg segment lengths as below:

	fore	mid	hind
femur	2.9	3.8	4.9
tibia	3.5	3.7	4.4
tarsus 1	1.41	1.58	n.a.
2	0.57	0.63	n.a.
3	0.27	0.30	n.a.
4	0.16	0.16	n.a.
5	0.25	0.24	n.a.

HEAD: Exact palpal segment proportions not determinable from material, but the palpus is very short and similar to that of the other species with two segments (morphologically, segments 2–3 fused). The indistinct intersegmental articulation 2–3, common to this organ in male *Paltostoma,* probably led to Alexander's remark in the original description that the palpus is apparently 1-segmented. Antennal segment proportions: 1.0, 1.1, **1.00**, 1.0, 1.0, 1.1, 1.0, 1.0, 1.0, 1.0, 1.0, 1.0, 1.0, 1.0, 1.5. Ultimate segment 1.5 length of penultimate.

LEGS: Progressive segment proportions as below:

foreleg	1.0	1.2	0.4	0.4	0.5	0.6	1.6
midleg	1.0	1.0	0.4	0.4	0.5	0.5	1.5
hindleg	1.0	0.9	n.a.	n.a.	n.a.	n.a.	n.a.

WING (Fig. 14): Venation and trichia typical for genus.

GENITALIA (Figs. 12–13): IXth tergite lobe prominent, symmetrically triangular, apex broadly acute; arms of ventral armature contiguous cephalad. Margin of outer dististyle entire, obtusely rectangular. Inner dististyle simple, apex slightly spatulate. Tegmen elongate, narrow; apex truncate; basal portion narrow, articulating with the contiguous arms of ventral armature of IXth tergite lobes. Phallosome lacking parameres, longitudinal striae evident in ventral plate; penis filaments short, evenly tapered, only slightly widened basad, basal fourth alveolate.

Female

Unknown.

Pupa (Not figured)

SIZE: Medium. Measurements (N=5): all females (?), length 5.0, width 3.6.

STRUCTURE: Outline elliptical, L/W 1.4–1.5, compressed, cross section hemilenticular, peripheral margin acute. Cephalic sclerite underfolded only a little more than half the distance to level of tips of palpus cases. Anterior margin of scutellar sclerite shallowly U-shaped. Cuticular spines proportionately long, longest lateral spines slightly longer than middorsal length of scutellar sclerite; only two spines in mesoposterior corner of scutum; parabasal spinelets commonly multiple (2–4) and of unequal length. Lamellae of respiratory processes parallel, erect, subequal in length; outer pair heavier than inner and triangular, inner pair about 0.5 width of outer at their bases; no. 3 the smallest and narrower than no. 2 and set mesad of same; apices of both inner lamellae straight; apices of lamellae no. 4 of each side convergent.

Larva (Figs. 30–33)

SIZE: Medium. Measurements (N=10): Body length 6.1; head capsule width 1.41.

CHAETOTAXY (trunk segments only): General secondary dorsal sensilla mostly small and coniform, grading to larger and spiniform laterad; a triplet (short series of 3, rarely 2) of conspicuously larger spiniform sensilla in the anterolateral and posterolateral tergal regions (latter triplet lateral to primary subtergal sensillum, **tp.**). Sensilla of antero- and posterolateral linear series large and spiniform; lateral and ventral members of both series with apices acuminate and sometimes multiple.

STRUCTURE: Pseudopods elongate, L/W about 3.5; arising from near apex of pleuron. Posterolateral lobe of anal division well developed, about half the size of the pseudopods, its apex directed posterolaterad. Lateral margin of anal division entire, set with a few larger spiniform secondary sensilla. Posterior extreme of anal division densely pigmented and heavily sclerotized and separated from posterolateral lobes by a deep depression. Ventral integument mesal to insertion of pseudopod mammillate over a broad area, the mammillae spinose laterad, grading to papillae mesad.

MATERIAL:

COSTA RICA, *San José Province,* 2 miles W Grecia, Río Trojas, 18 June 1972, C.L. Hogue (7 pupae, 24 larvae: LACM). Pan American Highway and Río Cajón, 22 June 1972, C.L. Hogue (11 larvae: LACM). Pan American Highway and Río Unión, 22 June 1972, C.L. Hogue (1 larva: LACM). Rivas, January 1934. D. Rounds (Holotype ♂, 1 paratype ♂: Alexander Collection). 10 miles E San Isidro del General, Río General, 22 June 1972, C.L. Hogue (1 larva: LACM). 1.8 miles S San Isidro del General, Río Pedregoso, 28 June 1972, C.L. Hogue (24 larvae: LACM).

REMARKS

Unfortunately, *delectata* is imperfectly known. The larva and pupa described here, although slightly large for the size of the adult, I judge to belong to this species since they were taken in the same drainage system (Rîo General) from whence the holotype comes (see Fig. 40). However, there are no collections of early stages associated with adults to confirm this.

Paltostoma diriageni NEW SPECIES

Figures 3–4, 15–19, 26, 34–36, 38, 40

DIAGNOSIS

Male genitalic features as follows set this species apart from its relatives: long penis filaments, gradually widening basally; bases of these structures non-alveolate internally. IXth tergite lobe asymmetrically triangular (similar to that of *zwicki* but the two lobes more divergent); arms of ventral armature widely separated anteriorly. Margin of outer dististyle entire.

DESCRIPTIONS

Male (Figs. 3, 15–19)

Based on 3 pharate specimens dissected from their pupal cases:

COLORATION: Not determinable.

SIZE: Measurements as follows: wing and leg dimensions not determinable. Head width 1.16. Clypeus-labrum length combined 2.88. Palpal segments 2–3 combined 0.35.

HEAD (Fig. 3): Palpus very short, segments 2–3 fused although limit of former marked by enlarged setae; segment 1 distinct, 2–3 constricted at presumed joint; segment proportions 1:(1:0.5). Antennal segment proportions: 1.0, 1.5, **1.00**, 1.2, 1.3, 1.3, 1.3, 1.2, 1.2, 1.2, 1.3, 1.3, 1.3, 1.4, 1.6; ultimate segment 1.2 length of penultimate.

LEGS: Segment proportions not determinable.

WING: Venation and trichia typical for genus.

GENITALIA (Figs. 15–19): IXth tergite lobe prominent, asymmetrically triangular, apex broadly acute; arms of ventral armature widely disjunct anteriorly. Margin of outer dististyle entire, roughly pentagonal. Inner dististyle simple, apex constricted, a ventromesal lobe present subapically; apicoventral lobe digitate, pronounced. Tegmen with narrow base, apex spatulate, basal portion broad, articulating laterally with the disjunct arms of the ventral armature of the IXth tergite lobes. Phallosome lacking parameres, complex striae evident in ventral plate; penis filaments long, evenly tapered, only slightly widened basad, extreme basal portions non-alveolate internally.

Female (Figs. 4, 26)

Based on 4 pharate specimens dissected from their pupal cases:

COLORATION: Not determinable.

SIZE: Measurements as follows: Wing and leg dimensions not determinable. Head width 1.19. Clypeus length 0.57. Labrum length 1.08. Palpal segments 2–3: 0.27, 0.44.

HEAD: Palpus very short, segments 1–3 distinct, proportions 2–3: 1.0, 1.6. Antennal segment proportions: 1.2, 1.2, **1.00**, 1.2, 1.3, 1.2, 1.1, 1.1, 1.0, 1.0, 1.1, 1.0, 1.1, 1.3; ultimate segment 1.2 length of penultimate.

LEGS: Segment proportions not determinable.

WING: Venation and trichia typical for genus.

GENITALIA (Fig. 26): Oviscapt elongate, ratio L/W=1.8. Setae of VIIIth sternite lobe long, 22–31 in number.

Pupa (Fig. 38)

SIZE: Large. Measurements (N=10): male length 6.7, width 4.4; female length 7.2, width 5.0.

STRUCTURE: Outline elliptical, L/W 1.4–1.5, compressed, cross section hemilenticular, peripheral margin acute. Cephalic sclerite underfolded only slightly more than half the distance to level of tips of palpus case. Anterior margin of scutellar sclerite shallowly V-shaped. Cuticular spines proportionately short, longest lateral spines distinctly less (about 0.75) than mid-dorsal length of scutellar sclerite; numerous spines in mesoposterior region of scutum, parabasal spinelets commonly multiple (2–4) and of unequal length. Lamellae of respiratory processes parallel, erect, subequal in length; outer pair heavier than inner and triangular, inner pair 0.6–0.7 width of outer at their bases; no. 3 the smallest and narrower than no. 2 and set mesad of same; apices of both inner lamellae slightly recurved but neither bent tortuously.

Larva (Figs. 34–36)

SIZE: Large. Measurement (N=10): body length 6.3; head capsule width 1.69.

CHAETOTAXY (trunk segments only): General secondary dorsal sensilla all small and coniform; those of antero- and posterolateral linear series much larger than general dorsals; cylindriform mesally, becoming coniform, flattened and sometimes ridged, laterally.

STRUCTURES: Pseudopods short, L/W about 2.3; arising from ventrolateral depression. Posterolateral lobe of anal division well developed, only slightly smaller than pseudopods, apex directed posterolaterad. Lateral margin of anal division with a conspicuous lobe anterior to posterolateral lobe, set with an arc of large, ovate sensilla. Posterior extreme of anal division densely pigmented and heavily sclerotized and separated from posterolateral lobes by a deep incision. Ventral integument mesal to base of pseudopod mammillate over a broad area, mammillae spinose laterad, grading to papillae mesad.

MATERIAL AND TYPE LOCALITY:

Types. COSTA RICA, *Alajuela Province,* Río Angel below El Angel Falls, 13 April 1975. C.L. Hogue: HOLOTYPE ♂ (pharate, dissected from and associated with pupal case; in alcohol: genitalia on slide No. CLH 75–219; head on slide No. CLH 75–233: LACM); ALLOTYPE ♀ (as ♂: genitalia on slide No. CLH 75–221; head on slide No. CLH 76–158: LACM); 3 ♂, 1 ♀ PARATYPES (pharate adults in alcohol, dissected from pupal cases with genitalia and heads on slides: LACM).

Additional. COSTA RICA, *Alajuela Province,* Río Angel below El Angel Falls, 13 April 1975, C.L. Hogue (19 ♂, 31 ♀ pupae and sexed whole pupal skins; 15 fragmentary pupal skins; 2 larvae: LACM). *Puntarenas Province,* Las Cruces, (rock quarry) 6 miles S San Vito de Jabá, Río Jabá, 27 June 1972, C.L. Hogue (1 pupa, 1 larva: LACM). 1.8 mi. W Rincón, Linguita Creek, 3 July 1963, C.L. Hogue (1 ♀, pharate, dissected from pupal case; 1 pupa, 3 partial pupal skins, 10 larvae: LACM). 11 March 1971, C.L. Hogue and J.P. Donahue (2 pupae, 2 larvae: LACM). *San José Province,* 2 miles W Grecia, Río Trojas, 18 June 1972, C.L. Hogue (1 pupa: LACM). 12.5 miles N San Isidro del General, 15 June 1963, C.L. Hogue (7 larvae: LACM).

ETYMOLOGY: The name was chosen to commemorate the name of one of Costa Rica's most famous and clever caciques. In 1522, Diriagen is reputed to have nearly defeated a force led by Gonzalez Davila in an ambush into which the latter's greed for Indian treasure led him.

Paltostoma exserta NEW SPECIES

Figures 10–11, 39, 40

DIAGNOSIS

This species is distinct from all other known *Paltostoma* in the form of the pupal lamellae. Normally the four plates of the branchia are more or less separate from one another and about equal in length (although the inner two may be narrower than the outer), but in *exserta* the inner pairs are appressed by the outer and extend about 20% of their own length beyond them.

Only small differences exist in other features, notably in the male genitalia, between *exserta* and the very similar *diriageni.* This applies principally to the shape of the inner dististyle which is considerably broader in the former than in the latter species. This structure also has a less pronounced apicoventral lobe in *exserta* than in *diriageni.* A further difference may be found in the outer dististyle lobe which is smoothly rounded in shape in *exserta* while it is asymmetrically hexagonal in *diriageni.*

The larva of *exserta* is unknown.

DESCRIPTIONS

Adults

The great similarity of this species to *diriageni* (see above) makes a full description of the adults superfluous. From the small amount of material available, which consists entirely of pharate individuals dissected from their pupal cases, nothing can be detected to distinguish the females. The same is true of the males except for a few characteristics in the genitalia. The latter are described as follows from the single fairly well sclerotized, but pharate, specimen:

MALE GENITALIA (Figs. 10–11): IXth tergite lobe prominent, asymmetrically triangular, apex broadly acute; arms of ventral armature widely disjunct anteriorly. Margin of outer dististyle entire, oval; dorsal portion concave. Inner dististyle simple, broad and angular, a ventromesal lobe present subapically; apicoventral lobe acute and moderately pronounced. Tegmen with narrow base, apex spatulate; basal portion broad, articulating laterally with the disjunct arms of the ventral armature of the IXth tergite lobes. Phallosome lacking parameres, complex striae evident in ventral plate; penis filaments long, evenly tapered, only slightly widened basad; extreme basal portions of filaments non-alveolate internally.

Pupa (Fig. 39)

SIZE: Large. Measurements: male (N=3) length 5.9, width 4.4; female (N=7) length 7.0, width 5.0.

STRUCTURE: Outline elliptical, L/W 1.4. Cuticular spines proportionately short, longest lateral spines distinctly less (about 0.75) than mid-dorsal length of scutellar sclerite; condition of parabasal spinelets not determinable due to abraded condition of available material. Branchial lamellae compressed, outer pair much heavier than inner and triangular, appressed to inner pair which are sagittate in form and extend considerably beyond the apices of the outer pair (by about 20% of their total length); outer lamellae covered by a dense, white, flocculent material of unknown origin.

Larva

Unknown.

MATERIAL AND TYPE LOCALITY:

Types. COSTA RICA, *Alajuela Province,* Río Angel below El Angel Falls, 13 April 1975, C.L. Hogue: HOLOTYPE ♂ (pharate, dissected from and associated with pupal case; in alcohol: genitalia on slide No. CLH 77–1; head on slide No. CLH 77–10: LACM); ALLOTYPE ♀ (as ♂: genitalia on slide No. CLH 77–3: LACM); 3 ♀ PARATYPES (pharate adults in alcohol, dissected from pupal cases with genitalia and heads on slides: LACM).

Additional. COSTA RICA, *Alajuela Province,* Río Angel below El Angel Falls, 13 April 1975. C.L. Hogue (2 ♂, 8 ♀ pupae: LACM).

ETYMOLOGY: *Exserta* is Latin, meaning "extended beyond" and is in reference to the protruding middle branchial lamellae of the pupa.

Paltostoma zwicki NEW SPECIES

Figures 20–24, 40

DIAGNOSIS

The following characteristics of the male genitalia distinguish this new species from its congeners: short penis filaments with basal third abruptly widened and alveolate internally. IXth tergite lobe asymmetrically triangular with an acute apex, arms of ventral armature contiguous anteriorly. Outer dististyle incised apicoventrally.

DESCRIPTIONS

Male (Figs. 20–24)

Based on the holotype and a single male paratopotype:

COLORATION: *Head.* — All sclerites medium-brown, darker towards vertex and caudad, with extensive velvety texture and silvery opalescent reflections; ocellar triangle dark-brown. Mouthparts and antenna dull brown, the latter darker. *Thorax.* — Generally medium-brown. Scutum, scutellum, episternum and meron darker and with reflections as on head; remaining sclerites dull yellow-brown. *Legs.* — Generally dull gray-brown, lighter basad, becoming darker distad; tarsi, including claws, almost black. Apices of femora darkened. *Wing.* — Membrane hyaline, veins brownish-black. *Haltere.* — Stem yellow basad, darkening distad; knob velvety brown. *Abdomen.* — Basal half of first tergite yellow, the remainder of this and other tergites velvety-brown with silvery reflections caudad, a distinct reflective black band basally. Sternites light-brown, also reflective. *Genitalia.* — Dark brown.

SIZE: Measurements as follows (from combined material, maximum N=2): Body length not determinable. Wing length 5.0, width 1.7. Head width 0.82. Clypeus length 0.23. Labrum length 1.66. Palpal segments 1–3 combined 0.21, 2–3 combined 0.15, 2 alone 0.06. Leg segment lengths as below (from Pedregosa specimen):

	fore	mid	hind
femur	3.3	4.2	5.0
tibia	3.9	4.1	4.8
tarsus 1	1.38	1.43	1.56
2	0.59	0.68	0.46
3	0.34	0.38	0.24
4	0.23	0.24	0.20
5	0.28	0.29	0.26

HEAD: Palpus very short, segments 2–3 fused, segment 1 distinct, 2–3 constricted at presumed joint; segment 2 short; proportions: 1:(1:1.4). Antennal segment proportions (from Pedregosa specimen, segments 9–14 damaged): 1.7; 1.7, **1.00**, 1.3, 1.3, 1.4, 1.3, 1.3, 1.3, 1.4, 1.1, 1.4, 1.3, 1.3, 1.9; ultimate segment 1.5 length of penultimate.

LEGS: Progressive segment proportions as below:

foreleg	1.0	1.2	0.4	0.4	0.6	0.7	1.2
midleg	1.0	1.0	0.4	0.5	0.6	0.6	1.2
hindleg	1.0	1.0	0.3	0.3	0.5	0.8	1.3

WING: Venation and trichia typical for genus.

GENITALIA (Figs. 20–24): IXth tergite lobe prominent, asymmetrically triangular, apex broadly acute; arms of ventral armature contiguous anteriorly. Outer dististyle incised apicoventrally, ventromedian margin not markedly produced. Inner dististyle slightly expanded apicad, apex abruptly narrowed and attenuate. Tegmen broad, apex rounded with a median, narrow sclerotized shaft; basal portion narrow, articulating with the contiguous arms of the ventral armature of IXth tergite lobes. Phallosome with slightly sclerotized straps in center of ventral plate, suggesting rudimentary parameres; penis filaments short, basal third abruptly widened, this portion alveolate internally.

Female, pupa and **larva**

Unknown.

MATERIAL AND TYPE LOCALITY:

Types. COSTA RICA, *San José Province,* Turrialba, 5–15 March 1954, C.H. Batchelder: HOLOTYPE ♂ (genitalia on slide No. CLH 76-161: USNM); PARATYPE ♂ (genitalia on slide No. CLH 76-162: USNM). March 1954. C.H. Batchelder (light trap).

Additional. COSTA RICA, *Province Unknown,* Pedregosa, no date, D.L. Rounds (1 ♂: USNM).

ETYMOLOGY: The species is named in honor of Peter Zwick, distinguished student of the family Blephariceridae.

REMARKS

I have not been able to locate the locality "Pedregosa" of Rounds' collection; it may be Pedregoso, 1 km W San Isidro del General.

ACKNOWLEDGMENTS

I owe gratitude to the following persons for making available the material upon which this report is based, either by providing funds and special help in the field, or by loaning specimens: Charles P. Alexander, John E.S. Dockweiler, Julian P. Donahue, Alan Landsburg, and Peter Zwick.

I would like to acknowledge also the invaluable assistance of Betty Birdsall and Carol Madle with preliminary drawings and to thank particularly Joy Roan for her fine rendering of figures of the larvae (Figs. 27–36).

RESUMEN

Se hace referencia a cinco especies de mosquitos de alas reticuladas de la familia Blephariceridae, procedentes de Costa Rica. Las cinco especies pertenecen al género *Paltostoma;* con excepción de *P. delectata* Alexander, ya descrita, las cuatro restantes *(costaricensis, diriageni, exserta* y *zwicki)* se describen como nuevas especies. La publicación incluye además un diagnóstico, acompañado de notas biológicas, referentes al género.

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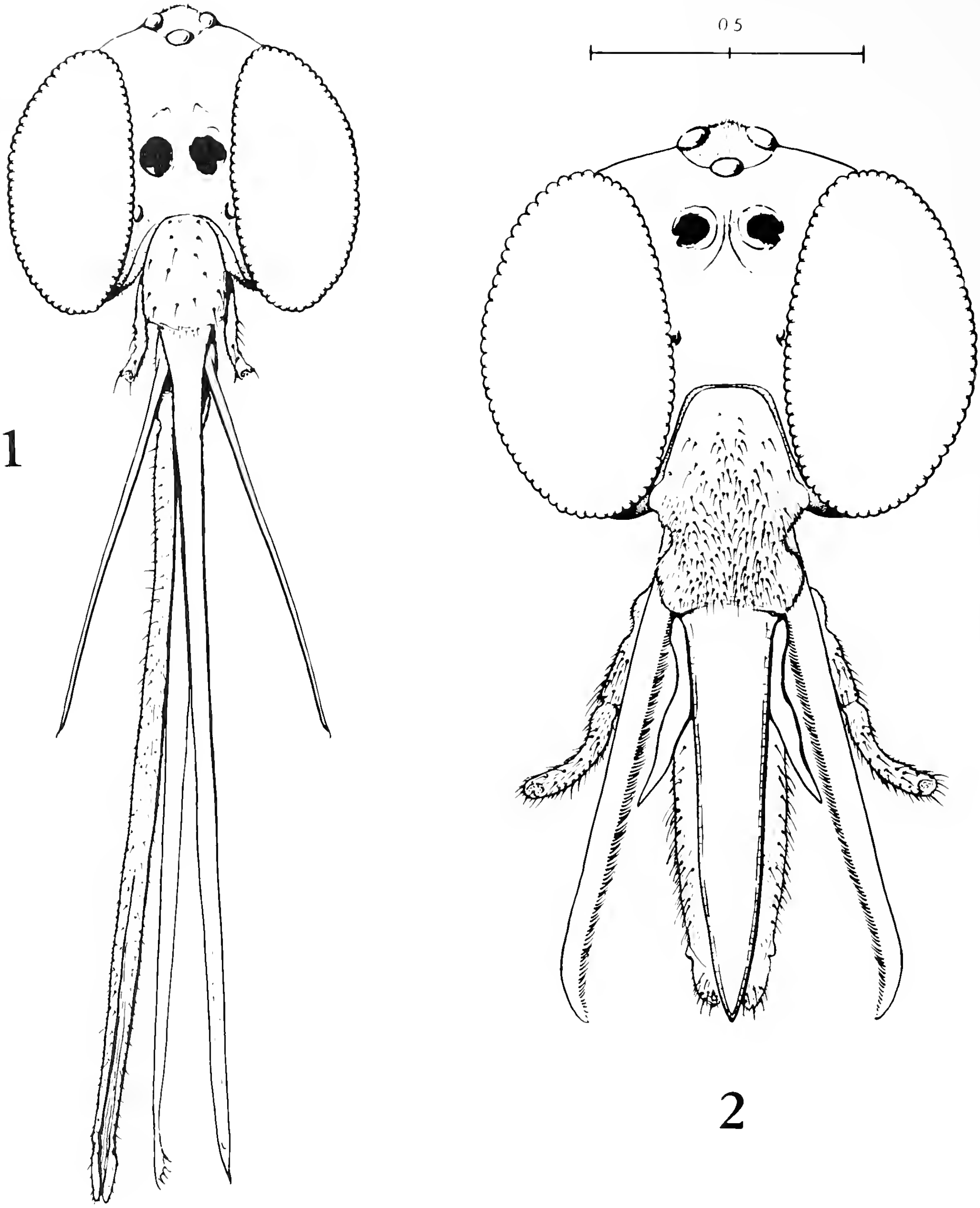
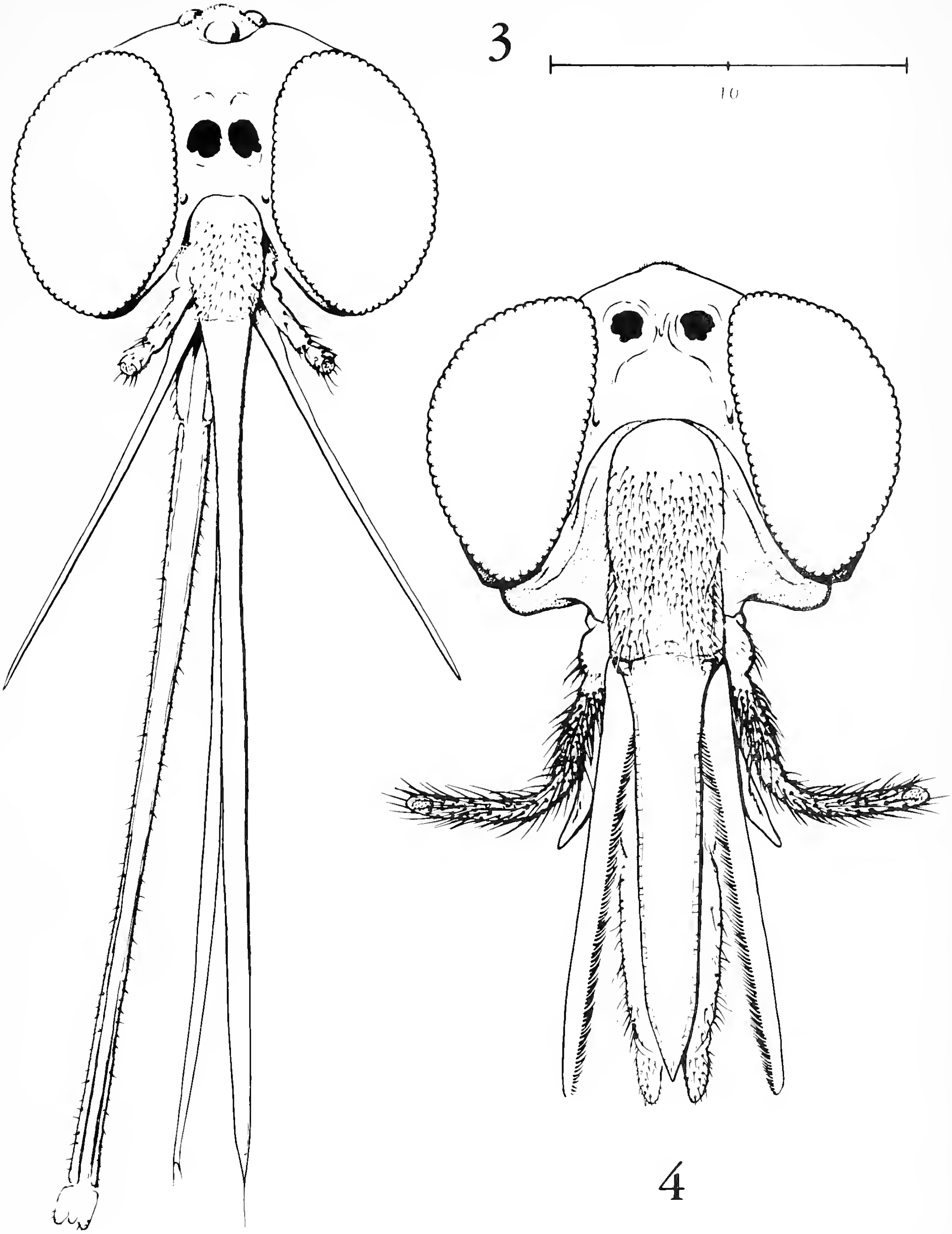
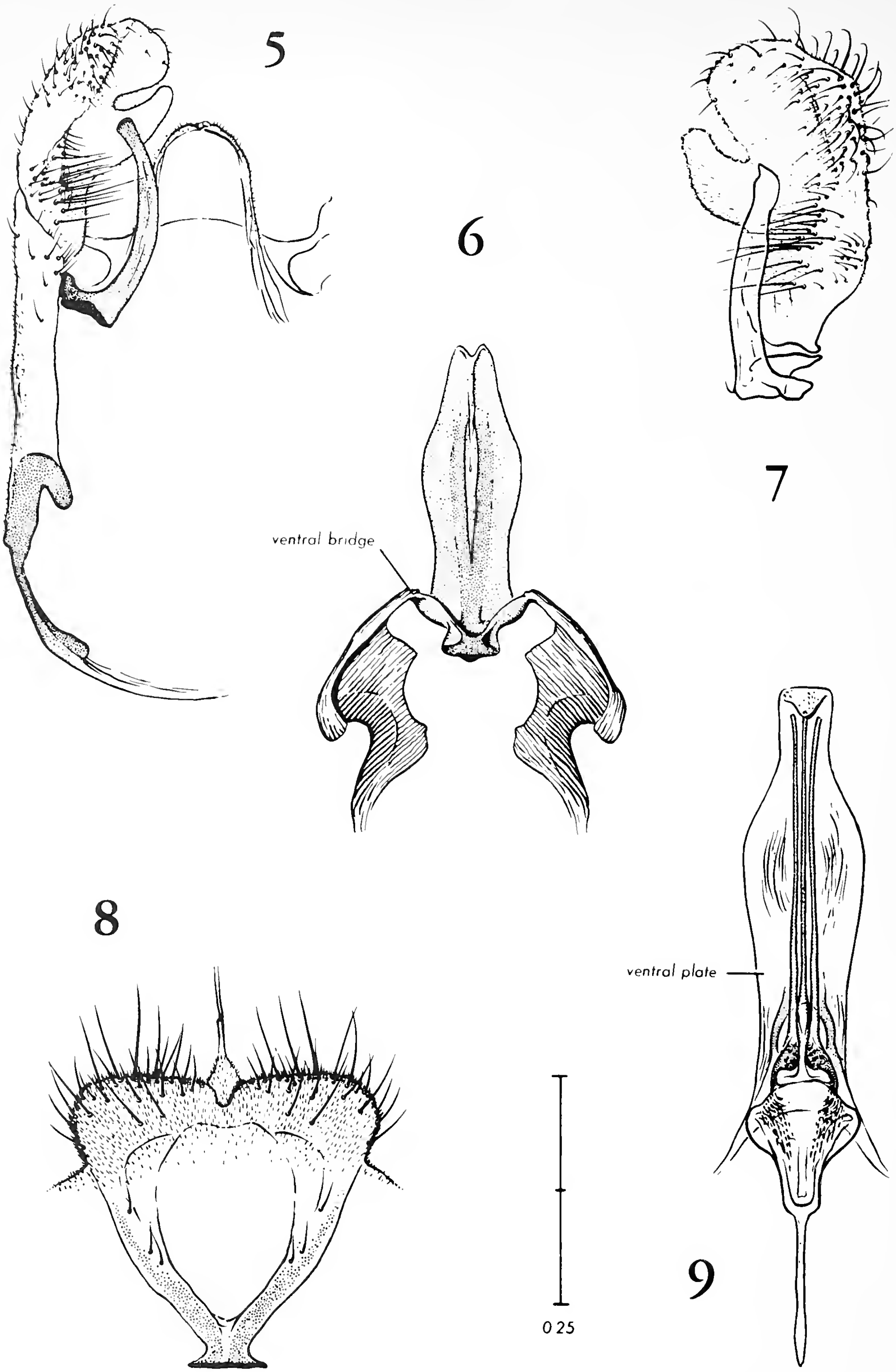


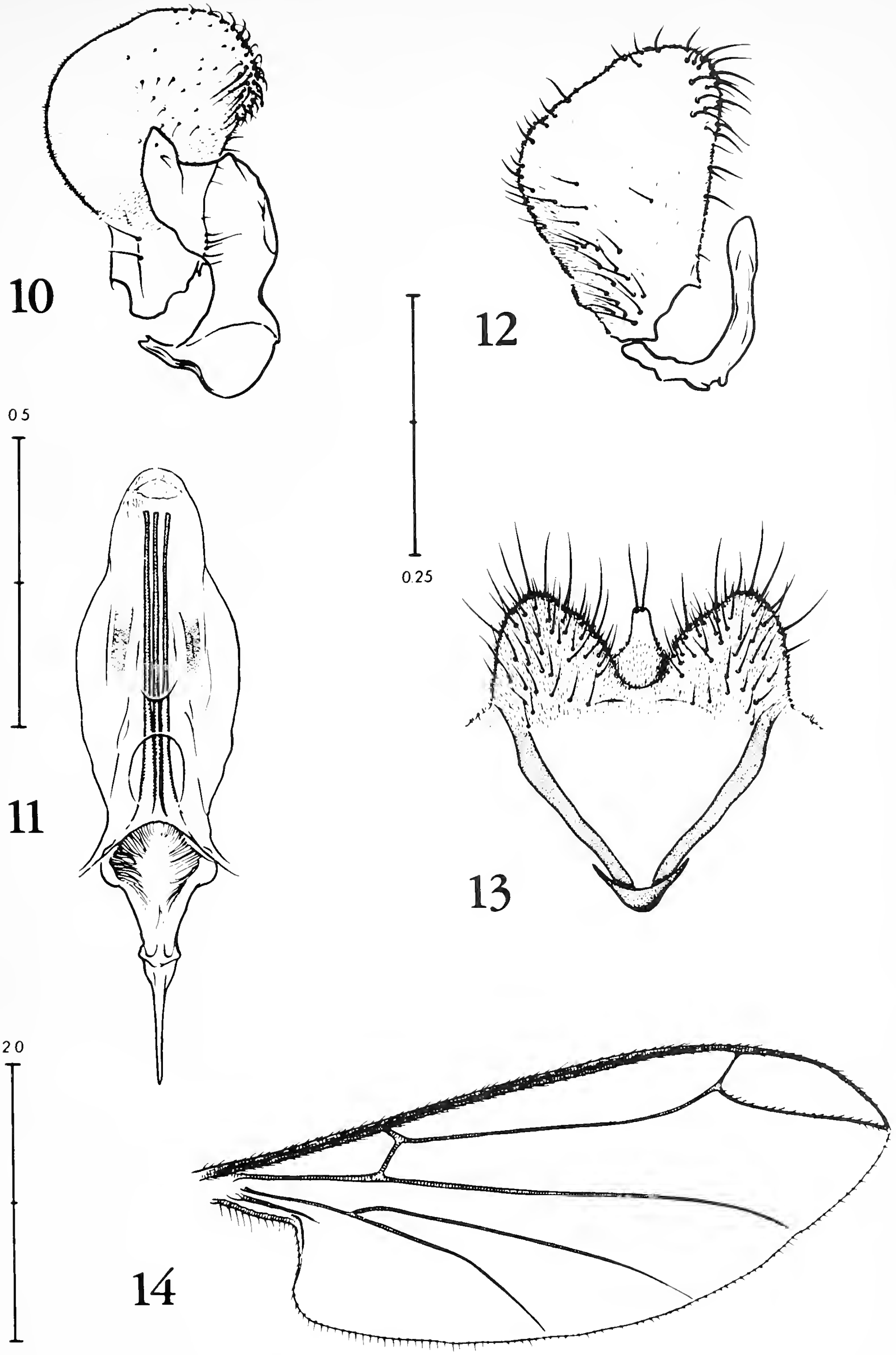
FIGURES 1–2. *Paltostoma costaricensis*, heads in frontal aspect. 1, male. 2, female.



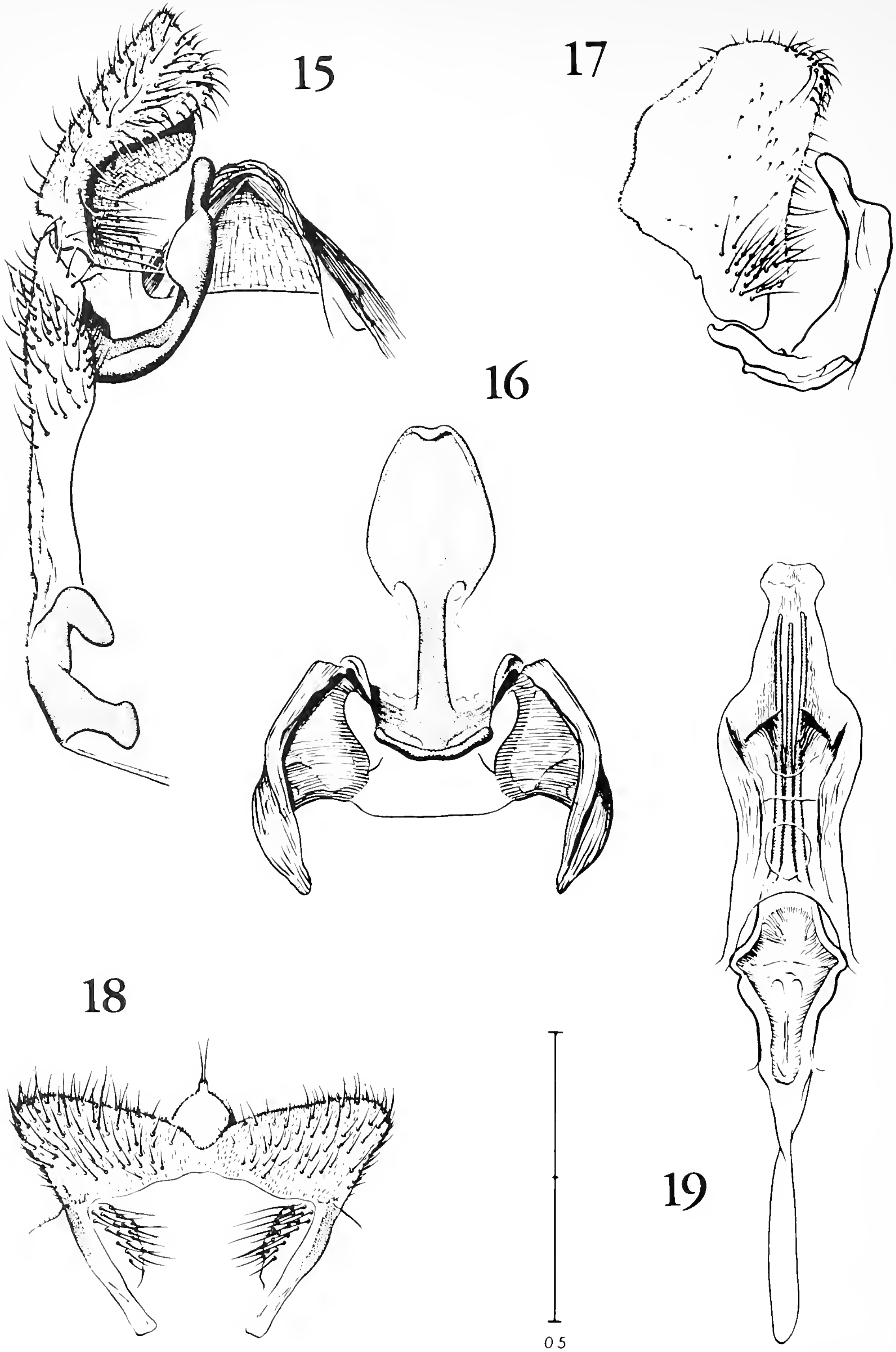
FIGURES 3–4. *Paltostoma diriageni*, heads in frontal aspect. 3, male. 4, female.



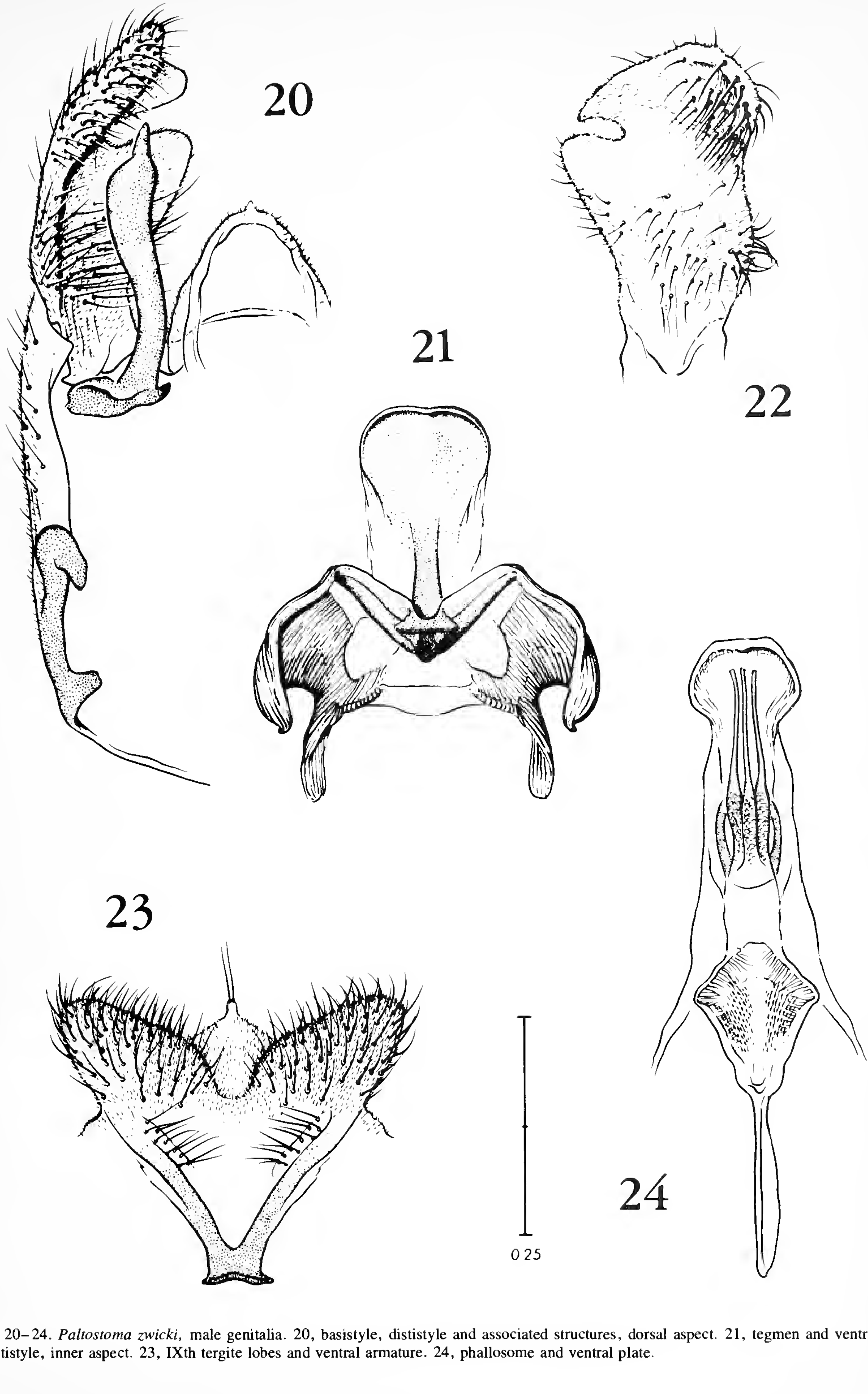
FIGURES 5–9. *Paltostoma costaricensis,* male genitalia. 5, basistyle, diststyle and associated structures, dorsal aspect. 6, tegmen and ventral bridge. 7, right diststyle, inner aspect. 8, IXth tergite lobes and ventral armature. 9, phallosome and ventral plate.



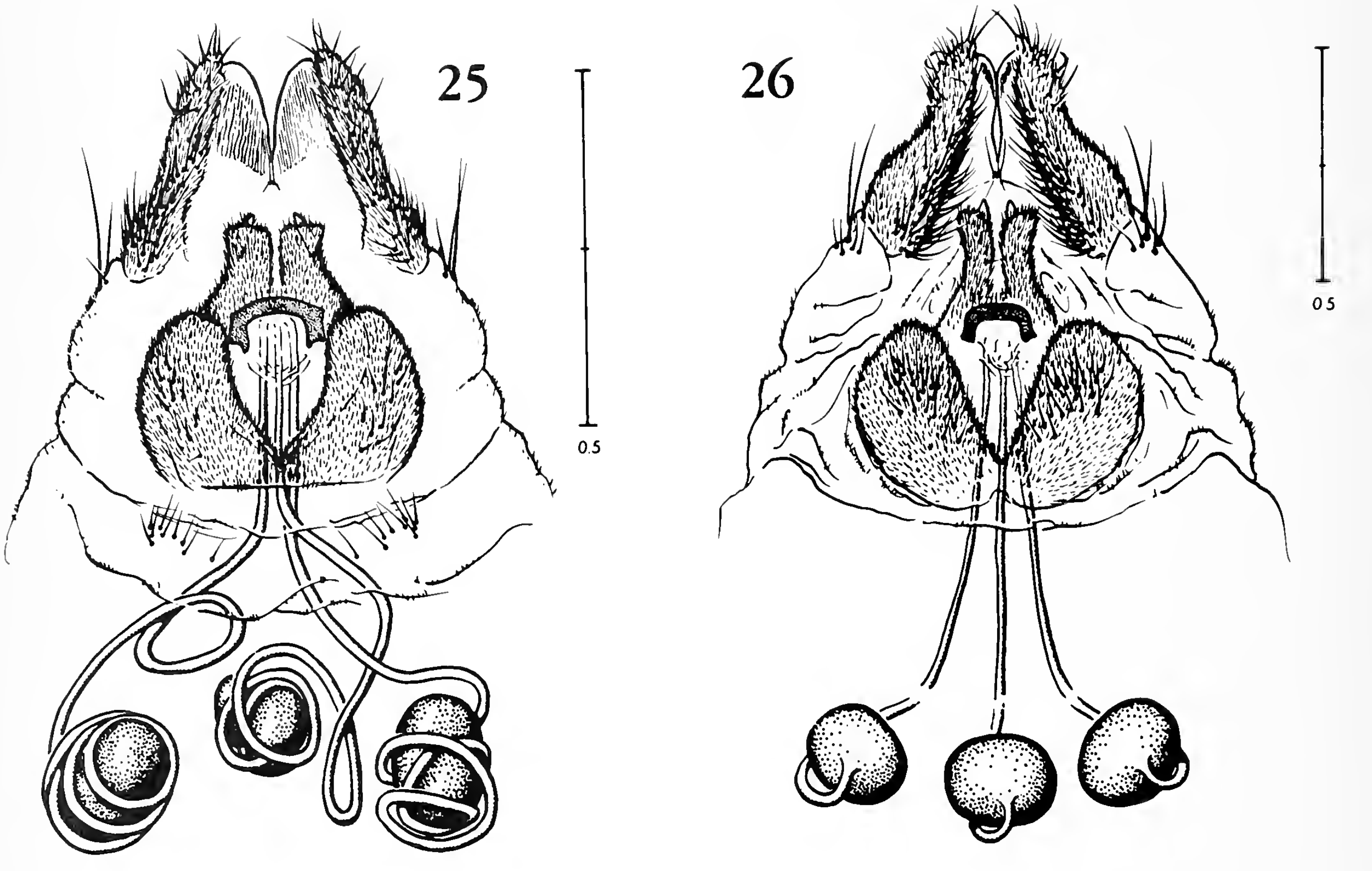
FIGURES 10–14. *Paltostoma*, male genitalia and wing. 10–11, *P. exserta*. 10, right dististyle, inner aspect. 11, phallosome and ventral plate. 12–14, *P. delectata*. 12, right dististyle, inner aspect. 13, IXth tergite lobes and ventral armature. 14, wing.



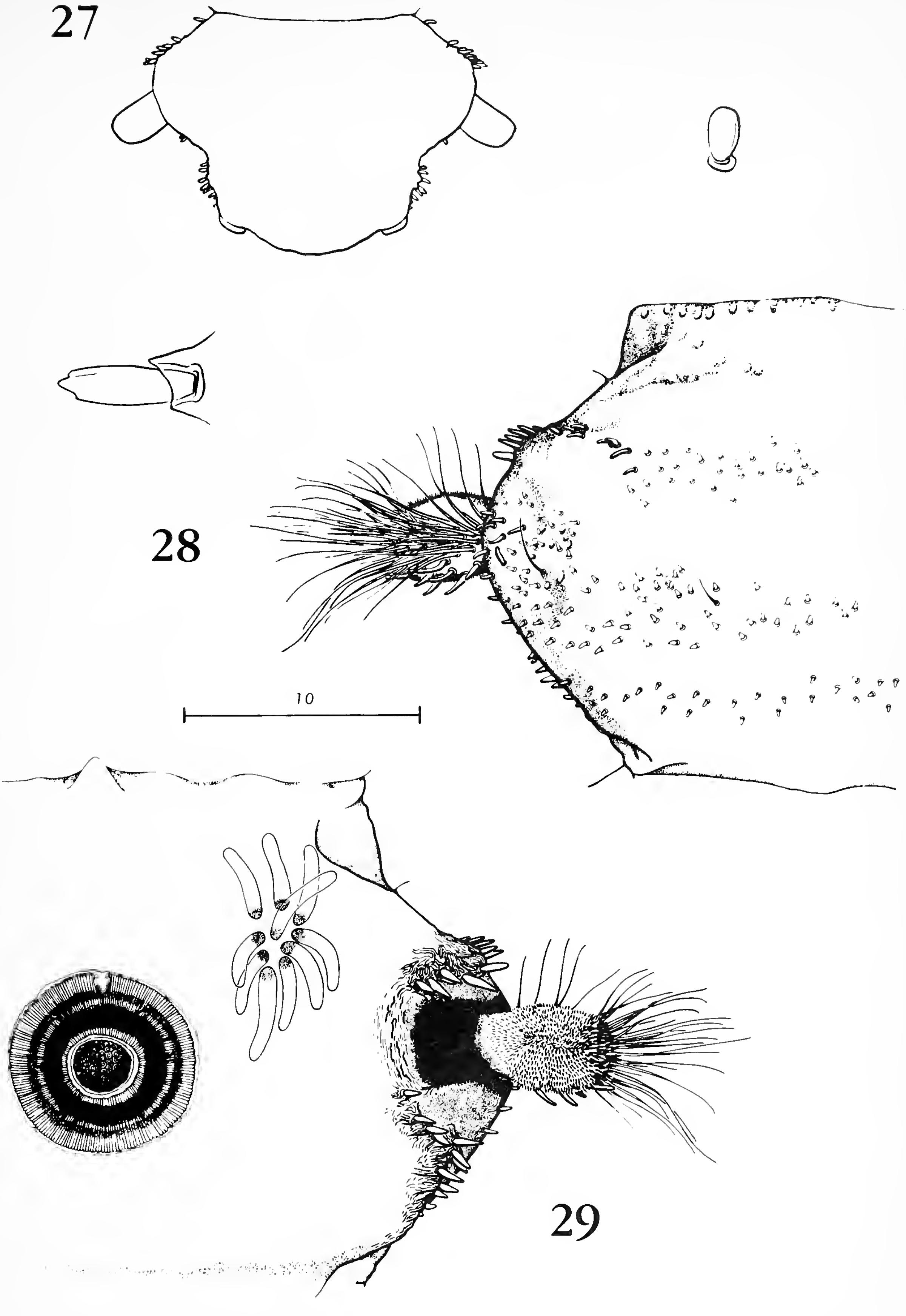
FIGURES 15–19. *Paltostoma diriageni*, male genitalia. 15, basistyle, dististyle and associated structures, dorsal aspect. 16, tegmen and ventral bridge. 17, right dististyle, inner aspect. 18, IXth tergite lobes and ventral armature. 19, phallosome and ventral plate.



FIGURES 20–24. *Paltostoma zwicki*, male genitalia. 20, basistyle, dististyle and associated structures, dorsal aspect. 21, tegmen and ventral bridge. 22, right dististyle, inner aspect. 23, IXth tergite lobes and ventral armature. 24, phallosome and ventral plate.



Figures 25–26. *Paltostoma*, female genitalia, ventral aspect. 25, *P. costaricensis*. 26, *P. diriageni*.



FIGURES 27–29. *Paltostoma costaricensis*, larva. 27, anal division, outline. 28, trunk division II, dorsal aspect. 29, same, ventral aspect.

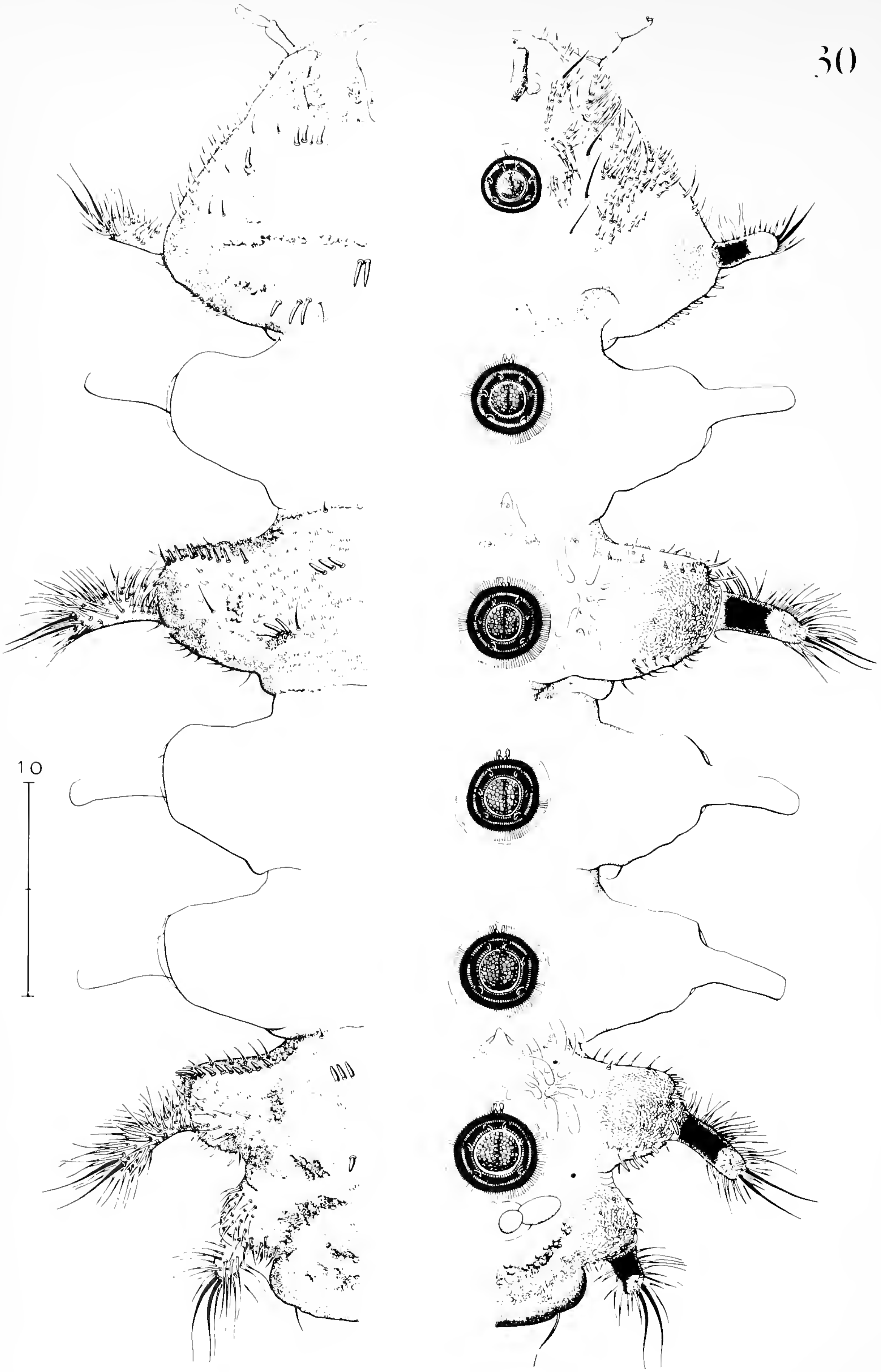


FIGURE 30. *Paltostoma delectata*, larva, dorsal aspect, left; ventral aspect, right.

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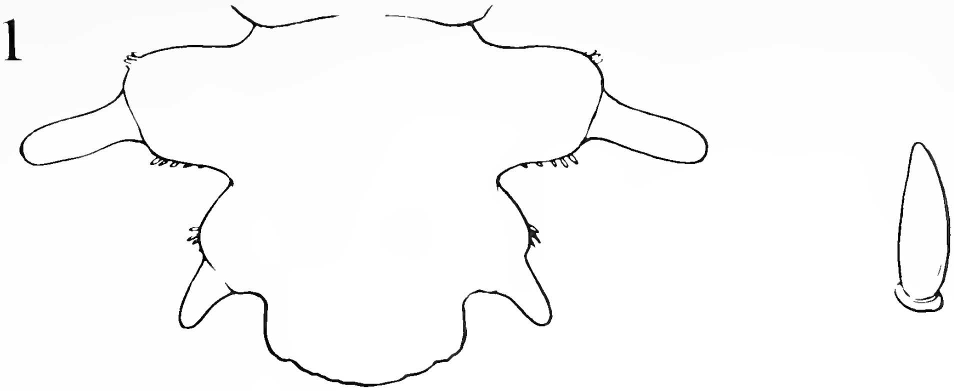

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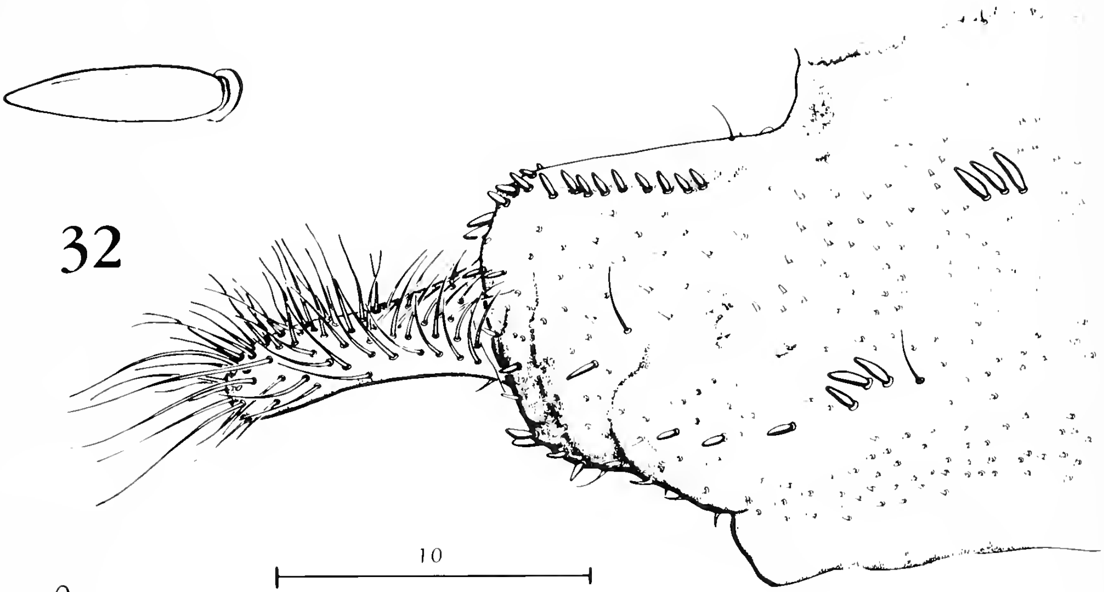

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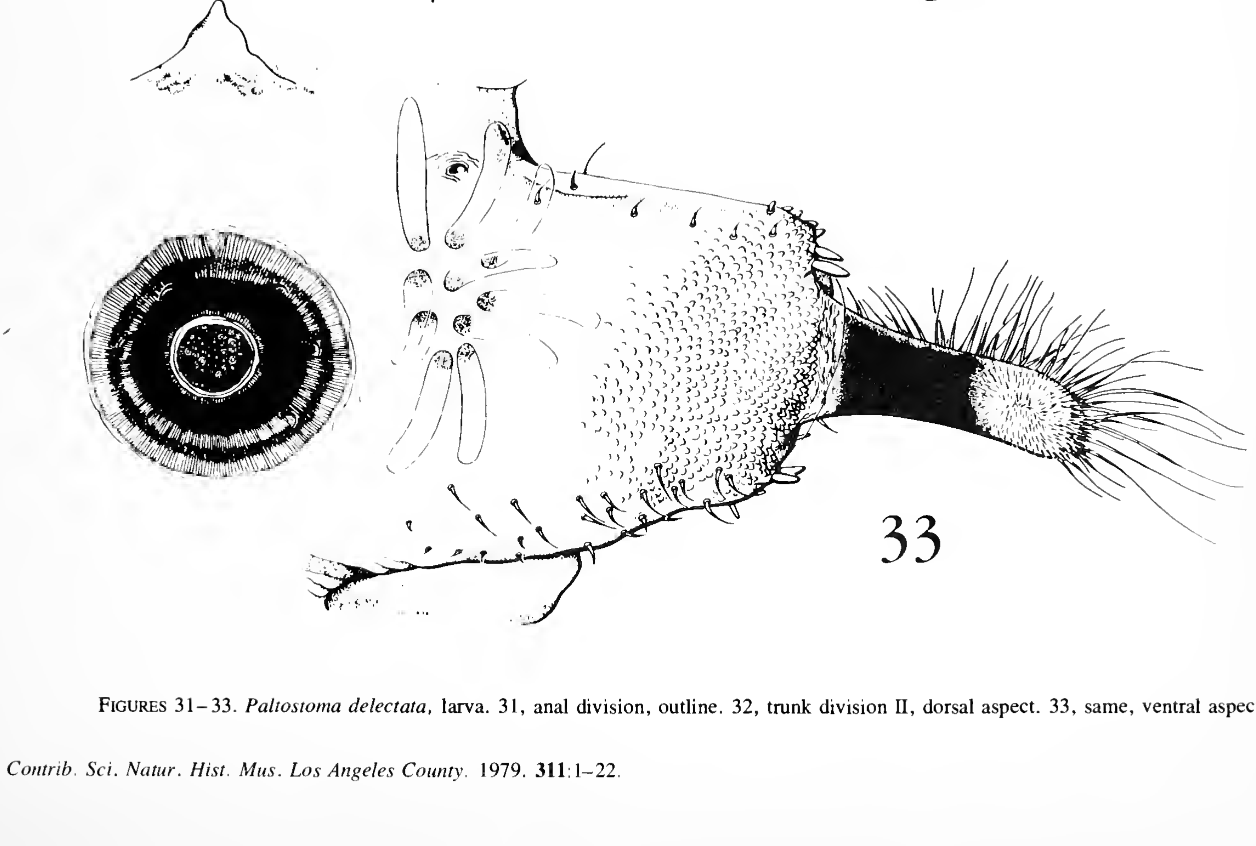

Figures 31–33. *Paltostoma delectata,* larva. 31, anal division, outline. 32, trunk division II, dorsal aspect. 33, same, ventral aspect.

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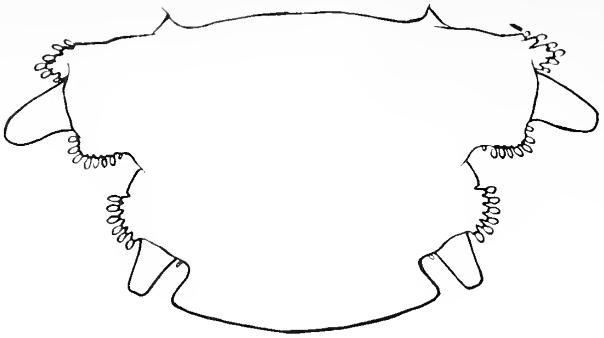

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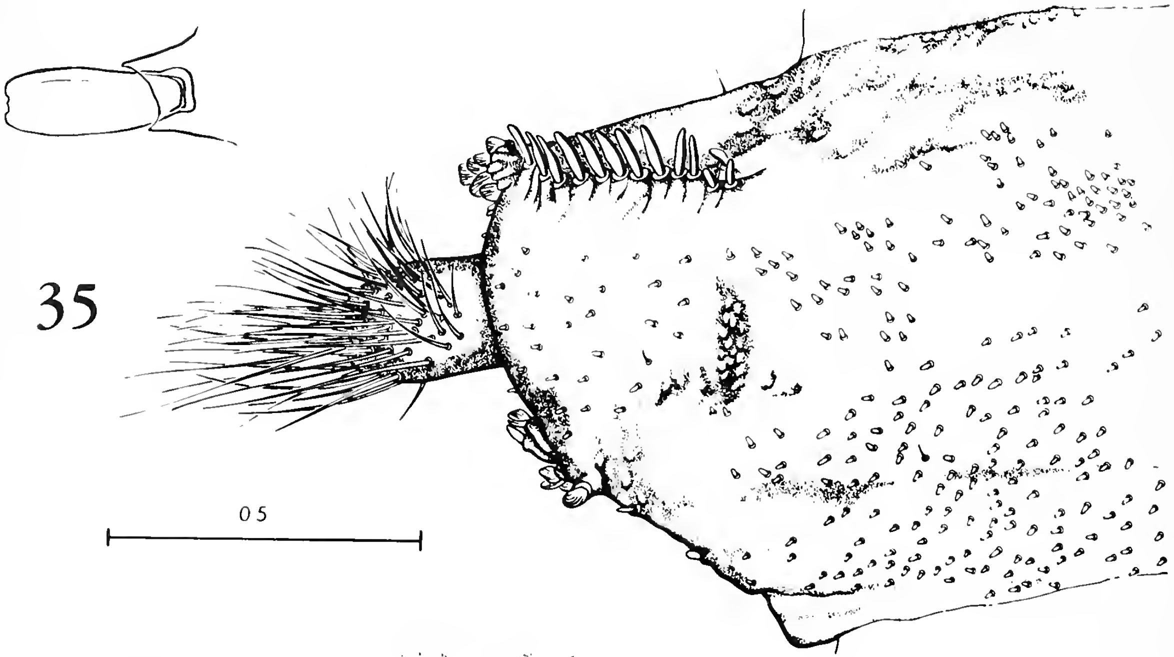

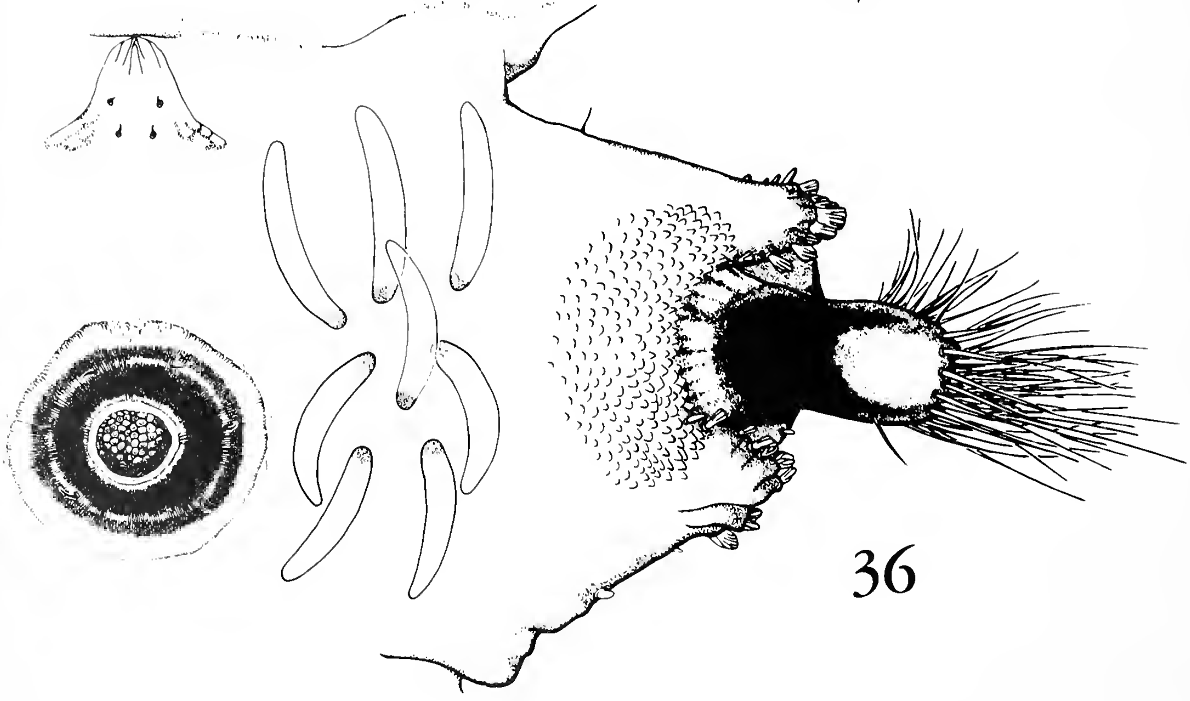

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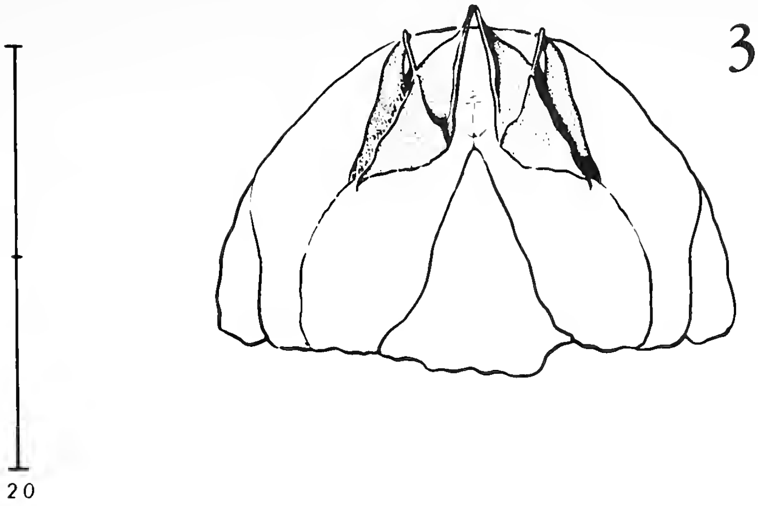
FIGURES 34–36. *Paltostoma diriageni*, larva. 34, anal division, outline. 35, trunk division II, dorsal aspect. 36, same, ventral aspect.



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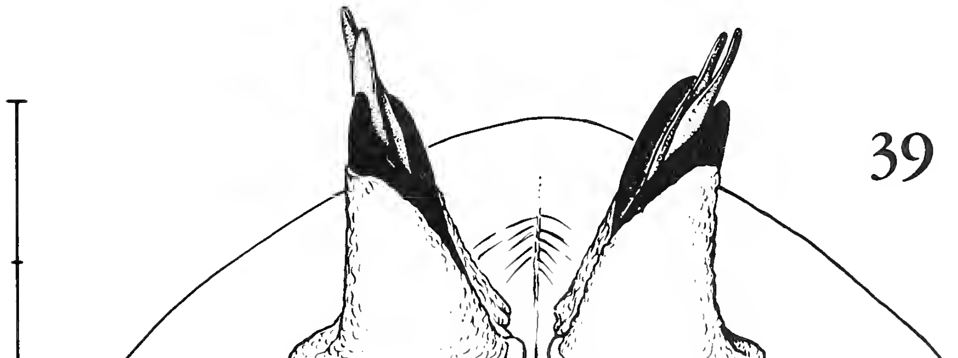

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FIGURES 37–39. *Paltostoma*, pupae, anterior aspect. 37, *P. costaricensis*. 38, *P. diriageni*. 39, *P. exserta*.

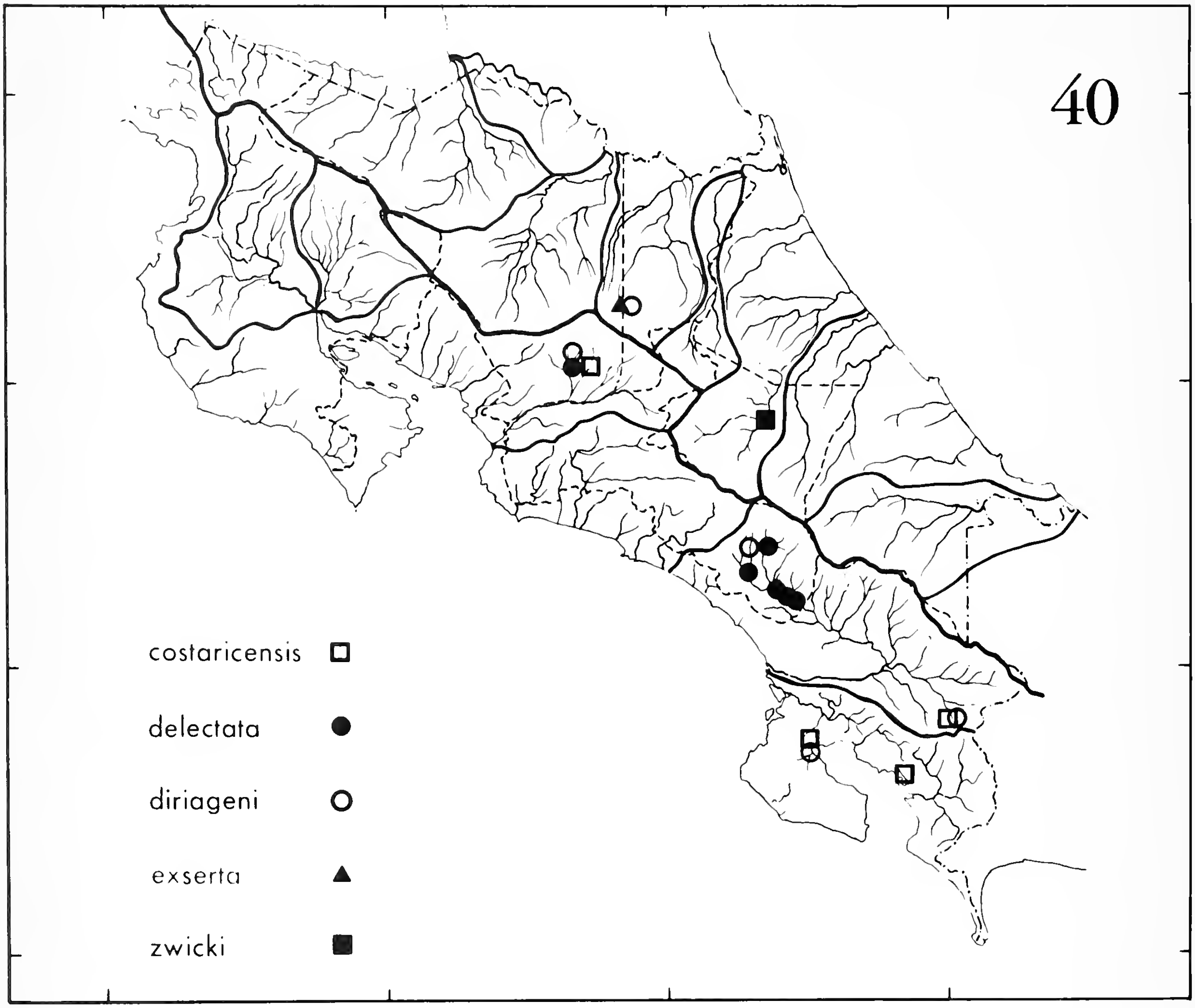

FIGURE 40. Map of Costa Rica with collection localities of *Paltostoma* shown by symbols. Heavy lines outline major drainage systems, heaviest indicating continental divide.

Number 312
March 16, 1979

CONTRIBUTIONS IN SCIENCE

NATURAL HISTORY MUSEUM OF LOS ANGELES COUNTY

PROMYLAGAULUS, PROGRESSIVE APLODONTOID RODENTS OF THE EARLY MIOCENE

By John M. Rensberger

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Edward Ostermeyer
Editor

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CONTENTS

The *Science Bulletin* and *Contributions in Science* of the Natural History Museum of Los Angeles County were merged into a single imperial octavo serial, retaining the name *Contributions in Science* and beginning with Number 301.

This serial has been newly formatted for maximum use of typography and illustrations per page, and sized for maximum use of paper. All photography has been produced utilizing a 200-line screen for detail.

Since most institutions rebind *Contributions in Science* collectively into hardbound volumes, and many researchers using them desire to photocopy material, two new features have been incorporated into the new format. A suggested citation line provides the abbreviated serial title, year, number of publication, and total pagination, and appears in the lower left corner of each page; and pages of *Contributions in Science* have been printed off-center to provide a two-inch gutter between adjacent pages for easier accessibility in photocopying.

ISSN: 0459-8113

Suggested Citation: *Contrib. Sci. Natur. Hist. Mus. Los Angeles County*. 1979. **312**:1–18.

Contributions in Science are articles in the earth and life sciences, presenting results of original research in Natural History. *Science Bulletin* (Numbers 1–30; 28 June 1965 to 10 April 1978) and *Contributions in Science* (Numbers 1–300; 23 January 1957 to 16 June 1978) were merged into a single imperial octavo serial beginning with Number 301.

PROMYLAGAULUS, PROGRESSIVE APLODONTOID RODENTS OF THE EARLY MIOCENE[1]

By John M. Rensberger[2]

ABSTRACT: *Promylagaulus*, until recently represented by only a single described species of uncertain age, *P. riggsi*, is a diverse and rather widely distributed genus, most members of which seem to occur in a restricted interval of the early Miocene. Of the two new species described here, *P. ovatus* is from an upper part of the Monroe Creek Formation in South Dakota, and *P. montanensis* occurs in a restricted interval in the Deep River Formation of Montana. A form from northern Wyoming, when better known, may represent another species. Each of these three occurrences is within the *Entoptychus-Gregormymys* Concurrent-range Zone of Fisher and Rensberger (1972). *P. lemhiensis*, from northern Idaho, is apparently from an only slightly older interval.

These species differ in hypsodonty, size and lophodonty. No trend toward characteristics definitive of the Mylagaulidae is evident among these species and a number of features indicate that *Promylagaulus* was not ancestral to the later mylagaulids. Although similar in a number of characteristics to an earlier and more primitive aplodontoid, *Meniscomys*, *Promylagaulus* frequently retained at least one primitive feature that was absent in the earliest known members of *Meniscomys*.

A few years ago, a biostratigraphic study of the Deep River and Fort Logan formations of Montana was undertaken in order to more clearly correlate Oligo-Miocene sequences of vertebrates of the far west with faunas within and east of the Rocky Mountain region. One of the taxa recovered in the course of this study is an aplodontoid rodent resembling specimens referred to *Promylagaulus riggsi* McGrew, described from the Monroe Creek Formation of South Dakota by J.R. Macdonald (1963, 1970) and L. Macdonald (1972), and *P. lemhiensis* Nichols (1976) from the early Miocene of Idaho.

The problem of assessing the relationships of small samples of *Promylagaulus* is difficult because the cheek teeth in this genus are high crowned and complex, with numerous enamel bordered lakes of different depths and which vary in size and shape with wear. The dentition in the type specimen of *P. riggsi* (McGrew 1941) has few characteristic features that are not made ambiguous by the advanced stage of wear. The more recently described specimens of *Promylagaulus* were reported upon in papers devoted to entire faunas and the comparative morphologies have not as yet been presented in detail. This paper compares the new material of *Promylagaulus* from the Deep River Formation with that from South Dakota and Idaho, and presents additional evidence concerning the relationship of these forms.

ABBREVIATIONS OF INSTITUTIONS

AMNH	American Museum of Natural History
FMNH	Field Museum of Natural History
ISU	The Museum, Idaho State University
LACM	Los Angeles County Museum of Natural History
SDSM	South Dakota School of Mines and Technology
UM	Department of Geology, University of Montana
UWBM	University of Washington, Burke Memorial Washington State Museum

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DENTAL NOMENCLATURE

The principal cusps of the cheek teeth in *Promylagaulus* (Fig. 1) correspond to those of *Haplomys* (Rensberger 1975: Fig. 1). Whereas the major cusps are homologous to those of other groups of rodents, the enamel inflections, fossettes and fossettids are frequently not homologous. Different authors have applied the terminology used by Stirton (1935) for the castorids to the mylagaulids, but in conflicting ways. Because of fundamental differences in the origins of the inflections and lakes in the castorids and aplodontoids, there is no obvious and natural way to transfer a number of the names from the former to the latter. Rather than introduce new terms for these structures in the aplodontoids at this time, and to avoid confusion with the several usages of the castorid nomenclature, I have simply used descriptive terms based upon the position of the structure with reference to the center of the tooth (Fig. 1). Thus the structures in any of the four quadrants are prefixed by anterolingual, posterolingual, etc., and those falling in the midsection of a side by labial, lingual, anterior or posterior. An advantage of this method is that when applied to fossettes and fossettids, it lends itself to situations in which a structure originates in different ways. For example, within a single species of *Promylagaulus* there may be both anterolingual and posterolingual fossettids on P_4, or there may be only a lingual fossettid in those positions, depending upon whether or not the mesostylid is joined to the mesoconid by a crest. This

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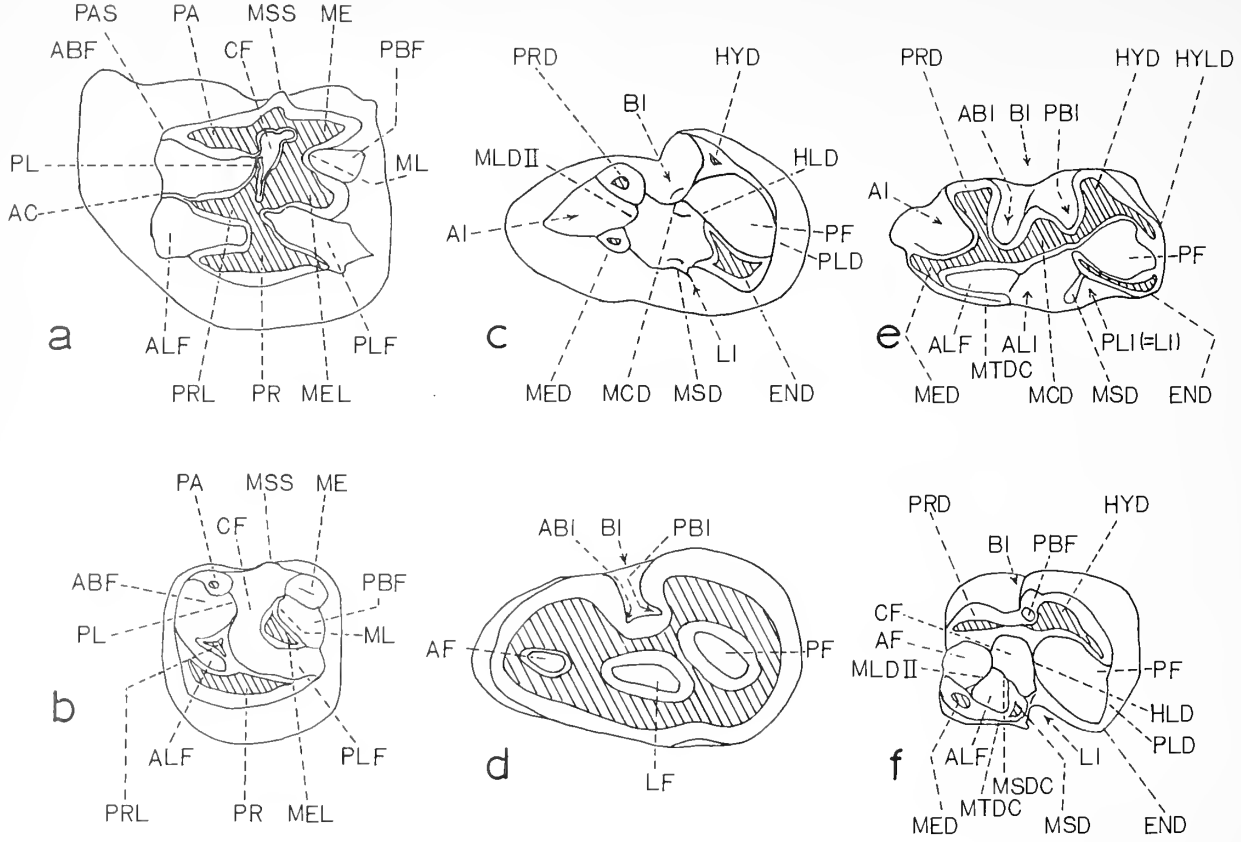

FIGURE 1. Nomenclature of occlusal structures in *Promylagaulus*. *a*–left P^4; *b*–left M^1 or M^2; *c*–little worn right P_4; *d*–well worn right P_4; *e*–right DP_4; *f*–right M_1 or M_2. Cross hatching = dentine; labial side toward top, anterior toward left. ABF = anterolabial fossette (-id); ABI = anterolabial inflection; AC = anterocone; AF = anterior fossettid; AI = anterior inflection; ALF = anterolingual fossette (-id); ALI = anterolingual inflection; BI = labial inflection; CF = central fossette (-id); END = entoconid; HLD = hypolophid; HYLD = hypoconulid; HYD = hypoconid; LF = lingual fossettid; LI = lingual inflection; MCD = mesoconid; ME = metacone; MED = metaconid; MEL = metaconule; ML = metaloph; MLDII = metalophulid II; MSD = mesostylid; MSDC = mesostylid crest; MSS = mesostyle; MTDC = metastylid crest; PA = paracone; PAS = parastyle; PBF = posterolabial fossette; PBI = posterolabial inflection; PF = posterior fossettid; PL = protoloph; PLD = posterolophid; PLF = posterolingual fossette; PLI = posterolingual inflection; PR = protocone; PRD = protoconid; PRL = protoconule (paraconule).

method somewhat simplifies the terminology in a group in which the occlusal structure can be very complex.

METHODS

The most objective information bearing on the relationship of the fossil jaws, teeth and skull representing *Promylagaulus* is the stratigraphic-geographic occurrence of the elements. Specimens from a single geographic and stratigraphic position and among which there is no evidence of a significant discontinuity in morphology were probably members of a single population or very closely related ones. This information, together with the complex combinations of morphologic similarities and dissimilarities presented in the following sections show that at least four distinct taxonomic groups are represented.

The distinct geographic-stratigraphic associations are:

Deep River Fm., central Montana, *(P. montanensis)*
Lemhi Valley, western Montana, *(P. lemhiensis)*
Anthills locality, uppermost Monroe Creek Fm., S. Dakota, *(P. ovatus)*
Specimen SDSM 6277, Monroe Creek Fm., S. Dakota, *(P. ovatus)*
P. riggsi, unknown locality, S. Dakota

MORPHOLOGIC RELATIONSHIPS

The material from the Deep River Formation consists of two right mandibles: UWBM 38075, with P_4–M_3; and UWBM 38103, with a lower incisor fragment and DP_4–M_2. The specimens are from approximately the same stratigraphic position in a 5 to 7 m thick massive sandstone at a single exposure. Although the relatively little worn and moderately worn occlusal patterns of the molars in the two specimens differ greatly, analogous differences are also present among the isolated teeth reported from an anthill locality in the Monroe Creek Formation of South Dakota and referred to *Promylagaulus riggsi* by L. Macdonald (1972). The specimens from the Deep River Formation probably represent a single population, or at least closely related ones.

LOWER INCISOR

The enamel face of the incisor in the Deep River taxon is broad and only slightly convex transversely. It closely resembles that of *Meniscomys hippodus* Cope, of the John Day Formation, except that the width is somewhat greater, consistent with the overall larger size of the mandible. The incisor is wider and slightly flatter than that of SDSM 6277, cf. *Promylagaulus riggsi*

(Macdonald 1970:33) from South Dakota, a specimen of smaller overall size.

Deciduous Lower Premolar

The DP$_4$ of the Deep River form (UWBM 38103) is well worn but still retains several fossettids (Fig. 2a). A central anterior fossettid is triangular with one angle in a posterior position and the remaining angles in anterolabial and anterolingual positions. The anterolingual corner of the fossettid is not quite closed at the existing stage of wear. The anterior fossettid in SDSM 6277 also opens anterolingually, although the fossettid is more worn and less triangular than in the specimen from Montana. In a specimen of *Meniscomys hippodus* (UWBM 29160), the anterior fossettid is oval, narrower transversely than that in SDSM 6277 or the Deep River form, and opens directly craniad. Three unworn to lightly worn deciduous lower premolars, 117384, 117436 from the anthill locality (LACM 1871 = SDSM 6229) were not described by L. Macdonald (1972), although they are questionably assigned on the specimen record to *Promylagaulus riggsi*. Although pronounced morphologic differences exist among these specimens, they probably belong to the taxon represented at that locality by permanent teeth, as will be shown below. The anterior fossettid or inflection in the specimens of DP$_4$ from the anthill collections (Fig. 3b) is triangular, as in the Deep River form,

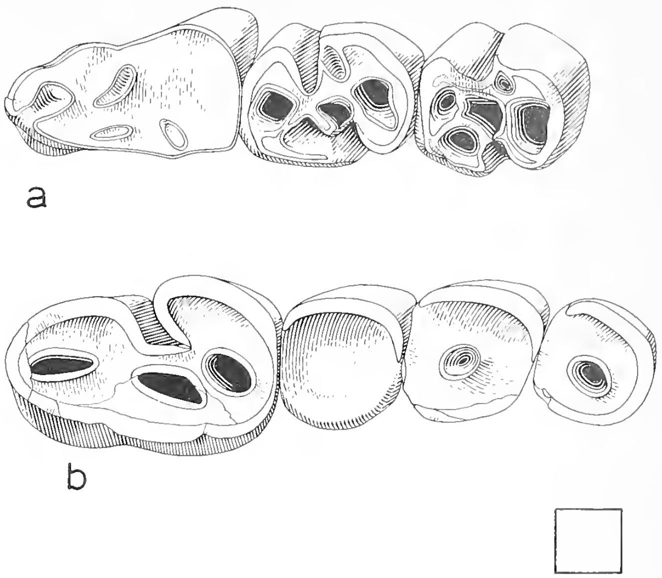

FIGURE 2. *Promylagaulus montanensis*. *a*–occlusal view right DP$_4$–M$_2$, UWBM 38103; *b*–occlusal view right P$_4$–M$_3$, UWBM 38075. Both specimens from level 1 of locality Spring Creek 1 (UWBM A5867), Deep River Formation, Montana. Labial side toward top of figure. Scale = 1 mm. Drawing by Mark Orsen.

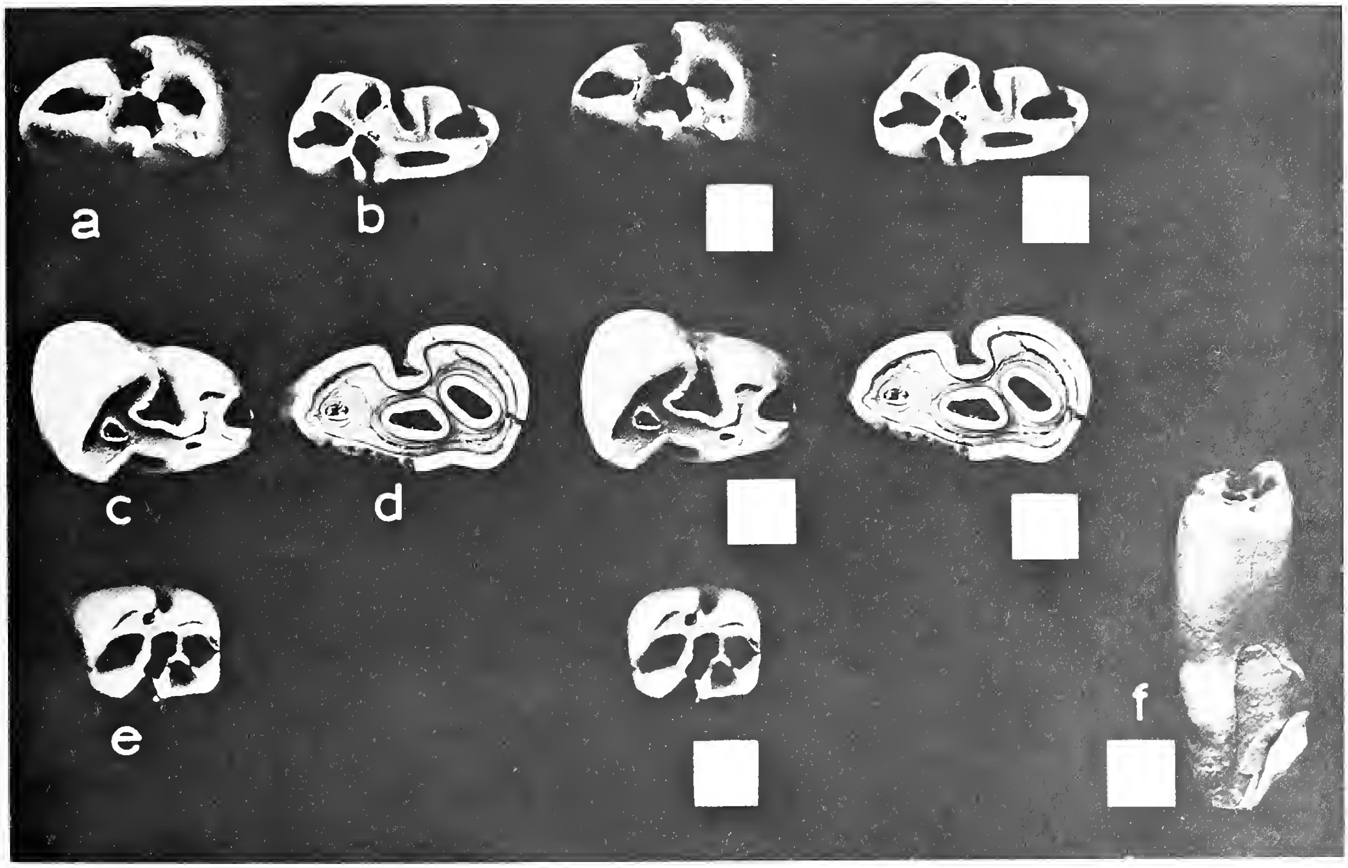

FIGURE 3. *Promylagaulus ovatus*, lower cheek teeth. *a*–occlusal view little worn right P$_4$, LACM 117372; *b*–occlusal view left DP$_4$, LACM 117436; *c*–occlusal view worn left P$_4$, LACM 117368; *d*–occlusal view worn right P$_4$, LACM 117370; *e*–occlusal view left M$_1$, LACM 117435; *f*–same, posterior view. All except *f* stereo pairs. Labial side toward top of figure. Scale = 1 mm.

TABLE 1

Length, Width of P_4; Depth of Labial Enamel on P_4 (mm)

MUSEUM NUMBER	LOCALITY	LP	WTR	WTA	DLEP	DLEP/LP
UWBM 38075	Deep River Fm (UWA 5867)	4.1	2.2	2.7	2.8	0.68
ISU 18594	Lemhi Valley (ISU 59003)	4.7	1.9	2.7	2.0	0.43
ISU 18601	Lemhi Valley (ISU 59003)	5.0	2.2	3.0	2.2	0.44
AMNH 56333	Darton's Bluff*	3.6	1.8	2.2	—	—
LACM 9340	Wolff Ranch (LACM 20051)	3.8	2.0	2.4	—	—
LACM 9342	Wolff Ranch (LACM 20051)	3.5	1.8	2.2	1.9	0.54
LACM 23530	Anthill (LACM 1871)	3.4	1.5	1.9	—	—
LACM 117367	Anthill (LACM 1871)	3.7	1.9	2.0	1.8	0.49
LACM 23532	Anthill (LACM 1871)	3.5	1.7	1.9	1.8	0.51
LACM 117437	Anthill (LACM 1871)	3.5	1.6	2.2	1.8	0.51

LP = anteroposterior length near base of crown.
WTR = transverse width of trigonid measured perpendicular to vertical axis of tooth.
WTA = transverse width of talonid, measured perpendicular to vertical axis of tooth.
DLEP = depth of labial enamel measured ventrad from apex of posterior dentinal tract.
* = measurements taken from published illustration (McKenna and Love 1972).

although the sequence of closure of the two anterior corners is variable.

An arcuate anterolabial inflection in UWBM 38103 lies in a transverse orientation near the anteroposterior center of DP_4 and anterior to the mesoconid. Opposite the inflection and near the lingual margin of the tooth is an anteroposteriorly aligned fossettid that is represented in *Meniscomys hippodus* by a shallow valley which doesn't form a fossettid. In both UWBM 38103 and *M. hippodus* the fossettid or valley is bounded lingually by an elongate metastylid crest at the margin of the tooth. Both the arcuate anterolabial fossettid and the elongate anterolingual fossettid are present in the teeth of the anthill locality (Fig. 3b). However, in one specimen of the latter the mesoconid lacks the labial spur that isolates the anterolabial fossettid in the other specimens.

The base of the posterolingual inflection is barely preserved in the specimen from the Deep River Formation. It lies near the lingual margin of the tooth between the areas of the entoconid and the mesostylid. The margin of the tooth is extended as a small, lingual protuberance slightly anterior to the opening of the inflection. These structures are similar to conditions present in the specimens of both *Meniscomys hippodus* and the anthill collection. The teeth in the anthill collection still retain the posterolingual fossettid, which is more posteriorly situated with respect to the posterolabial fossettid than is that in *M. hippodus*. The hypoconid of the specimens in the anthill collection is more anteriorly situated and less expansive posterolabially than in *M. hippodus* (Fig. 3b). It is this feature which relates the deciduous premolars most clearly to the molars in the anthill collection.

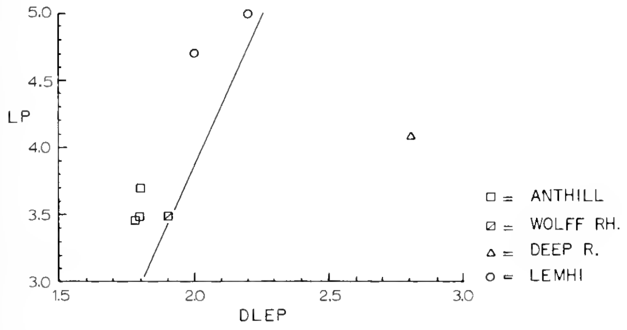

FIGURE 4. Bivariate plot of depth of labial enamel below highest point of posterior dentinal tract (DLEP) and anteroposterior length (LP) of P_4 in specimens of *Promylagaulus* from Anthill (LACM 1871), Wolff Ranch (LACM 2005), Deep River (Spring Creek 1, level 1; UWBM A5867) and Lemhi Valley (UM V-7303 = ISU 59003) localities.

LOWER PREMOLAR

The worn permanent premolar from the Deep River Formation is larger than those from the anthill collection, but its size, especially length, is exceeded by those from Lemhi Valley (Table 1). The anterior fossettid in the worn P_4 of UWBM 38075 from the Deep River Formation (Fig. 2b) is anteroposteriorly elongate and narrow, but slightly expanded anteriorly. In the Lemhi collection the fossettid is also elongate, but in SDSM 6277 and the numerous isolated teeth of the anthill collection (Fig. 3c,d) the fossettid is wider and shorter than that in the Deep River form.

The labial inflection in UWBM 38075 is directed posterolinguad, toward the center of the tooth (Fig. 2b). It ends internally at the flat surface of the mesoconid and lacks an anterior branch, but a narrow posterior portion representing the inflection posterior to the mesoconid in *Haplomys* (Rensberger 1975:6), the posterolabial inflection, extends to within 0.1 mm of the posterior fossettid. The hypoconid is posterolabially compressed and anteriorly expanded so as to contribute to the posterolingual trend of the labial inflection. In the Lemhi collection, SDSM 6277 and the unworn and little worn teeth in the anthill collection (Fig. 3a–d), the hypocone is similarly compressed and anteriorly expanded, the labial inflection abuts a normally flat mesoconid with little if any tendency to extend anteriad, and a narrow branch of the labial inflection extends behind the mesoconid toward the posterior fossettid, as in the Deep River form. There

TABLE 2

Ratios of Size of Posterior and Lingual Fossettids to Width of P^4

MUSEUM NUMBER	LOCALITY	WP	WPF4	$\frac{WPF4}{WP}$	WLIF4	$\frac{WLIF4}{WP}$	WC	$\frac{WC}{WP}$
ISU 18601	Lemhi Valley (ISU 59003)	2.7	1.1	0.41	0.8	0.30	1.8	0.67
LACM 117370	Anthill collection (LACM 1871)	2.2	0.7	0.32	0.6	0.27	1.5	0.68
LACM 117352	Anthill collection (LACM 1871)	2.2	0.8	0.36	0.6	0.27	1.4	0.64
LACM 117366	Anthill collection (LACM 1871)	2.2	0.7	0.32	0.6	0.27	1.3	0.59
UWBM 38075	Deep River Fm (UWA 5867)	2.7	0.8	0.30	0.6	0.22	1.5	0.55

WP = transverse width of P_4 across talonid.
WPF4 = transverse width of posterior fossettid on P_4, measured from outer margin of enamel.
WLIF4 = transverse width of lingual fossettid on P_4, measured from outer margin of enamel.
WC = transverse width of P_4 in center, from posterior end of posterolabial inflection.

is usually no mesoconid process on the hypoconid of *P. lemhiensis* or most of the specimens from the Monroe Creek Formation; however in several specimens from the anthill site a crest from the mesoconid joins the latter to the anterior process of the hypoconid to form a small posterolabial fossettid.

In *Meniscomys hippodus*, in contrast to many of the specimens from Montana, Idaho and South Dakota, the labial process of the mesoconid is persistent and joins at depth with a process from the hypoconid to enclose the posterolabial inflection as a fossettid. This tendency is present in the stratigraphically lowest of the known specimens of *Meniscomys*. As a consequence of this condition, the labial inflection in worn teeth of *M. hippodus* is confined to a transversely aligned slot that internally represents only the anterolabial inflection.

The posterior fossettid is still present in the moderately advanced stage of wear of UWBM 38075 (Fig. 2b). The lake is oval, with the long axis trending anterolabiad. The posterior fossettid in the teeth in the anthill collection is larger, relative to the width of the tooth (Table 2), than in the Deep River form (Fig. 3d). The fossettid is largest relative to tooth width in the Lemhi collection. In SDSM 6277 and *P. lemhiensis*, the fossettid is bounded in an early stage of wear by a distinct cusp joining the entoconid and mesoconid and forming the hypolophid, but in the anthill collection this cusp is much reduced.

A posteriorly elongate but slightly triangular lingual fossettid is present in the P_4 of the UWBM 38075. This fossettid is transversely wider relative to tooth width and more oval in the Lemhi and anthill collections (Table 2). The lake is bounded lingually by the surface of the metastylid crest, anterolabially by the surface of the mesoconid and posterolabially by the hypolophid (Fig. 2b). In all forms the posterolingual inflection extends as a shallow groove well below the stage of wear at which the fossettid closes. A considerable amount of variation in the structures bounding the fossettid is present among the little worn anthill specimens and SDSM 6277. Usually a strong metastylid crest (Fig. 3a) extends caudad to join either the hypolophid or a mesostylid cusp (or crest). There may be no mesostylid. When a mesostylid is present, it may be joined to both the metastylid crest and the mesoconid, so that the fossettid is restricted to an anterolingual position, at least in the upper part of the crown. In individuals in which the metastylid crest is undeveloped (Fig. 3c), the mesostylid tends to be flanked by anterolingual and posterolingual inflections which may not form fossettids at all, or only a small one. Specimens in the anthill collection in which the metastylid crest dominates and connects to the hypolophid (Fig. 3a, d) resemble those of the Lemhi collection and probably exhibit the structure that would be shown by UWBM 38075 in an earlier stage of wear.

In the primitive species of *Meniscomys* from the John Day Formation (Rensberger, in manuscript) individuals both with and without a metastylid crest are present. Those with the metastylid crest may lack a mesostylid, or if the latter is present, have an incipient lingual fossettid communicating (in the absence of a union between mesostylid and mesoconid) with the posterolingual fossettid. Individuals of later populations in the John Day Formation consistently have a mesostylid bounded by anterolingual and posterolingual inflections which do not close with wear to form fossettids.

The hypsodonty of the premolar in the Deep River form, as indicated by the depth of the labial enamel plate beneath the top of the posterior dentinal tract, exceeds that in the other collections (Fig. 4 and Table 1). Although the absolute length of the plate in the Lemhi collection slightly exceeds measurements in the anthill collection, the Lemhi specimens are the more brachyodont, as is shown by Figure 4 and the ratio of enamel length to tooth length (DLEP/LP in Table 1).

A locality (LACM 2005) northeast of Wolff Ranch in the Wounded Knee region of South Dakota yielded three lower cheek teeth, two of which are premolars which are not distinguishable in occlusal pattern or hypsodonty (Table 1) from the teeth in the anthill collection. The museum records indicate the specimens were derived from the Sharps Formation, but the color of the enamel is dark brown, like that of most of the teeth from the anthill collection in the Monroe Creek Formation.

A pair of mandibular rami with heavily worn teeth having a pattern similar to that of UWBM 38075 were found at Darton's Bluff, Big Horn Mountains, northern central Wyoming (McKenna and Love 1972:23). The wear is such that only two enamel lakes, the anterior and lingual fossettids, remain on the P_4 (McKenna and Love 1972: Figs. 15, 16), which makes difficult determination of the relationships of the form. The anteroposterior and transverse dimensions are smaller than those of UWBM 38075 and the Lemhi specimens but compare favorably with those from the anthill collection (Table 1).

TABLE 3

Length and Width of M_1, M_2, M_3 (mm)

MUSEUM NUMBER	LOCALITY	uL1	uL2	uL3	uW1	uW2	uW3	wL1	wL2	wL3
ISU 18594	Lemhi Valley (ISU 59003)	2.8	2.6	2.0	2.1	2.1	1.6	—	—	—
UM 5193	Lemhi Valley (UMV 7303)	—	—	—	—	—	—	—	2.4	1.9
UWBM 38103	Deep River Fm. (UWA 5867)	2.7	2.3	—	2.0	2.0	—	—	—	—
UWBM 38075	Deep River Fm. (UWA 5867)	—	—	—	—	—	—	1.9	2.2	1.8
AMNH 56333	Darton's Bluff (AMNH) left teeth†	—	—	—	—	—	—	2.0	2.3	1.7
SDSM 6277	Monroe Creek Fm. (SDSM V-6210)	2.4	2.2	—	1.8	1.7	—	—	—	—
LACM 23534	Anthill (LACM 1871)	2.8*	—	—	2.1	—	—	2.3	—	—
LACM 117441	Anthill (LACM 1871)	2.4	—	—	1.9	—	—	1.7	—	—
LACM 117435	Anthill (LACM 1871)	—	2.2	—	1.8	1.7	—	—	—	—
LACM 117374	Anthill (LACM 1871)	—	2.4	—	—	2.1	—	—	2.3	—
LACM 117373	Anthill (LACM 1871)	—	2.2	—	—	1.9	—	—	2.2	—
LACM 117415	Anthill (LACM 1871)	—	—	—	—	—	—	—	—	1.8
LACM 117404	Anthill (LACM 1871)	—	—	—	—	—	—	—	—	1.7
LACM 117406	Anthill (LACM 1871)	—	—	—	—	—	—	—	—	1 6
UCMP 75554	*Meniscomys hippodus* (UCMP V-6351)	2.0	2.0	1.9	1.8	1.8	1.5	—	—	—
UCMP 105101	*Meniscomys hippodus* (UCMP V-66104)	—	—	—	—	—	—	1.7	2.0	2.1
UCMP 105104	*Meniscomys hippodus* (UCMP V-66104)	—	—	—	—	—	—	1.8	2.1	2.1

u = unworn or only moderately worn occlusal dimension.
w = well worn or dimension taken near base of crown.
L = anteroposterior length.
W = transverse width.
1, 2, 3, = M_1, M_2, M_3.

* by far the largest molar in the anthill collection.
† measurements taken from published illustration.

LOWER FIRST AND SECOND MOLARS

The lower molars of the Deep River form are larger than those of the anthill collection but slightly smaller than those of the Lemhi collection (Table 3). In M_{1-2} of UWBM 38103 (Fig. 2a), an anterior fossettid is bounded posterolingually by the metalophulid II, which extends to the apex of the metaconid. The anterior fossettid in SDSM 6277 and the anthill and Lemhi collections is similarly formed.

In *Meniscomys* from the John Day Formation, only the labial arm of the metalophulid II is present. A slight expansion in the metalophulid II is present at the center of the tooth in the primitive species but no crest extends to the metaconid. In some individuals the expansion is stronger and restricts the anterior fossettid, but in others the fossettid is unrestricted. Occasionally the metaconid in *M. hippodus* is expanded and contacts the metalophulid II to create a small anterior fossettid in late stages of wear. In *M. hippodus,* the metalophulid II is continuous with a crest from the mesostylid; in UWBM 38103, the Lemhi collection, the anthill collection and SDSM 6277 the mesostylid crest appears to be an accessory to the metalophulid II, for it joins the latter at an angle.

The metastylid crest is stoutly developed in the Deep River form (Fig. 2a). It is slightly expanded opposite the middle of the tooth, in the position occupied by the mesostylid in primitive aplodontoids. In M_1 the crest extends 0.4 mm posterior to a transverse line through the center of the mesostylid expansion, thereby partially closing the lingual inflection. The metastylid crest of SDSM 6277 and the anthill collection (Fig. 3e) is similar but more lightly developed and seldom extends beyond the mesostylid. Though worn, the crest in ISU 18594 appears to have been less prominent than that in the Deep River form. The metastylid crest is absent in *Meniscomys hippodus*. However, in more primitive individuals of *Meniscomys* from the John Day Formation, the metastylid crest may be present as a very rudimentary structure.

An anterolingual fossettid is present in the Deep River form, the Lemhi collection and SDSM 6277, and is variably present in the anthill collection. It is bounded by the metalophulid II, the diagonally directed mesostylid crest, and the metastylid crest. When the anterolingual fossettid is not complete in the anthill collection, this is usually the result of weak development of the mesostylid crest. In M_1 of the Deep River specimen, the mesostylid crest from the metalophulid II is stout but barely makes occlusal contact with the mesostylid. In *M. hippodus* an anterolingual fossettid is seldom formed because the metalophulid II does not extend toward the metaconid.

In the specimen from the Deep River Formation, the Lemhi collection, SDSM 6277, the anthill collection, and *Meniscomys hippodus,* the central fossettid is the deepest of the four or five fossettids. In the M_1 of a primitive form of *Meniscomys* from the John Day Formation, a lingual inflection is present but there is little or no indication of a crest tending to enclose a central fossettid. In more advanced forms a central fossettid is formed in M_1. In the M_2 of *Meniscomys* the central fossettid is usually closed.

The lingual inflection in M_1 and M_2 of the Deep River form is closed at the lingual extremity by a low crest forming a basin or shelf at the base of the inflection, well below the closure of the central fossettid (Fig. 2a). A small, shallow fossettid is formed at the base of this inflection on M_1, but is not quite formed on M_2. In SDSM 6277, ISU 18594 and most of the anthill collection, the shelf is absent and the inflection usually fades out at depth. A shelf may or may not be present in *Meniscomys hippodus;* in primitive specimens of *Meniscomys* from the John Day Formation a shelf tends to be present but does not enclose a fossettid.

The mesoconid in the Deep River specimen is a triangular cusp, with a heavy labial spur that joins the anterior margin of the hypoconid to enclose a very small, shallow posterolabial fossettid (Fig. 2a). The configurations in SDSM 6277 and the anthill collection are similar except that the mesoconid in M_1 is smaller and less distinct (Fig. 3e). The mesoconid spur is directed anterolabiad in the Deep River specimen, whereas it runs posterolabiad in SDSM 6277 and strongly so in the anthill specimens (Fig. 3e). In *Meniscomys hippodus* the mesoconid is a distinct cusp, but the structure connecting it with the hypoconid is a thinner crest than that in *Promylagaulus*.

The hypoconid in the Deep River form, the Lemhi collection, SDSM 6277, and the anthill collection is posterolabially compressed and, as in P_4, expanded anteriorly (Figs. 2a, 3e). In the Deep River specimen the anteroposterior expanse of the labial inflection is less than in the other specimens and more deeply incised medially, especially in M_1. The posterolophid is posteriorly expanded and convex in the specimens from Montana, Idaho and South Dakota, but the convexity is most pronounced, especially at the transverse midpoint of the crest, in the Deep River form. The hypoconid of *Meniscomys hippodus* is expanded rather than compressed posterolabially, and the posterior surface of the posterolophid is relatively straight.

The posterior fossettid in the specimen from Montana is polygonal in shape, owing to prominence of the hypoconulid and entoconid, with the long diameter aligned anterolabially. In SDSM 6277 and the anthill collection, the fossettid has the same orientation but is more smoothly oval in outline. In *Meniscomys hippodus* the posterior fossettid is more compressed than in any of the other forms and the long axis is aligned anteroposteriorly.

M_1 in the lightly worn dentition from the Deep River Formation, UWBM 38103, as in the intermediately worn specimen from the Lemhi Valley (ISU 18594), appears somewhat larger than M_2 (Fig. 2a). In the heavily worn dentition from Montana, UWBM 28075, M_1 is slightly smaller in occlusal dimensions than M_2 (Fig. 2b). M_1 in the little worn dentition of SDSM 6277 is slightly larger at the occlusal surface than M_2. The isolated lower molars of the anthill collection vary greatly in size, probably in part due to such positional variation. In little worn dentitions of *Meniscomys* from Oregon, M_1 and M_2 are almost equal in size. However, in well worn dentitions M_1 becomes relatively smaller, especially in anteroposterior length, than in UWBM 38075.

At the late stage of wear represented in the Deep River form (Fig. 2b), the labial inflection has disappeared and the occlusal edge of the labial enamel forms a thick crest extending from the anterolabial corner of M_1 or M_2 across the labial face and onto the posterior face. The remaining three-fifths or more of the occlusal margin in M_1 lacks enamel. An isolated bit of lingual enamel persists in M_2. The only fossettid remaining in these teeth is the central one in M_2. The molars at this stage are reduced in size and rather oval in shape.

In the teeth from the anthill collection, the basal enamel of the hypoconid region extends more prominently posterolabiad than in UWBM 38075, giving the teeth an angular outline that persists with wear. Furthermore, the posterior surface at depth is invaginated, marking a division between the vestigial roots which is not indicated in UWBM 38075 nor ISU 18594. In *Meniscomys hippodus*, the labial inflection persists into late stages of wear, and the teeth retain an angular outline.

Full measurement of the degree of hypsodonty in the molars from the Deep River Formation is impossible because the enamel is either partially hidden by alveolar bone, or much of it has been worn away. Judging from the amount of enamel remaining on M_2 of UWBM 38075, the ratio of enamel length to tooth width was greater than that in a specimen of the Lemhi collection (Fig. 5 and Table 4). The relative length of enamel is greater in the anthill collection than in the Lemhi collection. An isolated molar from another locality (SDSM V59) is less hypsodont than that of the Lemhi collection or those of the anthill collection and may be more closely related to *P. riggsi*. The depth of the labial enamel in *Meniscomys hippodus* is one-third or less that in the Lemhi or anthill collections. Although the type of *Promylagaulus riggsi* lacks the lower dentition, an indication of the degree of hypsodonty of this specimen relative to that of the other collections is obtainable from the upper dentition, described in a later section.

A thin layer of cement extends over the lower part of the enamel in several of the lower molars of the anthill collection, and a rather heavy layer extends at least 1.3 mm above the base of the lingual enamel on UM 5193 of the Lemhi collection. Cement extends perhaps 0.5 mm up the lingual enamel of M_2 in UWBM 38075.

The first and second molars of AMNH 56333, from Darton's Bluff, lack fossettids, owing to the advanced stage of wear. These teeth are oval in occlusal outline — slightly more so than in the less worn molars of UWBM 38075, and differ in this respect from the angular pattern in the anthill collection. In contrast to UWBM 38075, the lingual and posterior enamel in this specimen still persists in spite of the deeper stage of wear with

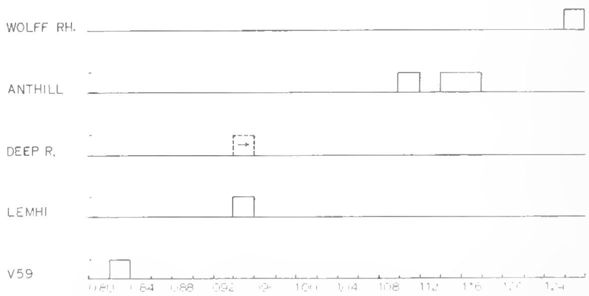

FIGURE 5. Frequency distributions of values of ratio of depth of labial enamel below highest point of posterior dentinal tract to transverse width of M_1 or M_2 in Promylagaulus. Localities are those in Fig. 4, plus SDSM V59. Base measurements for classes are listed. Arrow indicates incomplete measurement.

TABLE 4

Depth[1] of Labial Enamel on M_1, M_2 (mm)

MUSEUM NUMBER	LOCALITY, TAXON	DE1	DE2	DE1/W1	DE2/W2
UWBM 38075	Deep River Fm. (UWA 5867)	—	2.0+	—	>0.95
ISU 18594	Lemhi Valley (ISU 59003)	—	2.0	—	0.95
LACM 117435	Anthill Collection (LACM 1871)	—	2.5	—	1.14
LACM 117441	Anthill Collection (LACM 1871)	2.1	—	—	1.11
LACM 117373	Anthill Collection (LACM 1871)	—	2.1	—	1.17
LACM 9339	Wolff Ranch (LACM 20051)	1.9	—	1.27	—
SDSM 59158	Monroe Creek Fm. (SDSM V59)	—	2.1	—	0.83
UCMP 105066	*Meniscomys hippodus* (UCMP V-6506-1)	—	0.7	—	0.37
UCMP 105058	*Meniscomys hippodus* (UCMP V-6506-2)	—	0.6	—	0.33

[1] Measured from level of apex of posterior dentinal tract to lowermost margin of labial enamel.

DE1 = Depth of labial enamel on M_1.
DE2 = Depth of labial enamel on M_2.
W1 = Transverse width of enamel on M_1.
W2 = Transverse width of enamel on M_2.

respect to the bases of the lakes. This suggests that the dentinal tracts may not be as vertically extensive as in UWBM 38075.

LOWER THIRD MOLAR

This tooth is missing in the little worn dentition of the Deep River Formation, UWBM 38103, but is just emerging from the alveolus in SDSM 6277 and is present in ISU 18594. Several third molars are recognizable among the isolated teeth of the anthill collection. The mesostylid crest in the M_3 of SDSM 6277 and specimens of the anthill collection is, unlike the development in M_{1-2}, absent or incomplete. Metalophulid II extends from the ectolophid near the protoconid to the metaconid. An anterolingual fossettid is therefore not formed in these specimens. In ISU 18594 the mesostylid crest is complete. In *Meniscomys hippodus* the mesostylid crest is complete, as in M_{1-2}.

The region of the posterior fossettid in the M_3 of SDSM 6277, the anthill collection and ISU 18594 is shallower and anteroposteriorly shorter than that of M_{1-2}. This correlates with the size of the talonid, which is restricted in anteroposterior length. The posterolophid and ectolophid join at the hypoconid in an acute, labially prominent *V*, in correlation with a posterolabial flattening of the hypoconid. In *Meniscomys hippodus* the hypoconid is not flattened on its posterior surface, which is strongly convex, and the axis of the posterior fossettid is anteroposteriorly aligned. The hypolophid is frequently weak or absent in the specimens from South Dakota, but is present and moderately strong in *Promylagaulus lemhiensis*.

The labial inflection of M_3 in ISU 18595, SDSM 6277 and the anthill collection is more expansive anteroposteriorly than in M_{1-2}. No posterolabial fossettid is enclosed between hypoconid and mesoconid. A distinct labial spur is present on the mesoconid of ISU 18594 but is reduced or absent in the samples from South Dakota. The labial inflection of M_3 in *Meniscomys hippodus* is little if any larger than that of M_{1-2}, and a posterolabial fossettid is present.

The M_3 of ISU 18594, SDSM 6277 and the anthill collection is distinctly smaller in occlusal dimensions than M_{1-2}. In *Meniscomys hippodus* the size of M_3 more closely approximates that of the anterior molars.

UPPER INCISOR

The upper dentition of the Deep River taxon is unknown but in the Lemhi Valley collection all upper teeth are represented. The anthill collection contains teeth representing P^4, M^1, M^2, M^3, but not P^3 (L. Macdonald 1972:25–26). The dentition in the type of *Promylagaulus riggsi* (FMNH P26256) consists of the upper incisor, P^3, and well worn P^4–M^3.

The upper incisor in the Lemhi Valley collection is gently convex across the anterior face, the medial and lateral margins of which turn posteriad at approximately equal angles. The tooth closely resembles that of *Promylagaulus riggsi*, except that it is larger. The upper incisor in *Meniscomys* is similarly proportioned but appears to be anteroposteriorly relatively shorter in cross section.

UPPER THIRD PREMOLAR

The P^3 of *Promylagaulus riggsi* and the Lemhi collection is more slender and strongly compressed than that of *Meniscomys*. The crown lacks a basal swelling which is characteristic of *Meniscomys*. The long axis of the occlusal outline trends anterolabiad (Fig. 6a), whereas that in *Meniscomys* is aligned anteriorly or anterolingually. There is no distinct anterior or posterior carina on the crown, whereas both structures are present in *Meniscomys*. The tooth is curved from root to apex of crown, with the concave side facing anterolinguad, whereas the axis in *Meniscomys* is straight. The axial curvature in *P. riggsi* and UM 5285 places the apex of the tooth well forward of P^4, so that occlusal contact with P_4 during mastication may have been impossible. The worn surface in *P. riggsi* is polished and rounded, suggesting that only food abrasion, not contact wear, has occurred. In the Lemhi specimens no wear is apparent. A distinct facet, indicating contact wear, is characteristic of the P^3 in *Meniscomys*.

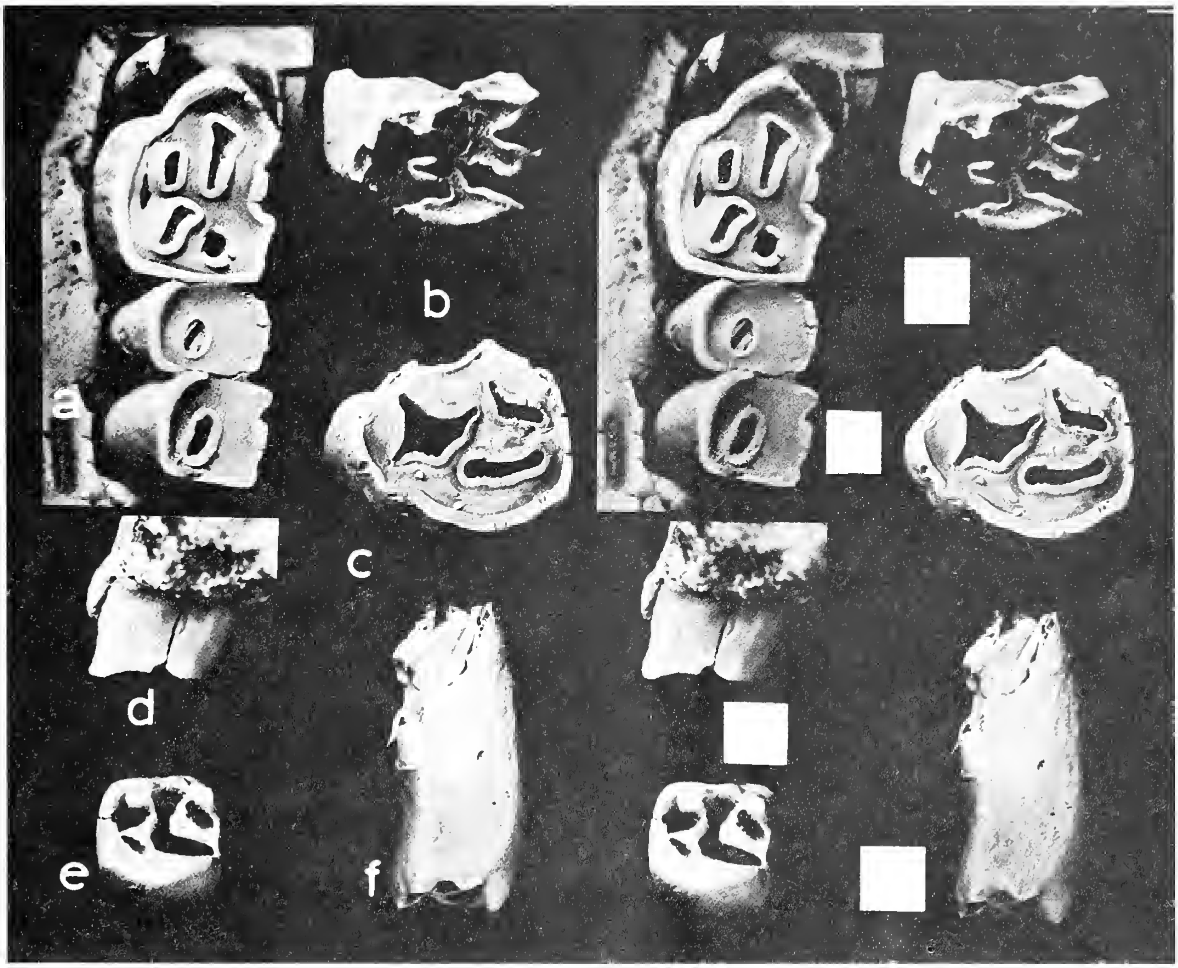

FIGURE 6. *Promylagaulus*, stereo views of upper cheek teeth. *a–P. riggsi*, occlusal view left P^3–M^2, FMNH P26256; *b–P. ovatus*, occlusal view little worn left P^4, LACM 117434, locality LACM 1871; *c–P. ovatus*, occlusal view worn left P^4, LACM 117378, locality LACM 1871; *d–P. riggsi*, posterior view left M^2, FMNH P26256; *e–P. ovatus*, occlusal view left M^1 or M^2, LACM 117428, locality LACM 1871; *f*–same, posterior view. Scale = 1 mm.

UPPER FOURTH PREMOLAR

The P^4 of the Lemhi collection is larger than that of the anthill collection. This tooth is smallest in *Promylagaulus riggsi* (Table 5). The anterocone, the anterolabial cusp characteristic of the P^4 of aplodontoids (Fig. 6a–c), is more lingually expanded in the specimens from the anthill locality and Lemhi Valley than in *Meniscomys*, and extends into the area occupied in the latter by a distinct cusp, the anterostyle. The anterostyle is poorly developed and sometimes absent in specimens of the anthill collection. The parastyle and mesostyle (Fig. 6a–c) are thinner and less prominent labially than in *Meniscomys*, and virtually absent in some individuals. A distinctive feature, shared by *Promylagaulus riggsi* and the specimens of the anthill and Lemhi collections, is a slight lingual displacement of the labial enamel just anterior to the mesostyle. The planes of vertical enamel in front of and posterior to the mesostyle more nearly approximate one another in *Meniscomys*. The worn occlusal outline of the tooth in the anthill and Lemhi collections (Fig. 6c) lacks much of the anterolingual notch between the region of the anterocone and the region of the protocone in *Promylagaulus riggsi* (Fig. 6a), making the tooth appear more oval. In the worn P^4 of *P. riggsi* (Fig. 6a), the plane of wear in the region of the parastyle and anterocone is more steeply inclined posteriad than in the teeth of the Lemhi Valley and anthill collections (Fig. 6c). No appression facet for P^3 is present on P^4 in the specimens of the anthill collection, which suggests that, as in *P. riggsi* and the Lemhi collection, the crown of P^3 does not occlude with P_4 during normal mastication. An appression facet is normally present in *Meniscomys hippodus*.

A conspicuous difference in the occlusal pattern from that in *Meniscomys* is the presence in all specimens of *Promylagaulus* of extreme anteroposterior length in the protocone, and corresponding lingual flatness of the cusp (Fig. 6b). The outline of the worn tooth in *Promylagaulus* is normally elongate anteroposteriorly

TABLE 5

Length and Width of Upper Cheek Teeth (mm)

MUSEUM NUMBER	LOCALITY, TAXON	LP4/	WP4/	LM1/	WM1/	LM2/	WM2/
UM 4038	*P. lemhiensis* (UMV 7303)	4.0	3.3	2.1(H)	2.9	2.4	2.7
UM 5193	Lemhi Valley (UMV 7303)	—	—	2.2(H)	2.9	2.2	2.7
UM 5285	Lemhi Valley (UMV 7303)	4.4	3.7	2.5(H)	3.0	2.7	2.8
ISU 18601	Lemhi Valley (ISU 18601)	—	3.9	2.9(H)	3.3	2.4	2.8
LACM 117376	Anthill (LACM 1871)	3.5	2.6	—	—	—	—
LACM 117377	Anthill (LACM 1871)	3.5	2.4	—	—	—	—
LACM 117378	Anthill (LACM 1871)	3.5	2.8	—	—	—	—
LACM 117380	Anthill (LACM 1871)	3.5	2.8	—	—	—	—
LACM 117418	Anthill (LACM 1871)	—	—	1.9	2.0	—	—
LACM 117422	Anthill (LACM 1871)	—	—	2.0	1.9	—	—
LACM 117425	Anthill (LACM 1871)	—	—	1.8	1.7	—	—
LACM 117374	Anthill (LACM 1871)	—	—	—	—	2.0	2.0
LACM 117419	Anthill (LACM 1871)	—	—	—	—	2.0	1.9
LACM 117424	Anthill (LACM 1871)	—	—	—	—	1.9	1.8
LACM 117417	Anthill (LACM 1871)	—	—	—	—	2.1	2.0
FMNH P26256	*P. riggsi*	3.3	2.6	1.5	2.0	1.7	2.0

LP4/ = Anteroposterior length of P^4, at occlusal surface.
WP4/ = Transverse width of P^4 at level of labial flexure of crown (below basal swelling).
LM1/ = Anteroposterior length of M^1 at occlusal surface (wear: H = heavy).
WM1/ = Transverse width of M^1 at occlusal surface.
LM2/ = Length of M^2 at level of labial flexure of crown.
WM2/ = Transverse width of M^2 at level of labial flexure of crown (below basal swelling).

(Fig. 6a–c), whereas the anteroposterior and transverse dimensions are almost equal in *Meniscomys*. The paracone, protoconule, and metaconule are also quite elongate anteroposteriorly and exhibit flattened labial and lingual surfaces. This trend toward lophodonty is advanced over that known for *Meniscomys*, although a similarly directed trend has commenced in the latter (Rensberger, in manuscript).

The crown of the premolar in the anthill and Lemhi collections and *Promylagaulus riggsi* is curved along the vertical axis, which is lingually convex and labially concave (Fig. 6b). Both labial and lingual surfaces are vertically convex in *Meniscomys*, so that the axis appears rather straight. The anterolingual fossette is altogether absent in one unworn specimen of the anthill collection, frequently disappears in early wear (Fig. 6c), and is absent in known specimens of the Lemhi collection (Nichols 1976). This fossette is present in both *P. riggsi* and *Meniscomys*. The area normally occupied by the anterolingual fossette in most aplodontoids is partially reached in the specimens of *Promylagaulus* lacking it by the anteriorly elongate posterolingual fossette and the lingually expanded anterolabial fossette. The posterolingual fossette is aligned almost anteroposteriorly in the Lemhi and anthill collections (Fig. 6c), whereas it slants anterolabially in *P. riggsi* (Fig. 6a) and *Meniscomys*.

UPPER MOLARS

The upper molars, like the premolar, are largest in the Lemhi collection and smallest in *Promylagaulus riggsi* (Fig. 7). The molars of *P. riggsi*, especially M^{1-2}, are rather rectangular in occlusal outline, and the anteroposterior length is less than the width (Fig. 6a). In the anthill and Lemhi collections the length and width are subequal (Fig. 6e). Poor development or lack of the mesostyle, at least in late wear, and limited lingual convexity contribute to the rectangular shape. In the little worn molars of the anthill collection, the anteroposterior length may be greater than the width, but with wear the width increases to essentially the length. In the stage of wear in which the labial (vertical) flexure of the crown has reached the occlusal surface, the length in the anthill collection is approximately equal to the width, whereas the width exceeds the length at the same stage in the Lemhi collection and *P. riggsi* (Table 5). In all groups including *Meniscomys*, the anteroposterior length of M^1 shortens more rapidly with wear than does that of M^2. The molars in *Meniscomys* bear strong mesostyles and strongly convex lingual mar-

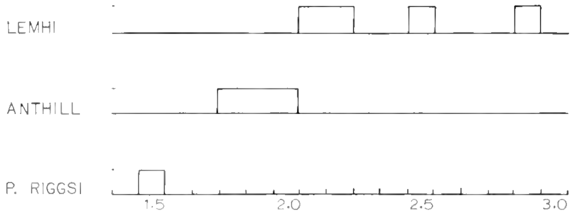

FIGURE 7. Frequency distributions of anteroposterior length of M^1 in specimens of *Promylagaulus* at localities Lemhi Valley (UM V-7303 = ISU 59003) and Anthill (LACM 1871), with value for type of *P. riggsi*. Base measurements for classes are listed.

TABLE 6

Depth[1] of Lingual Enamel on M^1, M^2 (mm)

MUSEUM NUMBER	LOCALITY, TAXON	DE1/	DE2/	DE1/ / WM1/	DE2/ / WM2/
LACM 117417	Anthill (LACM 1871)	—	2.9	—	1.38
LACM 117419	Anthill (LACM 1871)	—	2.3	—	1.15
LACM 117424	Anthill (LACM 1871)	2.2	—	1.16	—
LACM 117428	Anthill (LACM 1871)	—	2.3	—	1.21
ISU 18601	Lemhi (ISU 59003)	2.0+	1.9+	0.61+	0.56+
UM 5285	Lemhi (UMV 7303)	—	2.2	—	0.82
UM 4038	*P. lemhiensis* (UMV 7303)	—	2.4+	—	0.89+
FMNH P26256	*P. riggsi*	—	1.4	—	0.70
UWBM 29232	*Meniscomys hippodus* (UWA 5183–2)	—	0.5	—	0.23

[1]measured from level of apex of posterior enamel-dentine chevron to uppermost margin of lingual enamel.

WM1/ = Transverse width of M^1 near apex of posterior dentinal tract.
DE1/ = Depth of lingual enamel on M^1.
WM2/ = Transverse width of M^2 near apex of posterior dentinal tract.
DE2/ = Depth of lingual enamel on M^2.

gins. The width of M^1 or M^2 in *Meniscomys* is greater than the length in all but the earliest stages of wear. The transverse dimension of the anterior margin of the tooth in the three groups of *Promylagaulus* is only slightly if at all less than that of the posterior margin (Fig. 6e), whereas a very narrow anterior dimension is characteristic of *Meniscomys*. With moderate wear, only the posterolingual fossette remains in *Promylagaulus*, whereas several of the smaller fossettes are present until late stages of wear in *Meniscomys*.

The unworn M^3 in the anthill collection contains anterolabial, anterolingual, posterolabial and posterolingual fossettes, but no central fossette. The posterolabial fossette is usually the largest and deepest, although in several specimens the posterolingual fossette is dominant. A single, probably posterolabial, fossette is present in the well worn M^3 of *Promylagaulus riggsi* and the Lemhi collection. In *Meniscomys* the central fossette is present and moderately persistent, and the posterolabial fossette is the largest and deepest.

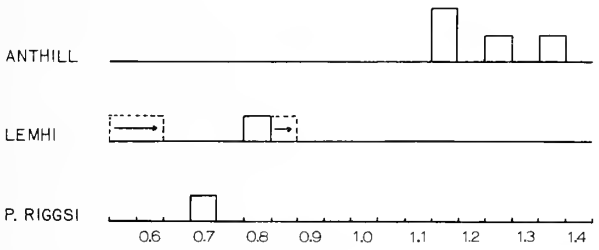

FIGURE 8. Frequency distributions of ratio of depth of lingual enamel above lowermost point of posterior dentinal tract to width of M^1 or M^2 in *Promylagaulus*. Localities as listed for Fig. 7. Base measurements for classes are listed. Arrows indicate incomplete measurements.

As in P^4, the crowns of the molars in *Promylagaulus* are vertically curved with the concave side labial (Fig. 6f). No comparable curvature is apparent in *Meniscomys*. Long dentinal tracts extend down the anterior and posterior sides of the molars in the anthill collection. A tract is visible on the posterior side of the left M^2 in *P. riggsi* (Fig. 6d) but is shallower than the corresponding plate in specimens of the anthill collection (Fig. 6f). The margins of the chevron-shaped enamel edges bordering the dentinal tracts are more steeply inclined in the anthill specimens (Fig. 6f) than in *P. riggsi* (Fig. 6e) and suggest greater hypsodonty. Furthermore, the lingual enamel plate, measured from the apex of the chevron (lowest part of the tract), is considerably longer in the anthill specimens than in *P. riggsi* (Fig. 8 and Table 6). This difference in enamel length is, for example, approximately equivalent to the change in length of the enamel of the upper and lower molars spanning three chronologically successive taxa of early Miocene pocket gophers, *Entoptychus minor, E. cavifrons,* and *E. transitorius* (Rensberger 1971:79–85). The depth of the lingual enamel relative to tooth width on M^2 is apparently intermediate in the Lemhi collection between that of *P. riggsi* and that in the anthill collection (Fig. 8 and Table 6). The roots of the upper molars in the anthill collection are greatly reduced compared to those in the Lemhi collection and *P. riggsi*.

SYSTEMATIC PALEONTOLOGY
Order RODENTIA
Superfamily Aplodontoidea Matthew 1910
Family Mylagaulidae Cope 1881
Promylagaulus McGrew 1941

GENOTYPIC SPECIES: *Promylagaulus riggsi* McGrew 1941.

DEFINITION (REVISED): More hypsodont than *Meniscomys*. P^3 slender, curving anterolinguad, with long axis of cross section slanting anterolabiad, lacking occlusal contact. P^4 with lingually expanded anterocone, parastyle and mesostyle more reduced than in *Mylagaulodon*, ectoloph anterior to mesostyle displaced linguad, protocone expanded anteroposteriorly and relatively flat lingually, posterolabial fossette smaller, less persistent than in other mylagaulids or *Meniscomys*, anterolingual fossette reduced or absent, posterolingual fossette extended craniad, anterolabial fossette expanded linguad.

M^{1-2} rectangular in occlusal outline, at least in earlier stages of wear; with mesostyle reduced or absent, tendency for anteroposterior elongation of lower part of crown, persistence of posterolingual fossette long after others have worn away. P^4–M^2 with vertically elongate, curved (labially concave) crowns, anterior and posterior dentinal tracts.

P_4 with long, strong metastylid crest from metaconid to mesostylid, enclosing lingual fossettid; mesostylid usually indistinct; mesoconid flattened labially in mature stages of wear; poor development of anterior branch of labial inflection, smaller than in other mylagaulids or *Meniscomys*, extensive development of posterior branch; posterolabially compressed, anteriorly expanded hypoconid, narrow entrance to labial inflection.

M_1 with strong central fossettid. M_{1-2} with strong metastylid crest; hypoconid posterolabially compressed, anteriorly expanded; posterolophid posteriorly convex; posterior fossettid trending anterolabiad; metalophulid II extending to apex of metaconid; crest from mesostylid bending craniad to join center of metalophulid II; anterior and lingual fossettids present; mesostylid indistinct, lacking lingual prominence, especially on M_1; tendency to lose rectangular outline and labial inflection in late wear.

M_3 with hypoconid posteriorly flattened; labial inflection relatively larger anteroposteriorly than in M_{1-2}; absolute occlusal dimensions much smaller than those of M_{1-2}; no mesostylid crest; metalophulid II extending from metaconid to protoconid; no posterolabial fossettid.

SPECIES: *P. riggsi* McGrew, L. Mioc. S. Dak.; *P. ovatus* (n. sp.) L. Mioc., S. Dak.; *P. lemhiensis* Nichols, L. Mioc. Idaho; *P. montanensis* (n. sp.) L. Mioc. Montana.

Promylagaulus riggsi McGrew 1941

(Fig. 6a,d)

McGrew, P.O., 1941, Figs. 1, 2c, 3.

TYPE: Skull, lacking anterior extremities of nasals, zygomatic arches and cranium posterior to orbits; with right and left I, P^3–M^2; right M^3; FMNH P26256.

TYPE LOCALITY: Four miles south of Porcupine, South Dakota.

STRATIGRAPHIC POSITION: "Top of lower Rosebud beds" (McGrew 1941:6); "Probably Rosebud Formation" (J.R. Macdonald 1963:179). Monroe Creek Formation or Harrison Formation or Rosebud Formation (L. Macdonald 1972:25).

AGE: Arikareean or Hemingfordian, early or middle Miocene, based on the range of possible stratigraphic positions cited above. Older than late Arikareean, based on comparative stages of advancement of other species.

REFERRED SPECIMEN: SDSM 59158, M_2, from locality SDSM V59.

DIAGNOSIS (REVISED): Smaller than other species. Worn occlusal surface of anterocone on P^4 with pronounced inclination posteriad; anterolingual fossette of P^4 present in known specimen; posterolingual and anterolabial fossettes more restricted than in *P. ovatus, P. lemhiensis;* posterolingual fossette with strong anterolabial slant; worn occlusal outline with distinct notch separating anteriorly prominent anterocone from protocone; with angular posterolingual corner.

Anteroposterior length of M^1 and M^2 becoming less than transverse width well before wear reaches labial flexure of crown; ratio of depth of lingual enamel on M^2 to width of tooth 0.70, less than in other species; sides of posterior dentinal tract of M^{1-2} less vertical than in other species.

Promylagaulus lemhiensis Nichols 1976

Nichols, R., 1976, Figs. 7, 8b; Pl. 1, Figs. 5–10.

TYPE: Fragment of rostrum and palate with root of right I, worn left P^3–M^2, UM 4038.

TYPE LOCALITY: Big Wash (Univ. of Montana locality MV 7303, in part). NW¼NW¼ sec. 17, T. 17 N., R. 25 E., Lemhi quadrangle, Idaho.

STRATIGRAPHIC POSITION: Specimens from middle part of 400 foot section, Peterson Creek beds, an informal unit (Nichols, 1976).

ZONE: Upper *Meniscomys* Concurrent-range Zone (Nichols, 1976:13).

AGE: Arikareean, early Miocene.

REFERRED SPECIMENS: UM 5193, cranial and mandibular fragments with worn M^{1-3}_{2-3}; UM 4039, worn P^4; UM 4055, little worn P^4; UM 5285, partial skull with I, worn P^3–M^3; ISU 18594, mandible with little worn P_4, moderate to little worn M_{1-3}; ISU 18601, associated P^4 (fragment), M^{1-3}, P_4. All from a series of closely related exposures, University of Montana locality MV 7303 (= ISU 59003); ISU 18594 from stratigraphically 21 m above type specimen.

DIAGNOSIS (REVISED): Overall size greater than that of *P. riggsi, P. ovatus*. Occlusal surface of anterocone on P^4 nearly horizontal in mature stages of wear; anterolingual notch, posterolingual corner of tooth less pronounced than in *P. riggsi,* making occlusal shape more oval; posterolingual fossette aligned more nearly anteroposteriorly than in *P. riggsi;* tooth in known specimens lacking distinct protoconule and anterolingual inflection.

Transverse width of M^{1-2} greater than anteroposterior length at level of labial flexure of crown, as in *P. riggsi,* unlike *P. ovatus;* ratio of depth of lingual enamel of M^2 above apex of posterior dentinal tract to width of tooth 0.82–0.89+, greater than in *P. riggsi,* less than in *P. ovatus*. Root branches of M^{1-2} more prominent than in *P. ovatus*.

Posterior and lingual fossettids of P_4 wider relative to tooth width (ratios 0.41, 0.30, resp.) than in *P. montanensis;* central width of tooth greater relative to overall width than in *P. montanensis* (ratio 0.67); length (4.7–5.0 mm) greater than in *P. montanensis, P. ovatus;* ratio of depth of labial enamel to length of tooth (.43–.44) less than in *P. ovatus, P. montanensis*.

Ratio of depth of labial enamel on M_2 to tooth width (0.95) less than in *P. ovatus*. Metastylid crest of M_{1-2} with less posterior prominence than in *P. montanensis;* no posterolingual fossettid, unlike *P. montanensis;* labial inflection relatively more expansive anteroposteriorly than in *P. montanensis;* central posterior convexity less pronounced than in *P. montanensis*. Heavier layer of cementum overlapping enamel of cheek teeth than in *P. ovatus, P. montanensis*.

Promylagaulus ovatus[1] NEW SPECIES

(Figs. 3a–f; 6b,c,e,f)

Macdonald, J.R., 1970, Fig. 14 *(Promylagaulus* cf. *riggsi).*
Macdonald, L., 1972:25–26 *(Promylagaulus riggsi).*

TYPE: Little worn left M_2. LACM 117435.

TYPE LOCALITY: Anthills of LACM 1871 (=SDSM V6229) SW ¼, sec. 9, T. 39N., R. 42 W., east of Porcupine Creek, Sharps Corner quadrangle, South Dakota.

STRATIGRAPHIC POSITION: Upper part of Monroe Creek Formation (Harksen 1970). Fossils, although recovered from anthills, apparently derived from two or three 0.6 cm thick bone bearing layers in nearby vertical cliffs (Harksen, 1970; L. Macdonald 1972:6). Locality may be at transition between Monroe Creek and Harrison formations (James E. Martin, pers. comm.).

ZONE: *Entoptychus-Gregorymys* Concurrent-range Zone (Fisher and Rensberger 1972).

AGE: Arikareean, early Miocene.

REFERRED SPECIMENS: LACM 117351–117370, 117372, 117392, 23530, 23532, 23535, 23536 (P_4); 117373–117375, 117403, 117406, 117410–117416, 117438–117441, 23534 (lower molars); 117384, 117436, 23637 (DP_4); 117376–117383, 117385–117391, 117393–117396, 117434, 23538 (P^4); 117371, 117397–117400, 117404, 117405, 117407, 117417–117433, 23528, 23529, 23531, 23534 (upper molars); from locality LACM 1871.

SDSM 6277, right mandible, DP_4–M_3; from locality V6210.

LACM 9339, right M_1; LACM 9340, right P_4; LACM 9342, right P_4; from locality LACM 2005, northeast of Wolff Ranch, South Dakota.

DIAGNOSIS: Smaller than *P. montanensis* and *P. lemhiensis*, slightly larger than *P. riggsi*. Worn occlusal surface of anterocone on P^4 less inclined posteriad than in *P. riggsi;* anterolingual fossette of P^4 only occasionally absent in unworn premolars, but frequently disappearing with early wear; posterolingual fossette expanded anteriad, with more nearly anteroposterior alignment than in *P. riggsi;* anterolingual notch and posterolingual corner less pronounced than in *P. riggsi*, making occlusal shape oval.

Transverse width of M^1 or M^2 approximately equal to anteroposterior length at level of vertical flexure of labial surface; ratio of depth of lingual enamel to width of tooth 1.15–1.21, greater than in *P. riggsi, P. lemhiensis;* sides of dentinal tracts more nearly vertical than in *P. riggsi;* root branches of less prominence than in *P. lemhiensis*.

Posterior and lingual fossettids of P_4 wider relative to tooth width (ratios 0.32–0.36, 0.27) than in *P. montanensis*, possibly narrower than in *P. lemhiensis;* ratio of depth of labial enamel to length of tooth 0.49–0.54, less than in *P. montanensis*, greater than in *P. lemhiensis*.

Ratio of depth of labial enamel on M_1 or M_2 to tooth width 1.11–1.27, greater than in *P. lemhiensis, P. riggsi;* metastylid crest with less posterior prominence than in *P. montanensis;* no posterolingual fossettid, unlike *P. montanensis;* labial inflection relatively more expansive anteroposteriorly, shallower transversely than in *P. montanensis;* labial part of posterolophid less extensive anteriorly than in *P. montanensis;* deep portion of posterolophid more protuberant posterolabially (less posteriorly) than in *P. montanensis*.

DISCUSSION: An isolated cheek tooth from the anthill locality was selected as the type of this species in lieu of the mandible from SDSM V6210, because of the much larger sample of *Promylagaulus* as well as other mammalian taxa at the anthill site. Furthermore, the cheek teeth are poorly exposed in the young mandible, leaving doubt as to the stage of advancement in hypsodonty.

It seems likely from this evidence that *P. riggsi*, for which the stratigraphic occurrence is uncertain, did not occur in a deposit which was contemporaneous with those of the anthill locality and other sites which have yielded *P. ovatus*. The preservation of the specimens also suggests this conclusion. The specimens of *Promylagaulus* from the anthill locality, that from SDSM V6210, and those from the Wolff Ranch locality (LACM 2005), all of which are referable to *P. ovatus*, are of medium to dark or blackish brown color, whereas the teeth of *P. riggsi* are very light in color.

Placement of the occurrences of *Promylagaulus ovatus* in the *Entoptychus-Gregorymys* Concurrent-range Zone is based upon the abundant association of *Gregorymys formosus* (L. Macdonald 1972:30) and the advanced morphology of *Promylagaulus* compared with that of *Meniscomys*. *Meniscomys* occurs only stratigraphically beneath the *Entoptychus-Gregorymys* Concurrent-range Zone in the John Day Formation (Fisher and Rensberger 1972).

Promylagaulus montanensis NEW SPECIES

(Fig. 2)

TYPE: Right mandible with DP_4, M_{1-2}, incisor fragment; missing upper part of ascending ramus. UWBM 38103.

TYPE LOCALITY: Spring Creek 1 (UWA 5867–1). SE-NW trending draw 46°37.4′ N, 111°3.6′ W; SE¼ sec. 14, R. 5 E., T. 10 N., Hanson Reservoir quadrangle, Montana.

STRATIGRAPHIC POSITION: Deep River Formation. Specimens from stratigraphically lower of two units. Brownish tan, massive sandstone.

ZONE: *Entoptychus-Gregorymys* Concurrent-range Zone.

AGE: Arikareean, early Miocene.

REFERRED SPECIMEN: Right mandible with worn P_4–M_3; lacking incisor, ventral margin, condylar process and ascending ramus; geographic locality and stratigraphic position exactly that of type specimen. UWBM 38075.

DIAGNOSIS: Larger than *P. ovatus* and *P. riggsi*. Anteroposterior length of P_4 4.1 mm, less than in *P. lemhiensis;* ratios of width of posterior and lingual fossettids to tooth width less than in *P. lemhiensis, P. ovatus;* ratio of depth of labial enamel to length of tooth 0.68, greater than in *P. ovatus, P. lemhiensis;* ratio of central width to overall width of tooth 0.55, smaller than in *P. ovatus, P. lemhiensis*.

Metastylid crest of M_{1-2} with greater posterior prominence than in *P. ovatus, P. lemhiensis;* small posterolingual fossettid on M_2, incipient posterolingual fossettid on M_1, unlike *P. ovatus, P. lemhiensis;* labial inflection anteroposteriorly more compressed, transversely relatively deeper than in *P. ovatus, P. lemhiensis;* central posterior convexity of posterolophid more pronounced than in *P. ovatus, P. lemhiensis*.

DISCUSSION: The placement of this form in the *Entoptychus-Gregorymys* Concurrent-range Zone is based upon an associated assemblage of taxa, including *Gregorymys*, to be described later.

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[1] *ovatus:* L., egg shaped, in reference to the occlusal outline of P^4.

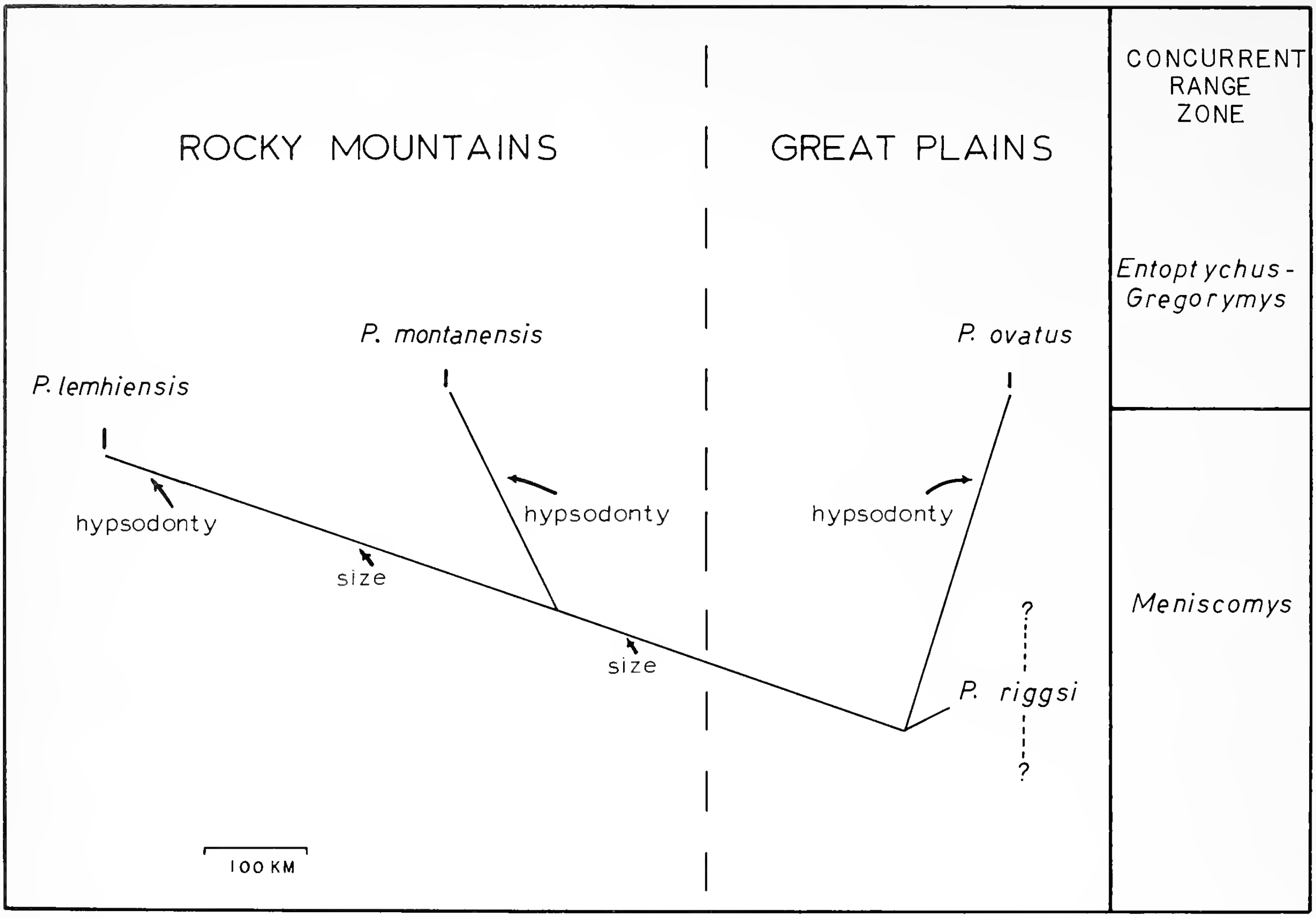

FIGURE 9. A possible phylogeny for the described species of *Promylagaulus* which would explain the morphological and geographical differences. Arrows designate chronologic intervals during which increases in size and hypsodonty presumably occurred. The stratigraphic position of *P. riggsi* is uncertain.

Promylagaulus sp.

McKenna and Love 1972, Figs. 15, 16.

LOCALITY: Darton's Bluff (AMNH) Big Horn Mountains, SW¼NE¼, sec. 19, T. 48 N., R. 85 W., Hazelton Peak quadrangle, Johnson County, Wyoming. Exposure along bluff near head of Canyon Creek.

STRATIGRAPHIC POSITION: In 22 m thick, light tan, grading upward to light gray, massive, fine-grained sandstone within 43 m Miocene section.

ZONE: *Entoptychus-Gregorymys* Concurrent-range Zone.

AGE: Later Arikareean, early Miocene.

MATERIAL: Right mandible, P_4–M_2, I; left mandible P_4–M_3, fragmentary incisor. Posterior parts of both rami missing. AMNH 56333.

DISCUSSION: Judging from the illustrations of this specimen, it may be distinct from *Promylagaulus ovatus*, *P. montanensis*, *P. riggsi*, and *P. lemhiensis*. Lingual enamel is present on the occlusal surface at a stage of wear in which the occlusal outline is oval, unlike the condition in *P. ovatus*. In late stages of wear in *P. ovatus*, the originally rectangular outline remains until the lingual enamel disappears. The Wyoming specimen more closely resembles *P. montanensis* and *P. lemhiensis* in this character. However, the size is smaller than that of *P. montanensis*, *P. lemhiensis*, or *P. riggsi* and the dentinal tracts seem to be less extensive than in *P. montanensis*, judging from the greater continuity of enamel surrounding the heavily worn molars. It appears to be more hypsodont than *P. riggsi*.

That this occurrence seems to be within the *Entoptychus-Gregorymys* Concurrent-range Zone is based upon the presence of *Entoptychus* as well as the association with what may be *Pleurolicus* (McKenna and Love 1972:17–21). Although these geomyoids are not contemporaneous in the John Day Formation, the range of *Entoptychus* commences immediately above the range of *Pleurolicus* (Fisher and Rensberger 1972:24).

PHYLETIC RELATIONSHIPS OF THE SPECIES

The greater size of the species of *Promylagaulus* from the Rocky Mountains and the fact that the most primitive form, *P. riggsi*, is the smallest suggests that the group may have originated in the Great Plains. *P. ovatus*, the youngest known form in the Plains, was only slightly larger than *P. riggsi* but conspicuously advanced in hypsodonty. The species occurring farthest west, *P. lemhiensis*, is the largest but is only slightly more hypsodont than *P. riggsi*. These relationships suggest (Fig. 9) that an early divergence from the primitive stock may have dispersed westward and radiated again in the Rocky Mountain region. The amount of time involved in this dispersal, diversification and evolution was apparently not very great, judging from the occurrences of both *P. montanensis* and *P. ovatus* in the *Entoptychus-Gregorymys* Concurrent-range Zone, probably low in that zone, and *P. lemhiensis* in deposits not much older.

RELATIONSHIPS OF *PROMYLAGAULUS*

McGrew (1941:26), followed by subsequent workers, placed *Promylagaulus* in the Mylagaulidae. He believed, although with a degree of uncertainty regarding several characters, that *Promylagaulus* gave rise to *Mylagaulodon* and therefore to later mylagaulids. As McGrew noted, the upper premolar of *P. riggsi* displays the same general features as FMNH P26266 and is intermediate in degree of hypsodonty between the latter and *Meniscomys hippodus*. Wilson (1960:54) noted an apparent difference in the number of lakes in the molar talonid of *Promylagaulus* and *Mesogaulus*, but was uncertain as to whether wear in the specimen of *Promylagaulus* accounted for the discrepancy. Other characters in the worn dentition of *P. riggsi* raise at least some doubt about a relationship to the mylagaulids. The better represented taxa, *P. ovatus* and *P. lemhiensis*, unknown at the time of those earlier studies, exhibit features which differ more clearly from those of the mylagaulids.

The mesostyle in P^4, an early character in aplodontids and which in *P. riggsi* can be interpreted as almost worn away, is much smaller in *Promylagaulus* than in *Mylagaulodon* (FMNH P26266). The posterolabial fossette of P^4 is small and is worn away well before the other two major fossettes disappear in *P. ovatus*, whereas in the mylagaulids this structure is as persistent as the other fossettes, and in *Mylagaulodon* is large. The labial inflection of P_4 is undivided in *P. ovatus* and *P. lemhiensis* but is divided in both *Meniscomys* and the mylagaulids (for the latter see Black and Wood 1956, Fig. 1). The posterolabial fossettid of the lower molars, the one queried by Wilson, is absent or vestigial in the molars of *Promylagaulus*, relatively larger in *Meniscomys*, and still larger in *Mesogaulus* (Wilson 1960, Fig. 59) and *Mylagaulus* (McGrew 1941, Fig. 12). However, the posterolabial inflection above the fossettid is formed differently in *Mesogaulus* than in either *Meniscomys* or *Promylagaulus*, for in occlusal view (Black and Wood 1956, Figs. 8B,E) the channel is elongate, extends strongly posterolinguad, and the anterolabial margin of the hypoconid doesn't hook toward the mesoconid but joins the base of the protoconid to close the fossettid. In both *Meniscomys* and *Promylagaulus* the posterolabial fossettid is small and oval, and is formed by union of the anterolabial process of the hypoconid with the mesoconid.

One of the distinctive characters of *Promylagaulus* is the posterolabial flattening of the hypoconid in P_4–M_3. The hypoconid is usually rather protuberant posterolabially in *Mesogaulus* (Wilson 1960, Figs. 56–59; Black and Wood 1956, Figs. 6, 8), but in the unworn pattern of the molars may extend anterolabiad somewhat as in *Promylagaulus*.

On the other hand, *Promylagaulus* shares with the later mylagaulids reduction of the labial prominence of the stylar cusps in the upper cheek teeth and the tendency for the occlusal outlines to become oval. It also shares relatively large P^4_4 and, unlike the aplodontines, persistent fossettids. Although the reduction of stylar structures may have occurred independently, these events may have emerged from an early common adaptive trend and affinity.

The morphology of the mylagaulids and *Promylagaulus* seems therefore to suggest that the mylagaulids may possibly have evolved from a lineage leading eventually to *Promylagaulus*, as opposed to others going toward other aplodontoids, but if so, the ancestral form for *Promylagaulus* and the mylagaulids was so primitive that the posterolabial inflection of the lower molars was still unclosed — a stage more primitive than that of any aplodontid presently known from the *Meniscomys* Concurrent-range Zone.

Promylagaulus may represent a progressive group that was part of a rather profuse radiation of aplodontoid rodents in the early Miocene just prior to and during the *Meniscomys* Concurrent-range Zone, of which only a few groups, not *Promylagaulus*, survived into the middle Miocene.

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