PROCEEDINGS

OF THE

California Academy of Sciences

Volume 43

SAN FRANCISCO
PUBLISHED BY THE ACADEMY
1982–1984

(US ISSN 0068-547X)

The California Academy of Sciences
Golden Gate Park
San Francisco, California 94118

PRINTED IN THE UNITED STATES OF AMERICA
BY ALLEN PRESS, INC., LAWRENCE, KANSAS

INDEX TO VOLUME 43

(Compiled by Lillian J. Dempster)

New names in **boldface** type

PROCEEDINGS, OCCASIONAL PAPERS, AND MEMOIRS
of the
CALIFORNIA ACADEMY OF SCIENCES

INSTRUCTIONS TO AUTHORS

PUBLICATIONS

The California Academy of Sciences publishes at irregular intervals three series containing results of original scientific research. PROCEEDINGS comprise shorter papers (preferably no fewer than eight printed pages); OCCASIONAL PAPERS are catalogs, faunal lists, bibliographies, etc.; monographs, symposium proceedings, floras, etc. fall within the scope of MEMOIRS.

CONTENT

Subject matter generally coincides with the disciplines represented at the California Academy of Sciences (anthropology, botany, entomology, geology, herpetology, ichthyology, invertebrate zoology, ornithology, mammalogy, and paleontology), and the research foci of the institution—taxonomy, systematics, biogeography, and natural history.

COSTS

A charge of $40 per printed page is levied for PROCEEDINGS and OCCASIONAL PAPERS; $45 for MEMOIRS. For those without institutional affiliation, some funds may be available to defray these charges. Fifty separates are furnished free to the primary author. Additional separates may be purchased; an order form is supplied with page proofs.

PROCEDURES

A manuscript for consideration should be submitted in triplicate (including all illustrations) to: Editor, Scientific Publications, California Academy of Sciences, Golden Gate Park, San Francisco, California 94118. The editor may return a manuscript without review if it is not concise or fails to conform to the guidelines. Suitable manuscripts will be reviewed by members of the scientific publications committee of the Academy as well as by at least two outside experts.

PROOFS

First page proofs and the edited manuscript will be sent to the primary author; both must be returned within seven days of receipt unless arrangements for an extension have been made. Authors will be charged for changes other than corrections of printer's errors.

STYLE

Authors should follow the current edition of the CBE STYLE MANUAL (American Institute of Biological Sciences, 3900 Wisconsin Avenue NW, Washington, D.C. 20016) for general style and common abbreviations. Titles of periodicals should conform to the BIOSIS LIST OF SERIALS WITH CODEN, TITLE ABBREVIATIONS, NEW, CHANGED AND CEASED TITLES (Biosciences Information Service of Biological Abstracts, 2100 Arch Street, Philadelphia, Pennsylvania 19103). Geographical terms should be rendered as in WEBSTER'S NEW GEOGRAPHICAL DICTIONARY. Nomenclatural matters must conform to the most recent version of the relevant code (e.g., International Code of Botanical/Zoological Nomenclature, North American Stratigraphic Code). Scientific names and their spellings shall follow the standard work for a particular group except as otherwise defended. Generic names should be abbreviated so as to avoid confusion with other genera, and never at the beginning of a sentence. Equivalent common names should be provided whenever possible. Type-specimens for newly proposed taxa must be cited by their catalog numbers in an appropriate, specified scientific institution. A differential diagnosis is to be included with any newly proposed taxon.

FORMAT

The manuscript must be double-spaced, with margins of at least 3 cm. Avoid use of dot-matrix printers, hyphenation, and right justification. All pages shall be numbered consecutively in the upper right corner, where the surname of each author also appears. Each section begins at the top of a page.

Material not original to the author must be credited to its source; copyrighted material must be accompanied by a written statement of permission to reproduce it.

Measurements are in international units (SI) unless the use of others is defended.

Underlining should be used only for scientific names of generic and specific level, and for the word *in* when citing articles/chapters of books.

The **Title Page** contains the title of the paper, a suggested running head, and the name and institutional affiliation of the author(s), each on a separate line. The title should be brief, informative, and include Latin and common name(s) of the group(s) studied.

MEMOIRS and lengthy OCCASIONAL PAPERS may require a Table of Contents, List of Figures, and List of Tables immediately following the Title Page, and an Index at the end, all to be prepared by the author(s).

An **Abstract** no longer than three percent the total length of the paper concisely summarizes the new knowledge and main conclusions, and presents all scientific names introduced in the paper. A **Summary** in the language of the region dealt with in the paper, if not English, may be desirable. Otherwise the abstract suffices.

Each major section of text should begin on a separate page. Literature is cited by name and year in the text, as follows (note that commas are omitted in author-date citations): Jones (1970); Jones (1970:25); (Jones 1970); (Jones 1970:25); (Jones 1970; Smith 1980).

Appendices are designated with upper case letters (e.g., Appendix B).

Tabular and illustrative material, each item on a separate sheet, should be numbered with Arabic numerals in the order of first mention in the text. Numbered, self-explanatory legends/captions are to be submitted on a separate sheet; each table should also be titled. Desired placement in the text is to be indicated by lightly pencilled marginal notations.

Minimize the use and size of **Tables**. Each should be designed to decrease quantity of text, to avoid vertical lines and fold-outs, and to have clear, concise column/row headings.

Any and all line drawings, photographs, maps, graphs, charts, etc. are referred to as **Figures**. Preferably submitted as glossy, high-contrast photos, each mounted on stiff paper or light poster-board, figures should be mailed flat rather than folded or rolled. Each part of a composite figure (e.g., several charts with a single legend) receives a lowercase letter designation. Figures must be sufficiently clear and in proper proportions for reduction to bed width. For OCCASIONAL PAPERS and PROCEEDINGS this proportion is 14 cm for double column (page) width and 6.5 cm for single column; maximum height is 20 cm, less allowance for legends. (MEMOIR sizes may vary.) Lettering should be at least 1.5 mm high when reduced to publication size, yet should not overpower the figure. Some indication of scale is mandatory. Guidance may be obtained from STEPS TOWARD BETTER SCIENTIFIC ILLUSTRATIONS (Allen Press, Inc., Lawrence, Kansas 66044). Figure number, orientation, and approximate reduction desired, and surname of each author must be lightly pencilled on the reverse upper right corner of each item.

The following format should be followed for the **Literature Cited** section. Please take note of the spacing, capitalization, punctuation, and order of the elements.

Articles in a journal:

Smith, A. T. 1952. The ants: nature's own army. Ant Biol. 25:34–58.

———. 1971. Leaf-cutter ants of Oregon. Amer. Bull. Entomol. 43:1–8.

Smith, A. T., and L. O. Lee. 1969. Social organization of hymenopterans. Ecology 114:32–49.

Edited books:

White, L. M. Q., and J. T. Brown, eds. 1974. The biota of Gondwanaland. Harper and Row, Chicago, Illinois. 640 pp.

Articles/chapters in edited books:

Johnson, L. B., D. F. Black, and R. M. Hobbs. 1956. The acacias. Pp. 1093–1235 *in* Australian flora, I. Q. Doyle and M. Henry, eds. Kangaroo Press, Sydney, New South Wales, Australia.

Dissertation or thesis:

Green, J. P. 1960. Osmoregulation in sipunculids. Ph.D. Dissertation, University of Wyoming, Laramie, Wyoming. 122 pp.

For further guidance, consult the Editor, Scientific Publications, California Academy of Sciences.

CONTENTS OF VOLUME 43

PROCEEDINGS
OF THE
CALIFORNIA ACADEMY OF SCIENCES

Vol. 43, No. 1, pp. 1–16, 10 figs. June 15, 1982

THE SOUTHEAST ASIAN FRESHWATER PUFFERFISH GENUS *CHONERHINOS* (TETRAODONTIDAE), WITH DESCRIPTIONS OF NEW SPECIES

By
Tyson R. Roberts
California Academy of Sciences, Golden Gate Park, San Francisco, California 94118

ABSTRACT: The tetraodontid pufferfish genus *Chonerhinos*, restricted to fresh water in Southeast Asia, comprises five species, four of which are described as new. The species differ in adult size, coloration, orientation of squamation, depth of caudal peduncle, size of nasal organ, food habits, and geographical distribution. The most widely distributed, *C. nefastus* n.sp., occurs in southern, western, and northern Borneo, the Malay Peninsula, Thailand, Vietnam, Kampuchea, and Laos; it feeds mainly on fish fin rays and scales, and has a slender caudal peduncle and the smallest nasal organ. *Chonerhinos modestus* (Bleeker, 1850), in western Borneo and Sumatra, with perhaps the most varied diet, is the largest species and has the deepest caudal peduncle. The distinctively colored *C. amabilis* n.sp., with the largest nasal organ, occurs in western Borneo and Sumatra and feeds almost exclusively on large aquatic insects. The two new species *C. silus*, with a moderately deep caudal peduncle, and *C. remotus*, with a slender caudal peduncle, have varied diets including insects, and are known only from northern and northeastern Borneo.

INTRODUCTION

The freshwater pufferfish genus *Chonerhinos* currently includes a single species, *C. modestus* (Bleeker, 1850), reported from localities throughout much of Southeast Asia. The nominal species *C. africanus* Boulenger, 1909, known only from the holotype supposedly collected in the interior of the Congo basin, has been identified as a junior synonym of *C. modestus* with incorrect locality data (Roberts 1981; herein). The species formerly known as *C. naritus* (Richardson, 1848), from marine, brackish, and perhaps freshwater habitats along the coasts of the South China Sea and eastern Indian Ocean, has been placed in a monotypic genus, *Xenopterus* (Fraser-Bruner 1943; Tyler 1980; herein).

I undertook this revision because three species of *Chonerhinos* were obtained during my ichthyological survey of the Kapuas basin in western Borneo (Kalimantan Barat, Indonesia) in 1976.

MATERIAL EXAMINED AND METHODS

More than 250 specimens of *Chonerhinos* from throughout the range of the genus were examined during this study. These are deposited in the British Museum (Natural History), London, BMNH; California Academy of Sciences, San Francisco (CAS), including material formerly deposited at Stanford University, Stanford (SU); Field Museum of Natural History, Chicago (FMNH); Muséum Genève, Geneva (MG); Muséum National d'Histoire Naturelle, Paris (MNHN); Museum Zoologicum Bogorense, Bogor, Indonesia (MZB); Musée Royal de l'Afrique Centrale, Tervuren (MRAC); Natural History Museum, Basel (NHMB); Rijksmuseum van Natuurlijke Historie, Leiden (RMNH); University of Michigan Museum of Zoology, Ann Arbor (UMMZ); U.S. National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM); and Zoological Museum, Universiteit van Amsterdam, Amsterdam (ZMA).

Length of specimens is given as standard length unless total length is expressly indicated, and all proportional measurements are given as times in standard length (SL). Vertebral counts were made from radiographs prepared in the Department of Ichthyology, CAS. Sections of skin anterior and ventral to the pectoral fin were removed with a scalpel and stained in alizarin to facilitate illustration of the scales. Orientation of the scales is also obvious in radiographs and can be observed in whole specimens without special preparation.

Chonerhinos Bleeker

Chonerhinos Bleeker, 1854:259–260 (type-species *Tetraodon modestus* Bleeker, 1850, by subsequent designation of Fraser-Bruner 1943:16).
Chonerhinus Bleeker, 1865:213 (unjustified spelling change).

Designation of Type-species.—Fraser-Bruner (1943) is apparently the first author to have properly designated a type-species for *Chonerhinos*. The original description of the genus is as follows: "*Chonerhinos* Blkr [is gekenmerkt] door trechtervormige verdieping ter plaatse der neusopeningen met verhevene randen, lange rug- en aarsvinnen, zigtbare zijlijn en onegekielden rug . . . van *Chonerhinos* 2 t. w. *Chonerhinos modestus* Blkr = *Tetraödon modestus* Blkr olim (van Borneo, Sumatra), *Chonerhinos naritus* Blkr = *Tetraödon naritus* Richds (van Borneo)." Thus, Bleeker included two species in his original account of *Chonerhinos* and did not indicate a type-species. Hollard (1857) defined *Xenopterus* (type-species *X. bellengeri* = *X. naritus*, by monotypy) in such a way that it excludes *Chonerhinos*, which, however, he did not mention by name. Gill (1892) discussed the nomenclatural history of *Chonerhinos* (and *Xenopterus*) at length but oddly did not mention the lack of a type-species. Jordan (1919:256) incorrectly stated that *Tetraodon modestus* Bleeker is the "orthotype" of *Chonerhinos*, meaning that Bleeker (1854) indicated or distinctly implied that this species is the type-species.

Diagnosis.—*Chonerhinos* and its close relative *Xenopterus* differ from all other tetraodontids in having three lateral line canals on side of body instead of one, two, or none; dorsal fin with 22 or more rays; anal fin with 18 or more rays; at least 24 vertebrae; and prefrontal bones absent (Tyler, 1980). *Chonerhinos* differs from *Xenopterus* in its smaller adult size, less extensive squamation, less exposed olfactory lamellae, and fewer fin rays and vertebrae. The largest *Chonerhinos* I have examined is 106 mm; *Xenopterus* attains at least twice this size. In *Chonerhinos* the scales are relatively small and restricted to the head and body ventral to the level of the pectoral fin; in *Xenopterus* the scales are relatively large and extend dorsally to the pectoral fin. In *Chonerhinos* the olfactory lamellae are largely covered by nasal flaps in broad contact; in *Xenopterus* the nasal flaps are greatly reduced and the olfactory lamellae are consequently almost entirely exposed. *Chonerhinos* has 22–28 dorsal-fin rays, 18–22 anal-fin rays, 13–17 pectoral-fin rays, and 24–28 vertebrae; the same counts in *Xenopterus* are 32–38, 28–29, 18–19, and 29–30.

Remarks.—Tyler (1980) stated that *Chonerhinos* and *Xenopterus* are highly specialized tetraodontids which have secondarily increased the number of dorsal- and anal-fin rays and vertebrae, elaborated the lateral line system, increased the number and size of the olfactory lamellae, and increased the size of at least some of the scales; and that the greater numbers of vertebrae and fin rays in *Xenopterus* as well as the structure of the skull indicates that it is the more specialized of the two. In *Chonerhinos*, according to Tyler, apart from the absence of the prefrontal bones, the skull is not markedly different from that in many species of the tetraodontid genera *Monotreta*, *Chelonodon*, and *Tetraodon*, whereas in *Xenopterus* the frontals are much more laterally expanded and thickened than in *Chonerhinos*, forming a large plate over most of the dorsal surface of the skull, and the supraoccipital crest is wider and heavier; in large specimens the two frontals may become indistinguishably fused to each other in the middle of their lengths (Tyler 1980:340, fig. 274). I have examined two *X. naritus* from Sarawak, BMNH 1894.1.19.86–87, 71.2 and 108 mm. Radiographs reveal that the frontal bones, supraoccipital crest, supraneural bone, anteriormost

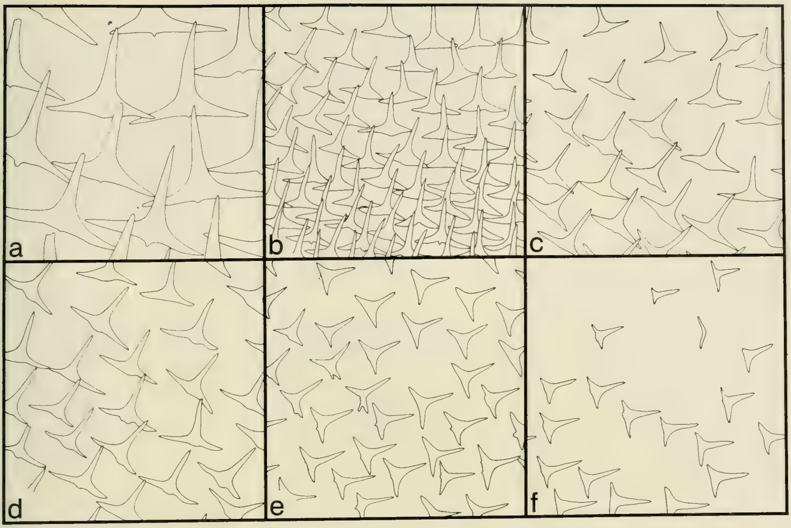


FIGURE 1. Scales on side of body immediately anterior and ventral to pectoral fin (each square = 5 × 5 mm): (*a*) *Xenopterus naritus*, 71.2 mm, BMNH 1894.1.19.86; (*b*) *Chonerhinos modestus*, 48.4 mm, USNM uncatalogued; (*c*) *Chonerhinos silus*, 48.5 mm, FMNH 68815; (*d*) *Chonerhinos remotus*, 49.9 mm, FMNH 68475; (*e*) *Chonerhinos nefastus*, 48.3 mm, CAS 49507; (*f*) *Chonerhinos amabilis*, 48.7 mm, MZB 3973.

anal-fin pterygiophore, and posteriormost neural and haemal spines are enormously thickened or hypertrophied, far out of proportion to neighboring bony elements. They appear to be hyperosteotic (and in the case of the frontal bones, partially synosteotic), and therefore, I am dubious about their phylogenetic significance and their being used as characters to distinguish *Xenopterus* from *Chonerhinos*. Other differences between the two genera, cited above and in Tyler (1980), are sufficient to merit their separation.

Chonerhinos is known only from fresh water. *Xenopterus*, so far as I have been able to determine, is marine or estuarine. There do not seem to be any museum specimens of *Xenopterus* with locality data from fresh water, and statements in the literature that *Xenopterus* occurs in fresh water (e.g., Cantor 1850:384; Weber and de Beaufort 1962:373) appear to be based at least partly on misinformation or confusion with *Chonerhinos*.

In *Chonerhinos* and *Xenopterus*, as in many other tetraodontids, each scale has a spinelike distal portion which projects more or less straight out from the skin when erected, as usually occurs when the fish inflates itself. When the scales are not erect, they are partially or wholly retracted beneath the skin, and the spines may be oriented dorsally, dorsoposteriorly, or posteriorly, depending upon the species (Fig. 1).

Size and shape of the jaw-teeth appear to be nearly identical in all species of *Chonerhinos*. One or two specimens of each species were dissected to permit observation of the gill rakers; all of the species have about 8–10 total gill rakers on each gill arch (sometimes fewer on the first arch). I have not attempted to distinguish the species by differences in the pathways of the lateral line canals. These are difficult to observe in many specimens, and they seem to be highly variable among individual specimens, often being irregularly interrupted or running into each other (Tyler 1980:fig. 223) and frequently differing in their courses on opposite sides of a specimen. Neither have I attempted to distinguish the species by counts of olfactory lamel-

TABLE 1. PROPORTIONAL MEASUREMENTS IN *Chonerhinos* (expressed as times in standard length).

	C. amabilis	*C. modestus*	*C. nefastus*	*C. remotus*	*C. silus*
n	20	13	54	31	33
SL mm	35.6–70.4	46.8–106	19.0–70.7	32.8–61.4	32.7–81.8
Eye	7.8–11.2	9.4–14.1	7.2–11.7	8.6–12.0	8.8–12.9
Nasal organ length	10.1–17.9	14.7–25.3	17.3–27.4	12.5–20.1	11.2–20.0
Snout length	6.0–7.2	6.4–7.5	5.8–7.1	6.6–8.7	6.3–8.1
Interorbital width	5.1–6.1	4.6–6.8	4.5–7.0	5.2–7.0	4.9–6.6
Pectoral-fin base length	10.5–12.2	9.5–11.5	9.9–13.5	8.9–11.1	9.1–12.4
Caudal peduncle depth	7.3–8.3	6.7–7.4	7.8–9.9	7.6–9.9	7.2–8.2
Caudal peduncle length	5.0–6.5	5.2–6.4	4.4–5.9	4.6–6.3	4.6–6.5

lae, the number of which seems to be highly variable within each species, as is the size of the nasal organ itself (Table 1).

PROPORTIONAL MEASUREMENTS; MERISTIC FEATURES

Proportional measurements, in most instances broadly overlapping and of little help in distinguishing species, are presented in Table 1. Frequencies of counts of fin rays and vertebrae, diagnostic for the genus but differing slightly among species and of little or no help in identifying individual specimens, are presented in Tables 2–3. Except in a few instances when counts or measurements are particularly useful for definition of species, these data are not repeated in the text.

KEY TO SPECIES OF *Chonerhinos*

1a. Scales on side of body anterior and ventral to pectoral fin with spines directed posteriorly (Fig. 1*e–f*) 2

1b. Scales on side of body anterior and ventral to pectoral fin with spines directed dorsally or dorsoposteriorly (Fig. 1*b–d*) 3

2a. A roundish dark spot in middle of caudal peduncle; dorsal and anal fins always with angulated margins; upper lip not projecting beyond lower lip; exposed portion of eye round; nasal organ relatively large, its length 10.1–17.9 (times in SL) .... *C. amabilis*

2b. No spot on caudal peduncle; dorsal and anal fins usually with rounded margins; upper lip usually projecting beyond lower lip; exposed portion of eye usually horizontally oval, especially in larger specimens; nasal organ relatively small, its length 17.3–27.4 .... *C. nefastus*

3a. Depth of caudal peduncle 6.7–7.4; upper and lower lips about equally projecting or lower lip slightly protruding; snout gently sloping; scales on side of body anterior and ventral to pectoral fin, very close-set with spines directed dorsally (Fig. 1*b*); anal-fin rays 20–22, modally 22 (Table 2); adult size to 106 mm .... *C. modestus*

3b. Depth of caudal peduncle 7.2–9.9; lower lip usually projecting beyond upper lip; snout strongly sloping; scales on side of

TABLE 2. FREQUENCIES OF FIN RAY COUNTS IN *Chonerhinos*.

	Dorsal fin							Anal fin					Pectoral fin				
	22	23	24	25	26	27	28	18	19	20	21	22	13	14	15	16	17
C. amabilis	–	–	1	12	6	1	–	–	–	14	6	–	–	3	16	1	–
C. modestus	–	–	–	4	12	8	1	–	–	1	7	17	–	1	9	14	1
C. nefastus	–	3	23	16	8	4	–	–	1	19	31	3	5	28	20	1	–
C. remotus	5	30	40	8	2	–	–	6	41	37	3	–	–	9	52	26	–
C. silus	–	1	8	18	27	3	1	1	2	19	34	3	–	2	36	15	1

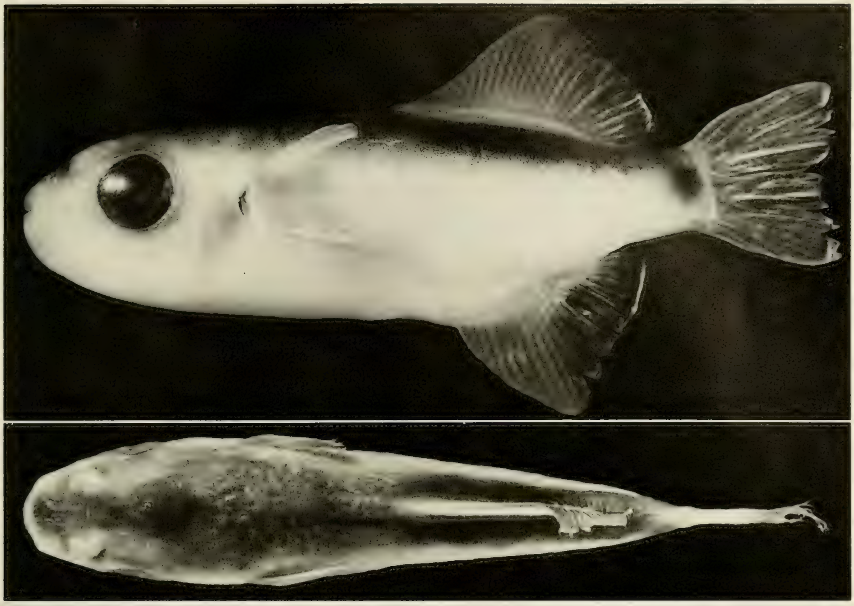


FIGURE 2. *Chonerhinos amabilis,* 45.2 mm, MZB 3972 (holotype).

body anterior and ventral to pectoral fin not as close-set and with spines directed dorsoposteriorly (Fig. 1*c–d*); anal-fin rays 18–22, rarely 22, modally 19 or 20 (Table 2); adult size to 82 mm 4

4a. Caudal peduncle moderately deep, its depth 7.2–8.2; dorsal-fin rays 23–28, average 25.4 .... *C. silus*

4b. Caudal peduncle slender, its depth 7.6–9.9; dorsal-fin rays 22–26, average 23.6 .... *C. remotus*

Chonerhinos amabilis new species

(Figure 2)

Chonerhinus naritus WEBER AND DE BEAUFORT, 1962:374 (specimens reported from "Labang hara, soengei Serawai").

Chonerhinus modestus WEBER AND DE BEAUFORT, 1962:fig. 84.

HOLOTYPE.—MZB 3972, 45.2 mm, Kapuas R. 6 km w of Putussibau, Kapuas Ichthyological Survey, 9 Aug. 1976.

PARATYPES.—CAS 49504, 45.0 mm, same data as holotype; MZB 3973, 48.7 mm, Kapuas basin, Sungai Landok at Ngabang, 83 km ENE of Pontianak, Kapuas Ichthyological Survey, 15 July 1976; MZB 3974, 41.8 mm, Kapuas basin, Sungai Pinoh 20–60 km upstream from Nangapinoh, Kapuas Ichthyo-

TABLE 3. FREQUENCIES OF VERTEBRAL COUNTS IN *Chonerhinos.*

C. amabilis	*C. modestus*	*C. nefastus*	*C. remotus*	*C. silus*
		9 + 15 = 24 (1)		
9? + 16 = 25? (1)		9 + 16 = 25 (2)	9 + 16 = 25 (1)	9? + 16 = 25? (1)
			10 + 15 = 25 (3)	10 + 15 = 25 (2)
9 + 17 = 26 (1)		9 + 17 = 26 (1)		
10 + 16 = 26 (9)	10 + 16 = 26 (3)	10 + 16 = 26 (1)	10 + 16 = 26 (8)	10 + 16 = 26 (8)
		10 + 17 = 27 (6)		10 + 17 = 27 (1)
	11? + 16 = 27? (1)		11? + 16 = 27? (2)	11? + 16 = 27? (1)

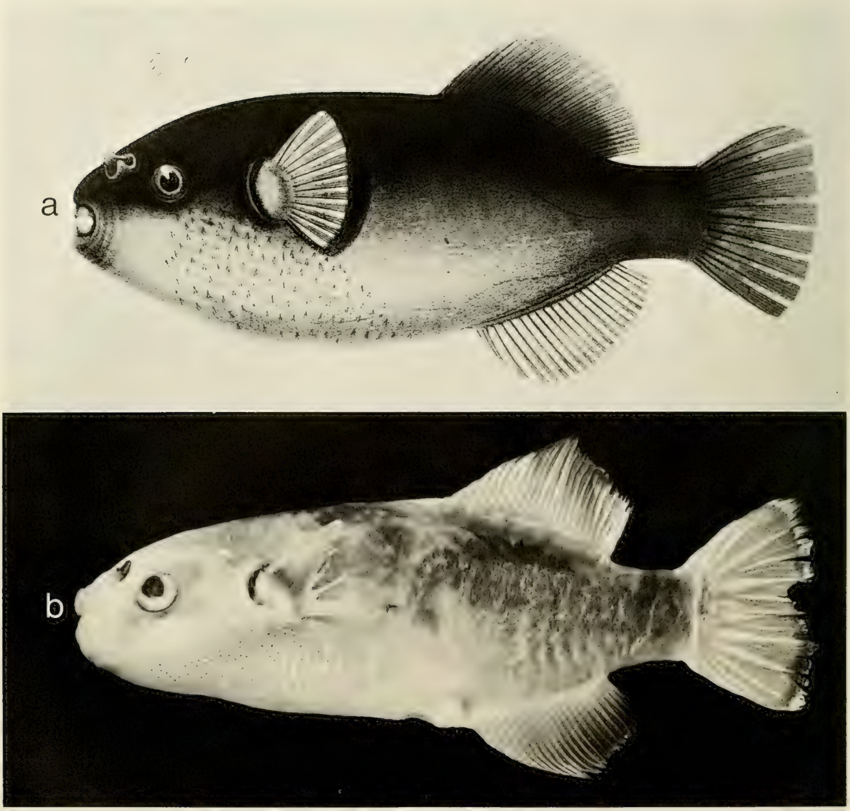


FIGURE 3. *Chonerhinos modestus*: (*a*) as illustrated in Bleeker 1865; length, locality, and present disposition of specimen unknown; (*b*) 78.7 mm, RMNH 26931 (neotype).

logical Survey, 22–26 July 1976; MZB 3975, 38.3 mm, Kapuas R. near Kampong Nibung, 7 km NE of Selimbau, Kapuas Ichthyological Survey, 5–6 July 1976; MZB 3976 and USNM 230359, 2:35.9–36.8 mm, Kapuas R. 53 km W of Putussibau, Kapuas Ichthyological Survey, 6–7 Aug. 1976; MZB 3977 and FMNH 94255, 2:35.6–46.0 mm, Kapuas R. about 23 km WSW of Putussibau, Kapuas Ichthyological Survey, 8–9 Aug. 1976; MNHN 91.216, 36.9 mm, Kapuas basin, M. Chaper, 1890; RMNH uncat., 2:40.9–41.2 mm, Kapuas basin, Sintang, July 1894; RMNH 7935, 4:55.5–68.1 mm, Kapuas basin, Raun, Mar.–May 1894; ZMA 108.912, 3:56.3–70.4 mm, Kapuas basin, Soengai Serawai, Lebang Hara, Witkamp, no date; UMMZ 171708, 2:36.2–38.3 mm, Sumatra, Moesi R. at Moera Klingi, A. Thienemann, 1913.

DIAGNOSIS.—*Chonerhinos amabilis* is readily distinguished from all other members of the genus by its highly distinctive coloration, almost all elements of which are visible in all specimens examined, including some century-old specimens which may have been dead for some time before being preserved. These unique features include a roundish dark spot in middle of caudal peduncle, visible in all specimens; a large, distinctively shaped dark mark on dorsal surface of head extending uninterrupted from just behind upper lip to well behind the eyes, set off by pale coloration on the upper lip, sides of snout, nasal flaps, and skin dorsal to orbits; pale white or milky coloration on ventral and lateral surfaces of body extending very far dorsally; dark col-

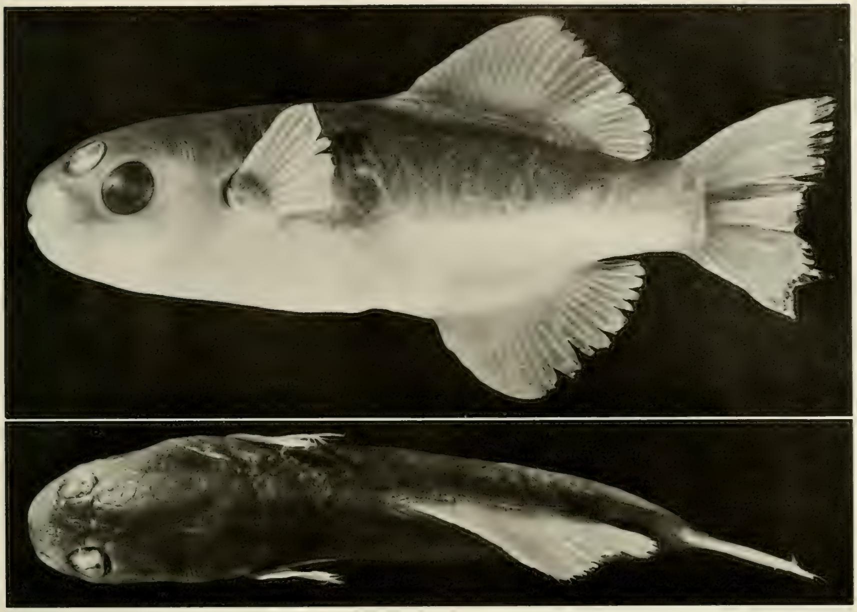


FIGURE 4. *Chonerhinos modestus*, 64.6 mm, CAS 49505.

oration on dorsal surface of body markedly enhanced around base of dorsal fin; and a small dark or dusky oval spot with indistinct margins near tip of chin (very faint or absent in some specimens). In addition, *C. amabilis* tends to have the largest nasal organ of any *Chonerhinos*, and thus of any tetraodontid (Tyler 1980:290); relatively large dorsal and anal fins with angulated (rather than rounded) margins; and scales on side of body anterior and ventral to pectoral fin relatively small, few in number, and with spines directed posteriorly (Fig. 1*f*).

ETYMOLOGY.—Latin *amabilis*, lovely.

Chonerhinos modestus (Bleeker)

(Figures 3–5)

Tetraödon (Arothron) modestus BLEEKER, 1850:16 (type-locality "Banjermassing, in fluviis").

Chonerhinos modestus BLEEKER, 1854:260.

Chonerhinus africanus BOULENGER, 1909:201 (type-locality "riv. Sankuru, à Kondué Kasai, Congo").

NEOTYPE.—RMNH 26931, 78.7 mm, Kapuas basin, Sanggau, Westenenk, 1894.

ADDITIONAL MATERIAL EXAMINED.—RMNH uncat., 2:49.2–59.2 mm, same data as neotype; RMNH 7934, 3:50.0–58.9 mm, Kapuas basin, Sintang, July 1894; CAS 49505 and MZB 3978, 2:64.6–106 mm, Kapuas R. about 23 km wsw of Putussibau, Kapuas Ichthyological Survey, 8–9 Aug. 1976; MZB 3979 and USNM 230360, 2:46.8–48.4 mm, Kapuas R. at Silat, Kapuas Ichthyological Survey, 17 Aug. 1976; BMNH 1846.6.22.75, 86.1 mm, Borneo, Frank Collection, no date; BMNH 1867.11.28.125, 87.3 mm, Borneo, Bleeker Collection, no date; RMNH 12004, 3:66.6–81.1 mm, Sumatra, Lahat, Bleeker Collection, 1850–60; NHMB 822–824, 3:44.7–73.5 mm, Sumatra, Indragiri, H. A. von Meckel, 1895; RMNH 7344 (part only), 8:47.9–62.0 mm, no locality data, Bleeker Collection, no date; MRAC 15306, 52.5 mm, "Congo, Sankuru River, Kasai" (holotype of *C. africanus*).

SELECTION OF NEOTYPE.—Identification of *C. modestus* presented a difficult and taxonomically important problem which I have resolved by selecting a neotype. The holotype is lost or at least it cannot be positively identified, and the original description fits all five species of *Chonerhinos* about equally well. In order to facilitate the following discussion the original description (Bleeker 1850:16) is reproduced here in its entirety:

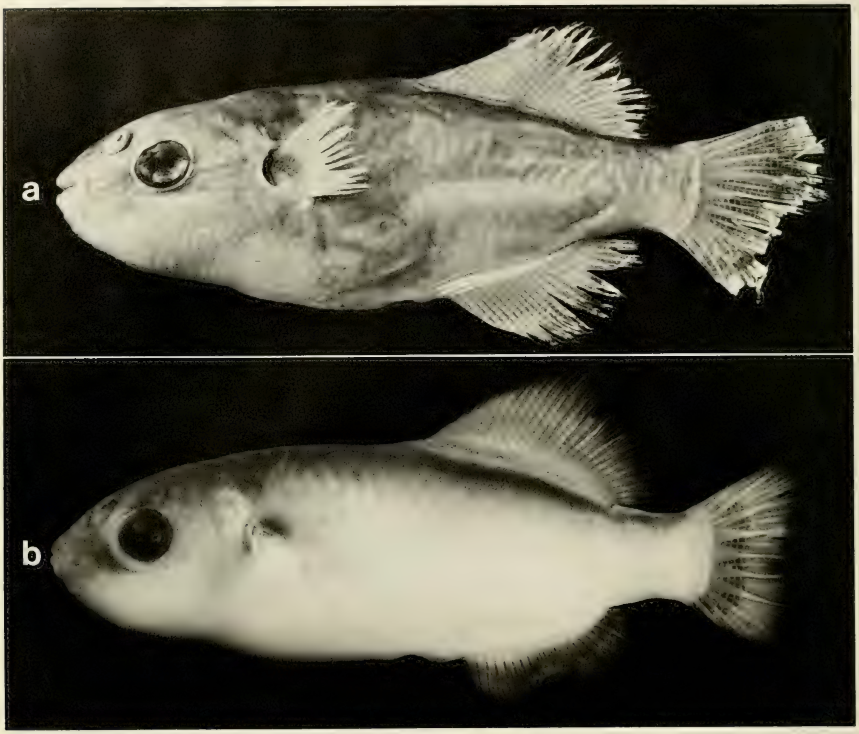


FIGURE 5. *Chonerhinos modestus*: (*a*) 52.5 mm, MRAC 15306 (holotype of *C. africanus*); (*b*) 48.4 mm, USNM 230360.

> *Tetraödon (Arothron) modestus* Blkr.
>
> Tetraöd. corpore oblongo compresso, altitudine 4 circiter in ejus longitudine, latitudine 2 in altitudine; vertice, dorso, lateribus caudaque laevibus, pectore genisque scabris; capite obtuso; lineo rostro-dorsali convexa; maxilla superiore paulo prominente; oculis paulo superis; tentaculis nasalibus 2 conicis obtusis loco narium; linea laterali inconspicua; sacco pneumatico parvo; ano ante pinnam dorsalem sito; pinnis dorsali et anali obtusis angulatis angulis rotundatis, pectoralibus emarginatis, caudali truncata vel leviter emarginata 5 in longitudine corporis; colore corpore supra viridi infra argenteo, pinnis hyalino-viridescente.
>
> D. 5/20. P. 2/12. A. 3/20. C. 9 vel 11 et lat. brev.
>
> Habit. Banjermassing, in fluviis.
>
> Longitudo speciminis unici 60'''.

Bleeker almost invariably recorded the length of his specimens as total length in millimeters (pers. commun. M. Boeseman, RMNH). Thus, the last two lines of the description indicate that it was based on a single specimen, the holotype, total length 60 mm, from riverine habitat at Bandjarmasin, southeastern Borneo (Barito basin). Bleeker obtained in all 59 specimens which he identified as *C. modestus*, total lengths 46–126 mm, from Palembang (=Lahat?), Sumatra, and Sambas, Pontianak, and Sintang as well as Bandjarmasin in Borneo (Bleeker 1865:78). All extant "*C. modestus*" from Bleeker's collection apparently are deposited in the BMNH, RMNH, and ZMA. The BMNH and ZMA each have a single Bleeker specimen, both of which are too large to be the holotype: BMNH 1867.11.28.125, 87.3 mm, Borneo, examined by me, and ZMA 102.263, 104 mm, Borneo, examined for me by H. Nijssen. The RMNH has two lots, RMNH 12004, 3:66.6–81.1

mm, Sumatra, Lahat (=Palembang?), and RMNH 7344, 52:29.0–74.0 mm (total lengths 37–88 mm), without locality data. If the holotype still exists, it presumably is in RMNH 7344. Among the 52 specimens are 4 which approximate 60 mm in total length; thus, on the basis of length alone, the holotype cannot be identified. Moreover, each of the four specimens differs by one or two fin rays in at least two of the three counts reported by Bleeker for the dorsal, anal, and pectoral fins of the holotype. In my opinion, none of these specimens can reasonably be identified as the holotype, and since their locality data are lost, a neotype should not be selected from among them. Unfortunately, I have been unable to find any specimen of *Chonerhinos* with locality data from Bandjarmasin or the Barito and do not know which of the species occur(s) there.

As noted above, the original description of *C. modestus* fits all five species of *Chonerhinos* about equally well. All species of *Chonerhinos* normally have 11 caudal-fin rays, and all species are represented by specimens with 25 dorsal-fin rays and 14 pectoral-fin rays. On the other hand, none of the more than 250 specimens examined have 23 anal-fin rays. The highest number of anal-fin rays observed, 22, is usually found in the species herein identified as *C. modestus,* but also occurs in *C. nefastus* and *C. silus*. Coloration and its variation in the species of *Chonerhinos* are too poorly known at present to be of much help in their identification, and Bleeker's description of coloration of the holotype cannot be accepted without reservation since he did not collect the specimen himself and could not have observed it until it had been in preservative for many days or weeks. Bleeker (1865:pl. 213, fig 8) published an excellent figure of a specimen which he identified as *C. modestus*. The length, locality, and date of collection of the specimen figured are not recorded, but it is not the holotype. It is evidently a much larger specimen, with lateral line canals on the body plainly visible, and differs also in fin-ray counts from the holotype as described by Bleeker. I have not tried to match up the figure with an extant specimen, although it may well be part of RMNH 7344. The figure does, however, show a number of features characteristic of the largest species of *Chonerhinos,* with which I unhesitatingly identify it. These features include its large size (indicated by the large size of the published illustration as well as by the relatively small eye); scales with dorsally oriented spines; relatively high counts of dorsal- and anal-fin rays; and deep caudal peduncle. All four specimens of total length 60 mm in RMNH 7344 also belong to this species. Thus, there is every reason to identify it as *C. modestus,* although we cannot be sure that this is the same species obtained for Bleeker at Bandjarmasin. In the absence of specimens with locality data from Bandjarmasin or the Barito, a specimen from the Kapuas basin has been selected as neotype. This specimen bears a strong resemblance to Bleeker's figure of *C. modestus* (Figs. 3*a–b*).

DIAGNOSIS.—*Chonerhinos modestus,* attaining at least 106 mm, apparently is the largest species of *Chonerhinos* and has the deepest caudal peduncle. Depth of caudal peduncle 6.7–7.4 (vs. 7.2–9.9 in all other *Chonerhinos*). Scales relatively large and close-set, those on body anteroventral to pectoral fin with spines directed dorsally, as in *Xenopterus* (vs. spines directed dorsoposteriorly or posteriorly in all other *Chonerhinos*). Upper and lower lips about equally projecting or lower lip slightly protruding. Exposed portion of eye round. Snout gently sloping. Nasal organ moderately large, its length 14.7–25.3. Dorsal-fin rays 25–28; and anal-fin rays 20–22 (generally fewer in other *Chonerhinos*).

REMARKS ON SYNONYMY.—Most records of *C. modestus* in the literature other than those cited in the synonymy above refer in whole or in part to other species of *Chonerhinos*.

Chonerhinos africanus was described briefly (and without a figure) on the basis of a single specimen supposedly obtained together with other fish specimens by E. Luja in the Sankuru River, Kasai, Congo basin, in 1908. No additional specimens of *Chonerhinos* have been found in Africa, and the holotype has not been compared previously to *Chonerhinos* from Southeast Asia. I have examined the 52.5-mm holotype (Fig. 5*a*), comparing it directly with specimens of all five species of *Chonerhinos,* and conclude that it is conspecific with *C. modestus*. It has 26 dorsal-fin rays; 22 anal-fin rays; 15 pectoral-fin rays; 10 + 16 vertebrae; scales relatively large, those on sides of body anteroventral to pectoral fin with spines directed dorsally; lower lip slightly protruding; snout gently

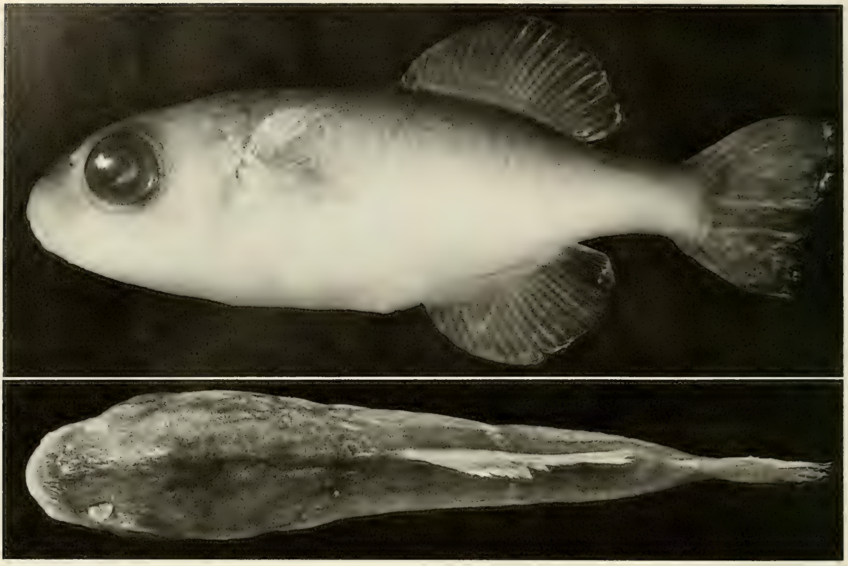


FIGURE 6. *Chonerhinos nefastus*, 47.0 mm, MZB 3980 (holotype).

sloping; eye 10.7; olfactory organ 18.7; snout 7.2; interorbital width 5.25; depth caudal peduncle 7.4; length caudal peduncle 5.9; and pectoral-fin base 10.8. The caudal peduncle depth and anal-fin ray count, while not conclusive, agree best with *C. modestus*. Presumably, the specimen originated somewhere in Southeast Asia and somehow became mixed with Luja's material when it was sent on loan to the BMNH for Boulenger to study.

Chonerhinos nefastus new species

(Figure 6)

Chonerhinos modestus d'Aubenton and Blanc, 1966:561 (Mekong basin, Kampuchea); Taki 1974:199–200, fig. 187 (Mekong basin, Laos); Imaki et al. 1978:29, pl. 18 (Kapuas R. at Sintang); Tyler 1980 (fig. 223?).

Holotype.—MZB 3980, 47.0 mm, Kapuas R. 29 km w of Putussibau, Kapuas Ichthyological Survey, 11 Aug. 1976.

Paratypes.—CAS 49506 and MZB 3981, 4:34.3–43.3 mm, Kapuas R. near Kampong Nibung, 7 km ne of Selimbau, Kapuas Ichthyological Survey, 5–6 July 1976; BMNH 1982.3.29. 254–5 and MZB 3982, 3:36.6–43.7 mm, Kapuas R. 53 km w of Putussibau, Kapuas Ichthyological Survey 6–7 Aug. 1976; IRSNB 632, MZB 3983, ROM 38601, and USNM 230361, 6:32.9–60.2 mm, Kapuas R. about 23 km wsw of Putussibau, Kapuas Ichthyological Survey, 8–9 Aug. 1976; MZB 3984, 51.7 mm, Kapuas basin, small tributary of Sungai Mandai 17 km wsw of Putussibau, Kapuas Ichthyological Survey, 10 Aug. 1976; MZB 3985, 64.9 mm, Kapuas basin, Sungai Mandai Kechil, 18 km wsw of Putussibau, Kapuas Ichthyological Survey, 11 Aug. 1976; CAS 49507 and MZB 3986, 3:36.7–57.8 mm, Kapuas basin, Sungai Tawang near Danau Pengembung, Kapuas Ichthyological Survey, 14–15 Aug. 1976; RMNH 7936, 61.8 mm, Kapuas basin, Sibau, June 1894; RMNH uncat., 25.5 mm, Kapuas basin, Sintang, July 1894; ZMA 110.220, 65.8 mm, Kapuas basin, Bunut, H. A. Lorentz, 26 June 1909; FMNH uncat. 3:38.2–50.1 mm, Sarawak, Niah R., T. Harrisson, 1 Apr. 1963; FMNH uncat., 2:64.8–70.7 mm, Sarawak, Niah, T. Harrisson, no date; FMNH uncat., 3:36.9–41.8 mm, Sarawak, Rejang basin, Baleh R. between Sungai Mujong and Sungai Gaat, R. F. Inger, 3 Aug. 1956; RMNH 7933, 2:56.6–68.0 mm, Mahakam basin, Tepoe, A. W. Nieuwenhuis, 1896–97; MG 2058.94, 34.9 mm, Kalimantan Tengah, Mentaya basin near Sampit, Pfeuffer, May 1980; UMMZ uncat., 50.1 mm, Sumatra, Moesi R. at Moera Klingi, A. Thienemann, 1913; SU 36040, 41.7 mm, Malay Peninsula, Perak, Chandra dam, A. W. Herre, 18 Mar. 1923; UMMZ 197038, 43.7 mm, Thailand, Songkhla Lake off Patalung, K. F. Lagler, 6 Jan. 1965; UMMZ uncat., 48.0 mm, Thailand, Mekong basin, Ubon Ratchtani, Huay Phai, 16 Oct. 1975; UMMZ uncat., 38.9 mm, Thailand, Mekong basin, Ubon Ratchtani, Huay Kwang, 1 Oct. 1976; UMMZ uncat., 42.5 mm, Thailand, Mekong basin, Huay Kwang s of Khong Chiam, Arden, 7 Oct. 1975; UMMZ uncat., 30.9 mm, Thailand, Mekong basin, Mun R. at Khong Chiam, Songrad and Buskirk, 19 July 1975; UMMZ uncat., 3:15.4–32.2 mm, Thailand, Mekong R. and

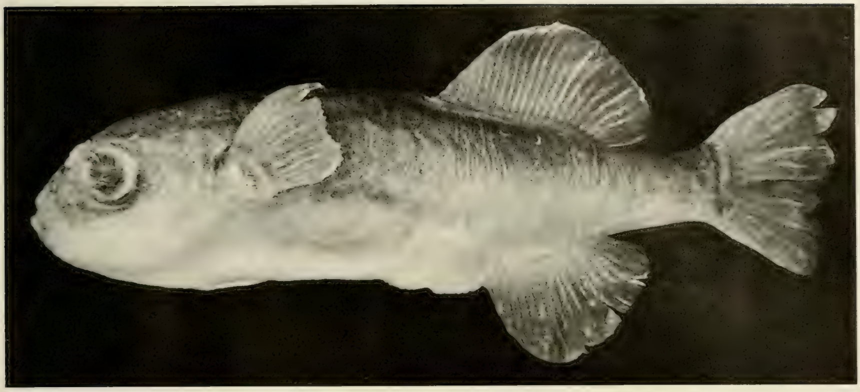


FIGURE 7. *Chonerhinos remotus*, 52.7 mm, FMNH 68475 (holotype).

tributaries from Ban Dan to Nakon Phanom, Mekong fish survey, Mar.–Apr. 1975; MNHN 1966.55–56, 9:21.6–48.1 mm, Kampuchea, Mekong basin, Prek Tasom, F. d'Aubenton, 5 June and 9 Nov. 1961; MNHN 1966.57, 12:19.0–47.5 mm, Kampuchea, Mekong basin, Prek Andor, F. d'Aubenton, 2 Dec. 1961.

DIAGNOSIS.—*Chonerhinos nefastus* differs from all other species of *Chonerhinos* in having upper lip usually projecting beyond lower lip; nasal organ relatively small (Table 1); and exposed portion of eyeball usually horizontally oval rather than round or vertically oval. It differs from all other species except *C. amabilis* in having scales on side of body anterior and ventral to pectoral fin usually with spines directed posteriorly (Fig. 1*e*), and from all except *C. remotus* in its slender caudal peduncle (Table 1). Body usually without distinct color marks except for a slightly darkened spot on dorsal surface of head posterior to eyes.

COMMENTS.—The exposed portion of the eyeball is distinctly horizontally oval in more than half of the specimens examined. It is usually round in very small specimens, however, and sometimes round in large specimens (including the holotype). Most specimens have the scales on the side of the body anterior and ventral to the pectoral fin with the spines directed posteriorly, as in Figure 1*e*. This character is variable, however, and in a few specimens the spines are directed posterodorsally or almost dorsally. This is most noticeable in the sample of 12 specimens from Prek Andor, 4 of which have the spines more dorsally directed than is usual in *C. nefastus*. The rest of the specimens in the sample have the spines directed posteriorly or posterodorsally. Specimens from the Mekong River differ from *C. nefastus* from other localities in having a dark transverse mark on the dorsal surface of the snout between the upper lip and the nostrils.

ETYMOLOGY.—Latin *nefastus*, wicked, abominable, in reference to the food habits (see below).

Chonerhinos remotus new species

(Figure 7)

Chonerhinos modestus HERRE, 1940:55 (Sandakan District, Sungei Segaliud and Sungei Sibuga); INGER AND CHIN 1962:190–191, fig. 101 (Kinabatangan District).

HOLOTYPE.—FMNH 68476, 52.7 mm, Kinabatangan basin, mouth of Sungai Deramakot, R. F. Inger and P. K. Chin, 27 Apr. 1956.

PARATYPES.—FMNH uncat., 9:32.8–54.4 mm, same data as holotype; CAS 49743 and FMNH 68475, 61:29.1–56.8 mm, Kinabatangan R. below mouth of Malubok R., R. F. Inger and P. K. Chin, 25 Apr. 1956; FMNH 68474, 3:47.2–54.4 mm, Kinabatangan R. at Deramakot camp, R. F. Inger and P. K. Chin, 24 Apr. 1956; FMNH 44931, 38.3 mm, Kinabatangan District, N. Borneo Fisheries Dept., 20 Jan. 1949; SU 33487, 2:60.5–61.4 mm, Sandakan District, Sibugal R. (=Sungai Sibuga), A. W. Herre, 19 Apr. 1938; SU 33563, 10:30.5–40.4 mm, Sandakan District, Segaliud R., A. W. Herre, 4 Feb. 1937.

DIAGNOSIS.—*Chonerhinos remotus* is most similar to *C. silus*, from which it differs in having a more slender caudal peduncle (Table 1); fewer dorsal- and anal-fin rays on the average

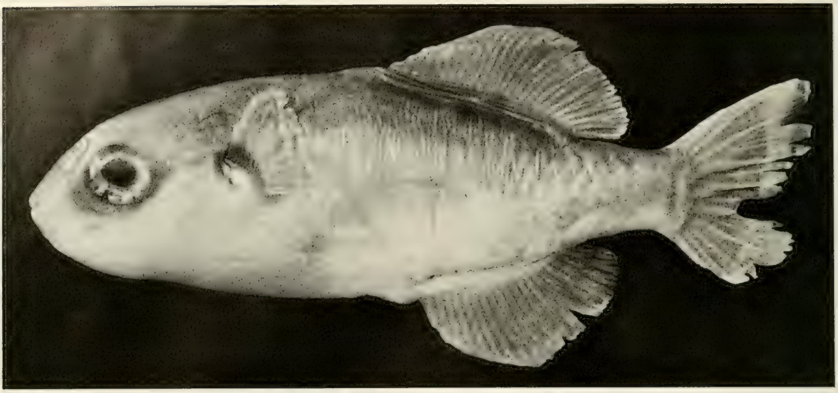


FIGURE 8. *Chonerhinos silus*, 44.9 mm, FMNH 68477 (holotype).

(Table 2); an even more strongly sloping snout; lower lip almost always strongly projecting beyond upper lip (vs. lower lip slightly projecting or equal to upper lip); and eye vertically oval or round (vs. usually round). Scales anterior and ventral to pectoral fin moderately large and close-set, with spines directed posterodorsally (Fig. 1*d*). No distinctive color marks except for a well-defined dark blotch on dorsal surface of head posterior to eyes.

ETYMOLOGY.—Latin *remotus*, remote, in reference to the type-locality.

Chonerhinos silus new species

(Figure 8)

HOLOTYPE.—FMNH 68477, 44.9 mm, Sarawak, Rejang basin, Sungai Baleh between Sungai Mujong and Sungai Gaat, R. F. Inger, 3 Aug. 1956.

PARATYPES.—CAS 49744, FMNH uncat., 36:35.0–60.1 mm, same data as holotype; FMNH 62987, 44.0 mm, Sarawak, Niah R., Niah, Lord Medway, 22 Aug. 1959; FMNH 68813, 81.8 mm, Sarawak, Niah, T. Harrisson, no date; FMNH 68814; 2:44.1–68.7 mm, Sarawak, Niah, Niah R., Pengkalan Lobang, T. Harrisson, 2–11 Nov. 1960; FMNH 68815, 16:37.1–72.9 mm, Sarawak, Niah R., T. Harrisson, 1 Apr. 1963; SU 33610, 32.7 mm, Sarawak, 16 miles [ca. 26 km] E of Kuching, A. W. Herre, 16 Feb. 1937.

DIAGNOSIS.—*Chonerhinos silus* is most similar to *C. remotus* and *C. modestus*. Differences between *C. silus* and *C. remotus* are set forth above in the diagnosis of *C. remotus*. It differs from *C. modestus* in attaining smaller adult size (largest specimen examined 82 mm vs. 106 mm); snout more strongly sloping; lips equally projecting, or lower lip variably protruding, frequently much more so than in *C. modestus*; scales anterior and ventral to pectoral fin with spines projecting dorsoposteriorly (Fig. 1*c*) rather than dorsally (Fig. 1*b*); and caudal peduncle relatively slender, its depth 7.2–8.2 (vs. 6.7–7.4). *C. silus* tends to have fewer dorsal-, anal-, and pectoral-fin rays than *C. modestus* (Table 2), but the counts are broadly overlapping and of little help in identifying individual specimens to species.

ETYMOLOGY.—Latin *silus*, pugnosed.

COLORATION IN LIFE

Most of the specimens of *Chonerhinos* collected during the 1976 Kapuas Ichthyological Survey were caught at night and preserved before their coloration in life could be properly observed. Colors of the 106-mm *C. modestus*, gill-netted at night and removed the next morning, are recorded in my field notes and in a 35-mm Kodachrome slide. It was pale blue dorsally, white on the sides and abdomen, and with a reddish eye. It is my impression that the three smaller *C. modestus* collected during the survey were similarly colored. *C. amabilis* is described in my field notes as lime-green dorsally, with a darkened area along the base of the dorsal fin, and a reddish eye; the round spot on the caudal peduncle, so evident in preserved specimens, was not observed during life (at least it is not recorded in my field notes, and I do not recall having seen it in the live specimens). I suspect that some *C. amabilis* were blue dorsally but this is not recorded in my field notes. My impression is that all *C. nefastus* caught during the survey were pale green dorsally; at least this was so in several specimens observed during the day. I doubt that any of them were blue dorsally. D'Aubenton and Blanc (1966) reported coloration of *C. nefastus* (as *C. modestus*) from the Mekong basin in Kampuchea as green on the back and white on the flanks and belly, while Taki (1974) reported specimens from the Mekong in Laos as having "back and upper surface of head and body olivaceous golden, underside pale yellow to white. Dorsal and caudal fins greenish yellow; anal fin pale yellow; pectoral fins hyaline."

SEXES

Secondary sexual dimorphism is unknown in *Chonerhinos*. I have examined ripe males and gravid or ripening females in all five species. Ovaries of the left and right sides are about equally well developed. The following approximate counts of eggs and measurements of egg diameters contained in the right ovary were made; *C. amabilis*, 57.4 mm, 180 eggs, 1.1–1.9 mm; *C. modestus*, 106 mm, 800 eggs, 1.5–2.1 mm; *C. nefastus*, 56.5 mm, 100 eggs, 1.4–1.5 mm, 57.8 mm, 80 eggs, 1.3 mm, and 64.9 mm, 230 eggs, 1.3–1.6 mm; *C. remotus*, 54.2 mm, 85 eggs, 1.9–2.3 mm; and *C. silus*, 58.7 mm, 200 eggs, 1.5–2.1 mm. All of these specimens are gravid except the three *C. nefastus*, which are nearly ripe. In *C. remotus* I observed two gravid females, 54.2 and 54.4 mm, and three spent females, 48.8, 51.4, and 52.7 mm (the holotype, Fig. 7), with genitoanal areas much swollen. Such swelling, perhaps present only in females just before or after spawning, has not been observed in other species.

FOOD HABITS

Food habits of *Chonerhinos*, determined by complete or partial examination of gut contents in more than 100 specimens, may be summarized as follows: *C. amabilis* feeds almost exclusively on large aquatic insects; *C. modestus* feeds mainly on terrestrial insects, shrimps, seeds, and to a less extent on whole fish, fin rays, or scales; *C. nefastus* feeds mainly on fish fin rays and scales, and to a lesser extent on insects (aquatic and terrestrial); *C. remotus* and *C. silus* feed mainly on insects aquatic and terrestrial), but also ingest vegetable matter and other items. No fish remains were found in *C. amabilis*, *C. silus*, or, excepting a single fish scale in one specimen, *C. remotus*. Pieces of clam flesh and gills were found in several *C. silus*, and numerous small, whole clams in a single *C. nefastus*, but otherwise molluscs were absent. The food of the five species may be described in more detail as follows.

In *C. amabilis*, 18 of 20 specimens contained more or less abundant remains of insects, mainly large aquatic forms; partial examination of the gut contents of these specimens failed to reveal any other food items. Of the remaining two specimens, one contained moderate amounts of an unidentified flocculent material, and one had empty guts. This species is noteworthy in that nearly all individuals had much food in their guts, and in being the most stenophagic of any species of *Chonerhinos*. In *C. modestus*, guts were examined in 10 specimens, half of which had empty guts. Of the remaining five, four contained moderate to large amounts of insects (mainly terrestrial), two had prawns, two had seeds, two had fish scales, one had fish fin rays, and one had the remains of a small whole cobitid fish (identified by its Weberian apparatus). The last *C. modestus*, the 106-mm specimen, is of particular interest because of its large size and because of the circumstances of its capture. It was gill-netted together with a large catfish, *Pangasius polyuranodon* (Fig. 9), which had much of its abdominal wall and portions of its anal and caudal fins and caudal peduncle bitten away. I suspected that part of the damage may have been done by the *C. modestus*, but careful examination of its gut contents failed to reveal any material from the *Pangasius*. While the *C. modestus* may have regurgitated, its stomach did contain other food items, and it seems more likely that the *Pangasius* was ravaged by some other predator, possibly *C. nefastus*. Of 31 *C. nefastus* in which the gut contents were examined, 11 had more or less substantial amounts of fish fin rays, six had fish scales, three contained small pieces of fish flesh, six had small to moderate amounts of insects (terrestrial and aquatic), two had unidentified debris or detritus, one had numerous small, whole bivalves, and one had a large amount of sand and grit; seven had

FIGURE 9. An 106-mm *Chonerhinos modestus* gill-netted together with an 80-cm *Pangasius polyuranodon* catfish ravaged by an unknown predator, possibly *C. modestus* or *C. nefastus* (Kapuas River near Putussibau).

empty guts. The Latin name *nefastus* refers to the predominantly pterygophagous and lepidophagous habits of this species. Inger and Chin (1962:191) reported gut contents of 11 *C. remotus* (as *C. modestus*) as follows: bits of leaves (6); parts of terrestrial insects (6); Plecoptera nymphs (3); Trichoptera larval cases (1); unidentified insect larvae (3); Acarina (2); unspecified parts of fishes (2). Of 21 *C. remotus* I examined, 18 had guts containing food items: 14 with insects (aquatic and terrestrial), 4 with parts of higher plants, 1 with a mite, 1 with a fish scale, and several with unidentified debris or detritus. In 33 *C. silus,* 22 had guts containing insects (aquatic and terrestrial), 6 contained higher plant material (fine rootlets, leaf, seeds, or seed pulp?), 1 had several pieces of a large, spinulose oligochaete, and 1 had chunks of spiny or hairy flesh (mammalian?); the remainder had empty guts.

INTRASPECIFIC BITING

Intraspecific biting, although infrequently documented, probably occurs in many members of the family Tetraodontidae. In *Fugu niphobles* (Jordan and Snyder, 1901), biting is an integral part of spawning behavior: egg laying occurs on the beach at high tide after a female has been bitten on the sides by two to four males (Uno 1955). Many of the specimens of *Chonerhinos* examined exhibited characteristically shaped bite marks on the flanks and, even more frequently, had portions of the median fins bitten off. I suspect that much of the biting, at least in *C. nefastus,* is inflicted by conspecifics. More than half of the specimens examined of this species had bite marks on the flanks or had portions of the dorsal, anal, or caudal fins missing. In many specimens these fins appear to have been bitten repeatedly, as evidenced by scar tissue and imperfect regeneration of fin rays. It is noteworthy that this species feeds predominantly upon fish fin rays (see above under Food Habits). *C. modestus* and *C. silus,* both of which occur sympatrically with *C. nefastus,* also exhibit high frequencies of specimens with bite marks and bitten fins, but it is unclear whether this is a result of intraspecific attacks, attacks by *C. nefastus,* or a combination of both. In all three species the bite marks and fin damage appear to be about equally distributed between the sexes, and between gravid and nongravid females. None of the specimens of *C. amabilis* and *C. remotus* examined exhibited bite marks on the flanks, and their fins were relatively undamaged, with little or no indication of fin-nipping. Perhaps the generally pterygophagous and lepidophagous feeding behavior of *C. nefastus* was preceded by the evolution of an exceptionally aggressive intraspecific biting and fin-nipping behavior.

GEOGRAPHICAL DISTRIBUTION

Tetraodontidae is the only one of the nine families of the large order Plectognathi or Tetraodontiformes which has representatives that occur in fresh water. About 25 of the approximately 140 described tetraodontid species are

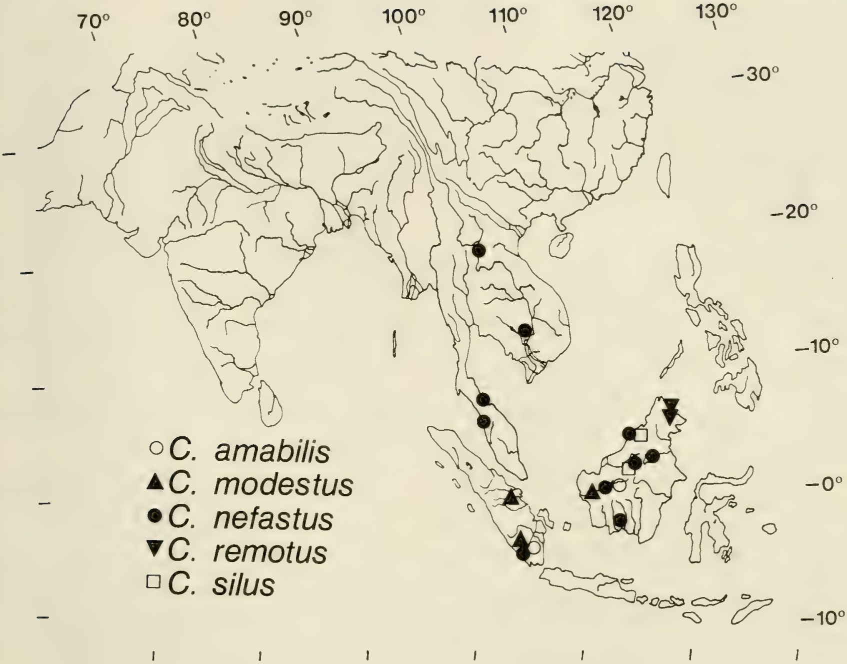


FIGURE 10. Geographical distribution of species of *Chonerhinos*.

endemic to fresh water. *Carinotetraodon* and *Chonerhinos*, both from Southeast Asia, are the only tetraodontid genera restricted to fresh water. Other genera with freshwater species include *Tetraodon* or *Monotreta* in India, Southeast Asia, and New Guinea; *Tetraodon* in Africa; and *Colomesus* in South America. Two features of the geographical distribution of freshwater Tetraodontidae merit comment. First, although marine tetraodontids extend into high latitudes in the Northern and Southern hemispheres, freshwater species occur only within tropical latitudes. Second, the tropical rivers with endemic tetraodontids generally have rich ichthyofaunas dominated by primary freshwater fishes.

Geographical distributions of the species of *Chonerhinos*, based mainly on material examined in this study, are illustrated in Figure 10. Two of the species, *C. amabilis* and *C. modestus*, have distributions lying within the hydrographic limits of the ancient Central Sundaland River basin, now fragmented by the Java and South China seas. I suspect that *C. modestus* also occurs in Thailand but have not examined specimens from there. The most widely distributed species, *C. nefastus*, occurs throughout the area occupied by the Central Sundaland River basin; it also occurs in northern and southern Borneo and in the Mekong basin. Whether the Mekong River once also formed part of the Central Sundaland drainage is a matter under investigation. *C. silus* and *C. remotus*, in northern and northeastern Borneo, have restricted distributions entirely outside the limits of the Central Sundaland drainage area. *C. amabilis*, *C. modestus*, and *C. nefastus* occur sympatrically in the Kapuas River and probably also in some rivers in Sumatra including the Indragiri and

Moesi. *C. nefastus* and *C. silus* occur sympatrically in Sarawak (Rejang and Niah basins).

ACKNOWLEDGMENTS

It is a pleasure to thank the following individuals for their help during this study: Oliver Crimmen, Gordon Howes, and Alwyne Wheeler, BMNH; Marie-Louise Bauchot, Jaques Daget, and Martine Desoutter, MNHN; Marinus Boeseman, Peter van Helsdingen, and M. J. P. van Oijen, RMNH; Han Nijssen, ZMA; Volker Mahnert, MG; Donald J. Stewart, FMNH; Walter Rainboth, UMMZ; Dirk Thys van den Audenaerde, MRAC; Maurice Kottelat, Université de Neuchatel; and Lillian Dempster, Madeleine Graham, W. I. Follett, Michael Hearne, and James Jackson, CAS. Photography is by Alphonse Coleman, Museum of Comparative Zoology, Harvard University, and Orrin Moon, The Darkroom, San Rafael.

The ichthyological survey of the Kapuas basin was sponsored by the Museum Zoologicum Bogorense, Indonesian National Research Council, and Smithsonian Tropical Research Institute. Soetikno Woerjoatmodjo, Leo Poerwadi, and Rajali assisted in the field. Research was done during visits to the BMNH, MNHN, RMNH, and ZMA, and at the California Academy of Sciences and Tiburon Center for Environmental studies, and was supported by National Science Foundation grant DEB77-24759.

LITERATURE CITED

BLEEKER, P. 1850. Bijdrage tot de kennis der ichthyologische fauna van Borneo, met beschrijving van 16 nieuwe soorten van zoetwatervisschen. Nat. Tijdschr. Ned. Ind. 1:1–16.

———. 1854. Vijfde bijdrage tot de kennis der ichthyologische fauna van Celebes. Nat. Tijdschr. Ned. Ind. 7:225–260.

———. 1865. Atlas ichthyologique des Indes Orientales Néêrlandaises, vol. 5.

BOULENGER, G. A. 1909. Catalogue des poissons du Congo du Musée d'Histoire naturelle de Luxembourg. Faune de Sankuru à Kondué (Collection Ed. Luja). Monatsber. Gesell. Luxemburg. Naturf., n. ser., 3:189–202.

CANTOR, T. E. 1850. Catalogue of Malayan fishes. J. Thomas, Calcutta. xii + 461 p., 24 pls.

D'AUBENTON, F., AND M. BLANC. 1966. Poissons tétraodontiformes du Cambodge. Bull. Mus. Natl. Hist. Nat. ser. 2, 38:554–561.

FRASER-BRUNER, A. 1943. Notes on plectognath fishes.—VIII. The classification of the suborder Tetraodontoidea, with a synopsis of the genera. Ann. Mag. Nat. Hist. ser. 11, 10:1–18.

GILL, T. N. 1892. Note on the genus *Chonerhinos* or *Xenopterus*. Proc. U.S. Natl. Mus. 14:696–699.

HERRE, A. W. 1940. Additions to the fish fauna of Malaya and notes on rare or little known Malayan and Bornean fishes. Bull. Raffles Mus. 16:27–61.

HOLLARD, H. 1857. Etudes sur les Gymnodontes et en particulier sur leur ostéologie et sur les indications qu'elle peut fournir pour leur classification. Ann. Sci. Nat. (Paris), zool., ser. 4, 8:275–328.

IMAKI, A., A. KAWAMOTO, AND A. SUZUKI. 1978. A list of freshwater fishes collected from the Kapuas River, West Kalimantan, Indonesia. The Institute for Breeding Research, Tokyo University of Agriculture, 50 p.

INGER, R. F., AND P. K. CHIN. 1962. The fresh-water fishes of North Borneo. Fieldiana: Zool. 45:1–263.

JORDAN, D. S. 1919. The genera of fishes, 2. Stanford Univ. Publ., univ. ser., i–x + 163–284 + i–xiii p.

ROBERTS, T. R. 1981. Identification of the presumed African freshwater fishes *Micracanthus marchei* (Belontiidae) and *Chonerhinos africanus* (Tetraodontidae). Cybium, ser. 3, 5:91–92.

TAKI, Y. 1974. Fishes of the Lao Mekong basin. USAID Mission to Laos, Agric. Div., vi + 232 p.

TYLER, J. C. 1980. Osteology, phylogeny, and higher classification of the fishes of the order Plectognathi (Tetraodontiformes). NOAA Tech. Rep. NMFS Circ. 434, 422 p.

UNO, Y. 1955. Spawning habit and early development of a puffer, *Fugu* (*Torafugu*) *niphobles* (Jordan et Snyder). J. Tokyo Univ. Fish. 41:169–183.

WEBER, M., AND L. F. DE BEAUFORT. 1962. The fishes of the Indo-Australian Archipelago, vol. 11. E. J. Brill, Leiden. ix + 481 p.

CALIFORNIA ACADEMY OF SCIENCES
Golden Gate Park
San Francisco, California 94118

PROCEEDINGS
OF THE
CALIFORNIA ACADEMY OF SCIENCES

Vol. 43, No. 2, pp. 17–24, 7 figs.

June 15, 1982

SYNONYMIES OF INDIAN OCEAN EELS, WITH THE DESCRIPTION OF *GYMNOTHORAX ENIGMATICUS*, A MORAY PREVIOUSLY KNOWN AS *G. RUPPELI*

By

John E. McCosker

Steinhart Aquarium, California Academy of Sciences, Golden Gate Park,
San Francisco, California 94118

and

John E. Randall

Bernice P. Bishop Museum, Honolulu, Hawaii 96818

ABSTRACT: The common, banded Indo-Pacific morays called *Gymnothorax petelli* (Bleeker, 1856) and *G. ruppeli* (McClelland, 1845) by recent authors are recognized as *G. rueppelliae* (McClelland, 1845) and *G. enigmaticus* n.sp., respectively. They are separable on the basis of coloration, vertebrae, and morphology and have different geographic ranges. *G. signifier* Bliss, 1883, is placed in the synonymy of *G. rueppelliae,* along with *Muraena umbrofasciata* Rüppell, 1852; *M. interrupta* Kaup, 1856; *Sideria chlevastes* Jordan and Gilbert, 1883; *G. leucacme* Jenkins, 1904; and *G. waialuae* Snyder, 1904. The moray *Uropterygius xanthopterus* Bleeker, 1859, is recognized as distinct from *U. marmoratus* (Lacépède, 1803), and *U. alboguttatus* Smith, 1962, is synonymous with it. *Ophichthus retifer* Fowler, 1935, from Durban, South Africa, is a synonym of *O. erabo* (Jordan and Snyder, 1901), an ophichthid also known from Hawaii, Japan, and Taiwan.

INTRODUCTION

In preparation for the publication of the eel section of the revised *Sea Fishes of Southern Africa* (McCosker and Castle, MS), we assign several poorly known taxa to synonymy and provide a description for a common, conspicuously banded Indo-Pacific moray, *Gymnothorax ruppeli* of earlier authors, which lacks a holotype and scientific name.

METHODS

Measurements are straight-line, made either with a 300-mm ruler with 0.5-mm gradations (for total length, trunk length, and tail length) and recorded to the nearest 0.5 mm, or with dial calipers (all other measurements) and recorded to the nearest 0.1 mm. Body length comprises head and trunk lengths. Head length is measured from the snout tip to the posterodorsal margin of the gill opening; trunk length is taken from the end of the head to mid-anus; maximum body depth does not include the median fins. Vertebral counts (which include the hypural) were taken from radiographs. Materials used in this study are housed at the following institutions: Academy of Natural Sciences of Philadelphia (ANSP); Bernice P. Bishop Museum (BPBM); British Museum of Natural History (BMNH); California Academy of Sciences (CAS); U.S. National Museum of Natural History (USNM); Museum of Comparative Zoology, Harvard University (MCZ); J. L. B. Smith Institute of Ichthyology, Rhodes University (RUSI); Natur-Museum Senckenberg (SMF); and the Scripps Institution of Oceanography (SIO). Paratypes of the new species will also be deposited at the

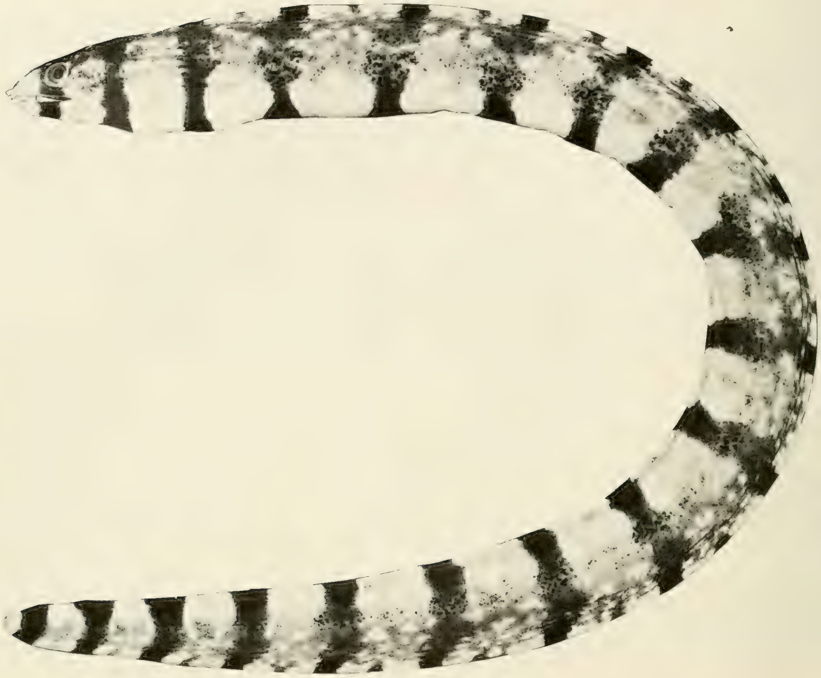


FIGURE 1. Paratype of *Gymnothorax enigmaticus* n.sp., BPBM 9491, 335 mm TL, from Palau.

Museum National d'Histoire Naturelle, Paris (MNHN), the BMNH, and the USNM.

FAMILY MURAENIDAE

Gymnothorax enigmaticus, new species

(Figure 1)

Holotype.—CAS 48815, 303.2 mm total length, a male (?) collected with rotenone in a 0–1-m tidal flat, off southern corner Ngatchab Beach, Angaur I., Palau, Western Caroline Is., by H. DeWitt, Sumang, and Sengich, 21 Oct. 1957.

Paratypes.—Collected in shallow coral reef flats and tidepools (0–3 m) using rotenone ichthyocides. PALAU: CAS 48823 (8; 51–299 mm), Angaur I., H. DeWitt et al., 22 Oct. 1957. CAS 48817 (293 mm), Auluptagel I., H. Fehlmann et al., 10 Aug. 1955. CAS 48816 (335.5 mm), Ngethil I., Sumang and R. Johaness, 13 July 1959. CAS 48822 (2; 238–257 mm), Aulong I., Sumang, 5 Nov. 1959. CAS 48826 (301.5 mm), Urukthapel I., H. Fehlmann et al., 19 Aug. 1955. BPBM 9491 (335 mm), Malakal Harbor, A. Emery, 21 Apr. 1970. KAPINGAMARINGI: CAS 48818 (163.8 mm), Thokotaman, R. Harry, 12 July 1954. IFALUK ATOLL: CAS 48819 (174 mm), Falarik Islet, R. Harry, 26 Sep. 1953. GUAM: CAS 48820 (214.4 mm), N of Cocos Is., Nangauta and H. Fehlmann, 8 Oct. 1958. ENEWETAK ATOLL: CAS 42377 (144 mm), Runit I., R. Nolan and L. Taylor, Jr., 23 Feb. 1974. BPBM 8184 (127 mm), Enewetek I., J. Randall, 1 Dec. 1967. BPBM 22339 (2; 219–233 mm), Enjebi I., J. Randall et al., 27 Apr. 1978. BIKINI ATOLL: BPBM 12354 (310 mm), Eman I., V. Brock et al., 18 June 1947. LINE IS.: CAS 48825 (302 mm), Palmyra I., E. Herald et al., 16 Aug. 1951. BPBM 7715 (2; 310–393 mm), Cooper I., J. Randall, 13 Nov. 1968. HONG KONG: CAS 48821 (3; 79–88 mm), Santa Cruz Is., Vanikoro I., R. Bolin, 30 Sep. 1958. INDONESIA: BPBM 20890 (2; 103–383 mm), Bali, Sanur Beach, J. Randall, 18 July 1977. THAILAND: BPBM 22827 (460 mm), Similan I., Ko Miang, J. Randall, 14 Feb. 1979. PHILIPPINES: CAS 48824 (2; 508–518.5 mm), Negros Oriental, D. Empero, 28 July 1958.

DIAGNOSIS.—A moderate-length species of *Gymnothorax* with anus before midbody; tubular anterior nostrils; uniserial jaw and vomerine teeth; and cream body coloration with 17–21 distinctive brown bands encircling head and body and extending onto fins.

DESCRIPTION OF HOLOTYPE (followed parenthetically by mean and range of the condition of holotype and nine paratypes).—Greatest depth

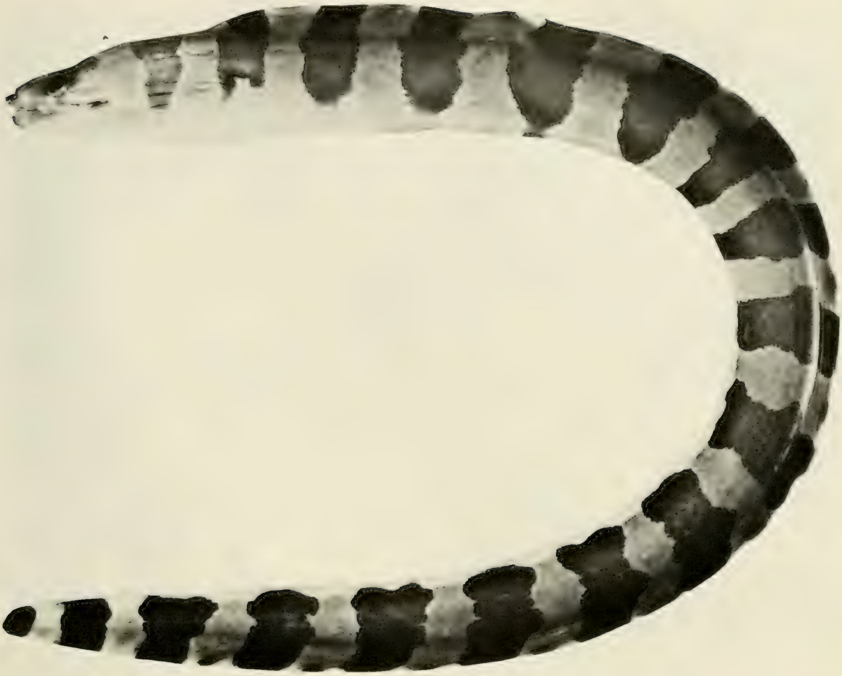


FIGURE 2. *Gymnothorax rueppelliae,* BPBM 18412, 339 mm TL, from Enewetak.

of body 16.8 (19.0; 15.4–22.7) times in total length (TL). Tail longer than body, its length 1.76 (1.76; 1.71–1.82) in TL. Head 7.94 (7.69; 7.19–8.19) and trunk 3.26 (3.30; 3.19–3.55) in TL. Dorsal fin low, its origin ahead of gill openings, arising above fourth vertebra. Snout 6.37 (5.76; 5.29–6.37), upper jaw 3.01 (2.78; 2.65–3.01) times in head length (HL). Eye 9.5 (9.4; 8.3–10.4) in HL and 1.5 (1.63; 1.4–1.9) in snout, closer to rictus than to tip of snout. Fleshy interorbital width 7.8 (8.4; 7.7–9.9) in HL. Gill openings nearly horizontal, their centers slightly below midbody, their length about equal to diameter of eye.

Anterior nostril tubular, elongate, slightly less than eye diameter in length. Posterior nostril a hole above eye, beginning in a line with eye.

Jaws subequal, the mouth closing completely. Teeth in jaws uniserial, stout, pointed and slightly retrorse. Six pairs of intermaxillary canines form a U-shaped margin around three central canines, the third the largest. Approximately six uniserial, small vomerine teeth. About 12 upper jaw teeth pairs, 18 lower jaw pairs; 3 pairs of depressible canines behind mandibular symphysis.

Number of vertebrae 130 (129.7; 128–131), 50.5 (50.8; 50–51.5) before anal fin. First dorsal pterygiophore arises above fourth vertebra.

Head pores present but not obvious. A single pore anterior and proximal to, and a second pore below base of anterior nostril. Six pores along the mandible, the second through fifth the largest. Four equally spaced pores along upper jaw, the first beneath nostril base, the last beneath rear of eye. A single pore between anterior and posterior nostrils.

Color in isopropyl alcohol cream, overlain with 17–21 distinctive brown bands which completely encircle head and body and extend onto

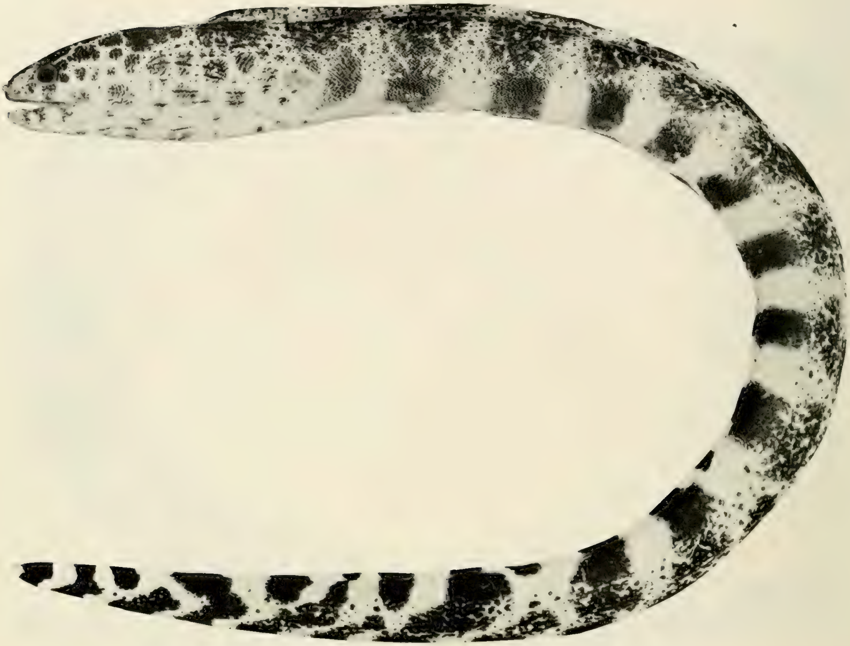


FIGURE 3. *Gymnothorax reticularis*, BPBM 18734, 492 mm TL, from Hong Kong.

median fins. The light interspacing of large individuals becomes mottled. The first brown band begins mid-snout, ends at the hind margin of the eye, and is continuous with lower jaw. The second begins at the rictus. Tail tip and anterior nostrils not dark, like body coloration. Bleeker's *Atlas* (1864: pls. 177 and 183, as *G. reticularis*) contains excellent illustrations showing juvenile and adult colorations.

DISTRIBUTION.—On the basis of our specimens, field records, and valid literature records, the new species is known to range widely within the central and western Pacific (excluding Hawaii and Australia) and Indian oceans to Aldabra and the Seychelles. Red Sea records (Günther 1910; Fowler 1956) are based on Klunzinger's (1871) misidentification of specimens of *G. rueppelliae*.

ETYMOLOGY.—Named *enigmaticus*, from the Latin *aenigma*, in the light of the nomenclatural confusion surrounding this species.

REMARKS.—Some recent authors have divided *Gymnothorax* into *Lycodontis* for those morays without serrated lateral jaw teeth, and *Gymnothorax* for those with serrated lateral jaw teeth. We conservatively recognize only *Gymnothorax* because species intermediate in this condition exist.

Two common Indo-Pacific species of *Gymnothorax* share a distinctive brown banding. These were treated by most recent authors as *G. petelli* (Bleeker, 1856) and *G. rupelli* (McClelland, 1845).* On examining the holotypes, the junior author (Randall 1973) discovered that they were both the *G. "petelli"* form. Thus, *G. petelli* was placed in the synonymy of *G. rueppelliae*, and the species described herein lacked a name. Following Schultz (*in* Schultz et al. 1953), Randall (1973) suggested that *G. reticu-*

---

* McClelland's species was named *Dalophis Rüpelliae*, properly *rueppelliae* (fide McCosker and Rosenblatt 1975), but has been variously and improperly emended to *rupelli, ruppeli, ruppelli,* and *ruppellii*.

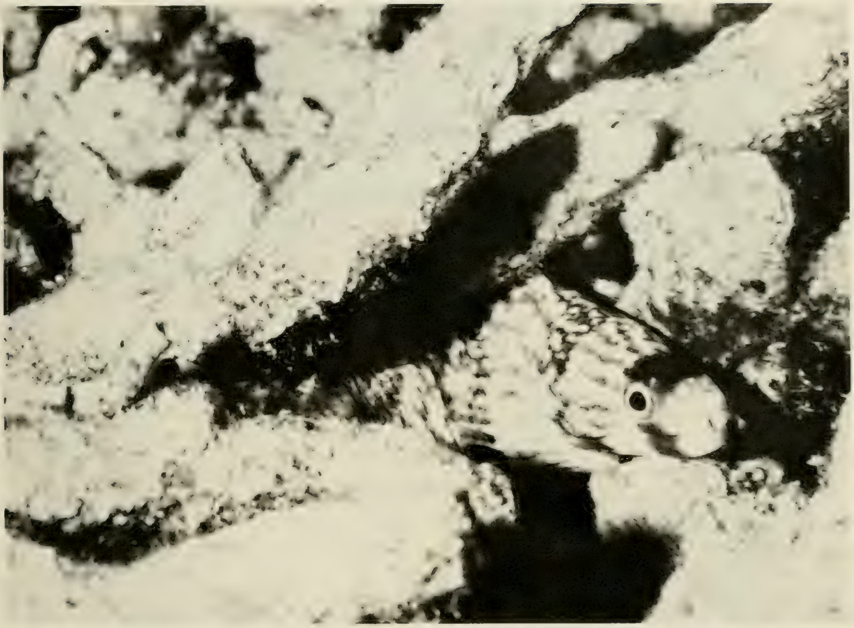


FIGURE 4. Underwater photograph of adult *Gymnothorax enigmaticus* taken at night by J. E. Randall, depth ca. 1 m, Sumilon Island, Philippines.

laris Bloch, 1795, was the next available name, but McCosker and Rosenblatt (1975) pointed out that it is a valid and different species. We have subsequently examined the 395-mm holotype (SMF 151) of *Dalophis Rüpelliae* and compared it to other Indo-Pacific specimens of the "*petelli*" form. It is in excellent condition and clearly conspecific. It has 135 vertebrae, with 50 preanal and 4 before the first dorsal pterygiophore.

Dr. Wolfgang Klausewitz has brought our attention to *Muraena umbrofasciata* Rüppell, 1852, an obscure species which has not been reported since its description. On the basis of McClelland's type-specimen of *Dalophis Rüpelliae* and two specimens from India (SMF 2870, SMF 7346) received by Rüppell in 1845 from M. Boissenau, Rüppell (1852:33) described *M. umbrofasciata,* which we herein recognize as a synonym of *Gymnothorax rueppelliae.*

Smith's (1962:434) suggestion that *Gymnothorax signifer* Bliss, 1883, was a synonym of *G.* "*ruppelli*" prompted us to examine the holotype, a 180-mm specimen from Mauritius. Its chin, throat, and anterior trunk bands are discontinuous, and it is clearly a specimen of the "*petelli*" form, *G. rueppelliae.* The holotype of *G. signifer* (MCZ 6147) has 132 vertebrae, 51 preanal; the vertebral range of six specimens of *G. rueppelliae* was 132–135, with a mean of 133.7.

The new species is closely related to *G. rueppelliae* (Fig. 2), and might also be confused with *G. reticularis* (Fig. 3). It differs from *G. rueppelliae* in possessing light, rather than dark, anterior nostrils, in having continuous chin and throat bands, in lacking a black mark at the jaw corner, and in attaining a considerably smaller adult size. It differs from *G. reticularis,* which is heavily spotted in the head and throat regions and lacks the three prominent intermaxillary fangs.

The "*petelli*" form, *G. rueppelliae,* is known from shallow water collections from Hawaii, throughout the Pacific and Indian oceans, and

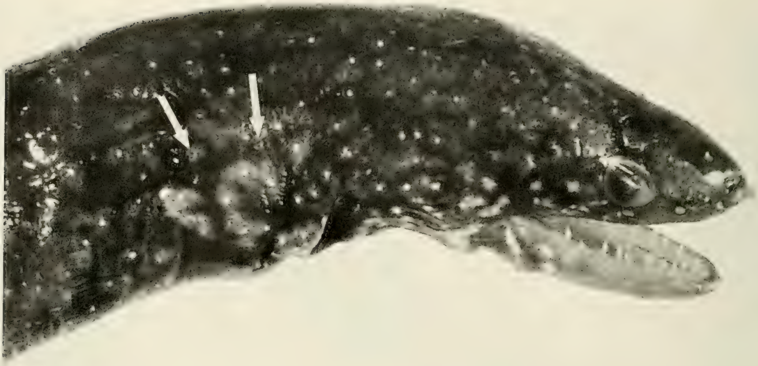


FIGURE 5. *Uropterygius xanthopterus,* CAS 35254, 245 mm TL, from Kapingamaringi, displaying white cephalic punctations. Arrows indicate the location of the anterior lateral line pores.

the Red Sea. Its synonyms also include *Muraena interrupta* Kaup, 1856; *Sideria chlevastes* Jordan and Gilbert, 1883; *Gymnothorax signifer* Bliss, 1883; *G. leucacme* Jenkins, 1904; and *G. waialuae* Snyder, 1904.

Whereas previous literature has suggested that most morays are nocturnal, it now appears that many, and possibly the majority of, moray species are diurnal but rarely observed due to their secretive nature (fide Chave and Randall 1971; Hobson 1974). On the basis of material collected and our observations while diving, we presume that *G. enigmaticus* is a shallow-water, nocturnally active piscivore (Fig. 4). It is noteworthy that *G. rueppelliae* is also a nocturnal predator (Hobson 1974, as *G. petelli*), as is *G. undulatus* (our observations), both of which are also strongly banded species.

Uropterygius xanthopterus Bleeker, 1859

Uropterygius xanthopterus Bleeker, 1859, has had a sketchy taxonomic history. We have located the type-specimen, recognize it as a valid species, and include *U. alboguttatus* Smith, 1962, in its synonymy.

Weber and de Beaufort (1916:397), without comment, included *U. xanthopterus* in the synonymy of *Gymnomuraena marmorata* Lacépède, 1803, a wide-ranging, elongate Indo-Pacific species of *Uropterygius* which possesses a single anterior lateral line pore and lacks white spotting on its head. Schultz (*in* Schultz et al. 1953:154) and Gosline (1958:226), on the basis of central Pacific specimens, recognized *U. xanthopterus* as a distinct small species (the largest of 213 specimens from 76 CAS rotenone collections in the Indian and central Pacific oceans which we examined was 345 mm) which possesses two anterior lateral line pores and white cephalic punctations (Fig. 5). Smith (1962:427) again synonymized *U. xanthopterus* with *U. marmoratus* and described *U. alboguttatus* on the basis of Indian Ocean and Schultz's central Pacific specimens. In describing *U. kamar* McCosker and Randall, 1977, we considered *U. alboguttatus* to be a possible synonym of *U. xanthopterus*. One of us (JEM) has subsequently examined the complete type-series of *U. alboguttatus* and was unable to find differences in coloration, meristic features, or morphometry.

The type-specimen of *U. xanthopterus* has not been clearly identified; however, through correspondence with Alwyne Wheeler, we have located the 275-mm specimen in the British Museum (cat. no. 1867.11.28.271) received from Bleeker and labeled "*Muraena xanthopterus.*" In that no specimen similar to Bleeker's type exists in the Rijksmuseum (M. Boeseman, in litt.), we presume that this is the type, and the specimen which Bleeker illustrated and described in his *Atlas* (1864:pl. CLXIV, fig. 4). A radiograph of the British Museum specimen clearly indicates that it is not *U. marmoratus,* a species which possesses obvious, large intramuscular bones.

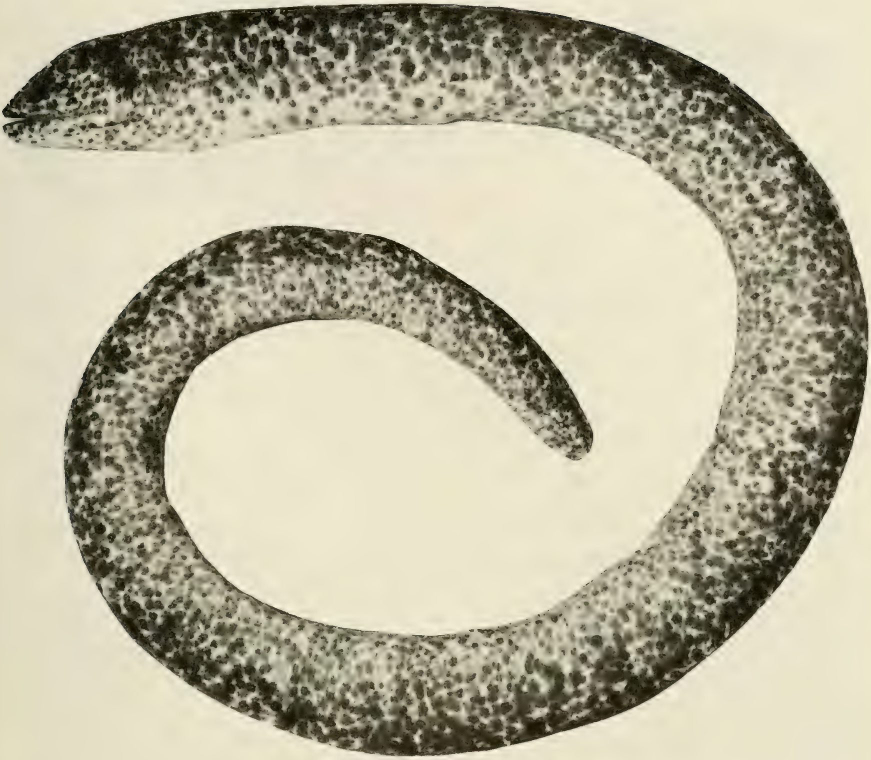


FIGURE 6. *Uropterygius marmoratus*, BPBM 12336, 701 mm, Nuku Hiva, Marquesas.

FAMILY OPHICHTHIDAE

Ophichthus retifer Fowler, 1935

Fowler (1935) described and illustrated *Ophichthus retifer* on the basis of a 718-mm specimen from Durban, Natal. Eugenie Böhlke has kindly examined the holotype (ANSP 63915) for us and compared it with a syntype (ANSP 26224) of *O. erabo* (Jordan and Snyder, 1901) from Japan. They do not significantly differ in coloration or proportions, yet there is a vertebral difference. A radiograph of the holotype of *O. retifer* shows 143 vertebrae, with 73 before the anal opening. McCosker (1979) reported that six specimens of *O. erabo* from Japan, Hawaii, and Taiwan had 152–155 vertebrae ($\bar{x}$ = 154). Fowler (1935) suggested that *O. retifer* was "greatly like *Microdonophis fowleri* Jordan and Evermann 1903" (=*O. erabo* fide McCosker 1979) "and its synonym *Ophicthys garretti* Günther 1910" (a valid species). We consider *O. retifer* to be conspecific with *O. erabo*, and account the vertebral difference to clinal variation.

ACKNOWLEDGMENTS

We thank the following individuals: Susan Middleton for photographic assistance; Michael Hearne for the preparation of the radiographs; M. Boeseman (Rijksmuseum van Natuurlijke Historie), Eugenie and James Böhlke (ANSP), William Fink (MCZ), W. Klausewitz (SMF), Margaret M. Smith (RUSI), and Alwyne Wheeler (BMNH), for assistance with museum specimens and records; Lillian Dempster and W. I. Follett (CAS) for nomenclatural advice; and the

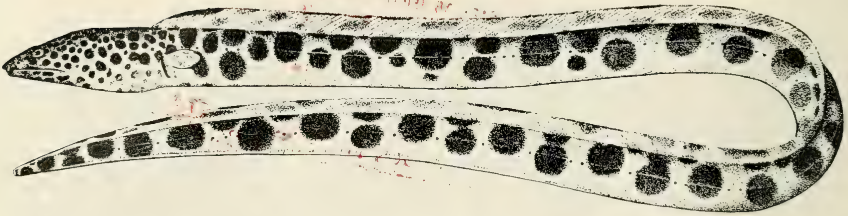


FIGURE 7. Adult *Ophichthus erabo,* from Jordan and Snyder (1901).

curators and staffs of many museums for allowing us to examine specimens under their care. Randall's collections were made possible in part by grants from the National Geographic Society and the American Philosophical Society. A portion of McCosker's work was supported by funds from the Charline Breeden Foundation.

LITERATURE CITED

BLEEKER, P. 1859. Over eenige vischsoorten van de Zuidkustwateren van Java. Nat. Tijdschr. Neder.-Indië 19:329–352.

———. 1864. Atlas ichthyologique des Indes Orientales Néerlandaises. Vol. 4. Amsterdam. 132 p.

BLISS, R. 1883. Descriptions of new species of Mauritian fishes. Trans. Soc. Roy. Arts Sci., Maurice 13:45–63.

BLOCH, M. E. 1795. Naturgeschichte der Auslandischen Fische. Vol. 9.

CHAVE, E. H., AND H. A. RANDALL. 1971. Feeding behavior of the moray eel, *Gymnothorax pictus.* Copeia 1971 (3):570–574.

FOWLER, H. W. 1935. South African fishes received from Mr. H. W. Bell-Marley in 1935. Proc. Acad. Nat. Sci., Philadelphia 87:361–408.

———. 1956. Fishes of the Red Sea and southern Arabia. 1. Branchiostomida to Polynemidae. Weizmann Sci. Press, Jerusalem. 240 p.

GOSLINE, W. A. 1958. Central Pacific eels of the genus *Uropterygius,* with the descriptions of two new species. Pac. Sci. 12(3):221–228.

GÜNTHER, A. 1910. Andrew Garrett's Fische der Südsee, . . . Heft IX. J. Mus. Godeffroy, Hamburg 17:389–515.

HOBSON, E. S. 1974. Feeding relationships of teleostean fishes on coral reefs in Kona, Hawaii. Fish Bull., U.S. 72(4):915–1031.

JENKINS, O. P. 1904. Report on collections of fishes made in the Hawaiian Islands, with descriptions of new species. U.S. Bur. Fish. Fish. Bull. 22:417–511.

JORDAN, D. S., AND C. H. GILBERT. 1883. Description of a new muraenoid eel from the Galapagos Islands. Proc. U.S. Natl. Mus. 6:208–210.

———, AND J. O. SNYDER. 1901. A review of the apodal fishes or eels of Japan, with descriptions of 19 new species. Proc. U.S. Natl. Mus. 23:837–890.

KAUP, J. 1856. Uebersicht der Aale. Arch. Naturges. 22(1):41–77.

KLUNZINGER, C. B. 1871. Synopsis der Fische des Rothen Meeres. II. Theil. Verh. Zool.-Bot. Ges. Wien 21:441–668.

MCCLELLAND, J. 1845. Apodal fishes of Bengal. J. Nat. Hist. Calcutta 5:150–226.

MCCOSKER, J. E. 1979. The snake eels (Pisces, Ophichthidae) of the Hawaiian Islands, with the descriptions of two new species. Proc. Calif. Acad. Sci., ser. 4, 42(2):57–67.

———, AND J. E. RANDALL. 1977. Three new species of Indo-Pacific moray eels (Pisces: Muraenidae). Proc. Calif. Acad. Sci., ser. 4, 41(3):161–168.

———, AND R. H. ROSENBLATT. 1975. The moray eels (Pisces: Muraenidae) of the Galapagos Islands, with new records and synonymies of extralimital species. Proc. Calif. Acad. Sci., ser. 4, 40(13):417–427.

RANDALL, J. E. 1973. Tahitian fish names and a preliminary checklist of the fishes of the Society Islands. Occ. Pap. Bernice P. Bishop Mus. 24(11):167–214.

RÜPPELL, W. P. E. S. 1852. Verzeichniss der in dem Museum der Senckenbergischen . . . Fische und deren Skelette. Frankfurt-a-M.

SCHULTZ, L. P., AND COLLABORATORS. 1953. Fishes of the Marshall and Marianas islands. Families from Asymmetrontidae through Siganidae. U.S. Natl. Mus. Bull. 202, 1. 685 p.

SMITH, J. L. B. 1962. The moray eels of the western Indian Ocean and the Red Sea. Ichthyol. Bull. Rhodes Univ. 23:421–444.

SNYDER, J. O. 1904. A catalogue of the shore fishes collected by the steamer "Albatross" about the Hawaiian Islands in 1902. U.S. Bur. Fish. Fish. Bull. 22:513–538.

WEBER, M., AND L. F. DE BEAUFORT. 1916. The fishes of the Indo-Australian Archipelago. Vol. 3. Leiden. 455 p.

PROCEEDINGS
OF THE
CALIFORNIA ACADEMY OF SCIENCES

Vol. 43, No. 3, pp. 27–42 June 15, 1982

NEW SPECIES OF NORTH AMERICAN *TACHYSPHEX* WASPS (HYMENOPTERA, SPHECIDAE)

By
Wojciech J. Pulawski
California Academy of Sciences, Golden Gate Park,
San Francisco, California 94118

ABSTRACT: **The following new North American species of *Tachysphex* are described (type-localities are given in parentheses): *acanthophorus* (Arizona: Willcox), *apricus* (California: Borrego Valley), *arizonac* (Arizona: 2 mi. NE Portal), *armatus* (Nevada: Sandy), *bohartorum* (California: Boca), *idiotrichus* (Arizona: 5 mi. W Portal), *irregularis* (California: Hallelujah Junction), *krombeiniellus* (Florida: Levy County), *lamellatus* (Mexico: Sonora: Alamos), *menkei* (California: Borrego Valley), *mirandus* (California: Palm Springs), *musciventris* (California: Borrego), *occidentalis* (California: 12 mi. E Lone Pine), *papago* (Arizona: Nogales), *solaris* (California: Borrego Valley), *spatulifer* (California: Arroyo Seco Camp), *verticalis* (California: 9 mi. W Beaumont), *yuma* (Mexico: Baja California: La Paz), and *yolo* (California: Davis).**

INTRODUCTION

For several years, I have been working on a monographic revision of North American *Tachysphex*. Because of the size of this undertaking, it will be some time before it is finished. Therefore, I am describing some of the new species now so their names will be available to those persons working on *Tachysphex* behavior. Furthermore, many hundreds of paratypes have been deposited in 34 collections in the USA and abroad, and it is desirable to validate these manuscript names now to avoid their possible use as nomina nuda in the works of others. The descriptions given below are restricted to those features which enable unambiguous recognition of each species. More complete characterizations will be given when my revision is published.

The terminology used below is based mainly on Bohart and Menke (1976). A few terms which need clarifications are the following:

clypeus: the clypeus has a midsection and two lateral sections; the midsection usually has a densely punctate, setose basomedian area, a sparsely punctate shiny bevel, and a marginal lip.
scutum: this term is used here for brevity's sake instead of mesoscutum.
tergum, sternum: short terms for gastral tergum, gastral sternum.

Many collectors are cited numerous times in the lists of material examined. Their names have been abbreviated to initials, as follows: ASM, A. S. Menke; BV, B. Villegas; DRM, D. R. Miller; EEG, E. E. Grissell; EIS, E. I. Schlinger; GEB, G. E. Bohart; GDB, G. D. Butler; FDP, F. D. Parker; FGW, F. G. Werner; FXW, F. X. Williams; HKC, H. K. Court; JCH, J. C. Hall; JAP, J. A. Powell; JMD, J. M. Davidson; JWMS, J. W. MacSwain; LAS, L. A. Stange; MAC, M. A. Cazier; MEI, M. E. Irwin; MSW,

M. S. Wasbauer; PDH, P. D. Hurd; PMM, P. M. Marsh; PFT, P. F. Torchio; RCB, R. C. Bechtel; RMB, R. M. Bohart; ROS, R. O. Schuster; RRD, R. R. Dreisbach; TG, Terry Griswold; WJP, W. J. Pulawski.

In the geographic names below, the following words have been abbreviated: County, Co.; Creek, Cr.; Highway, Hwy.; Island, I.; miles, mi.; Mountain(s), Mt(s).; River, R.; Station, Sta. The name Lower California has been used for the peninsula rather than Baja California, because the latter may refer either to the peninsula or to a state in Mexico. Altitudes and distances are given as they appear on the original labels—in feet and miles. Multiplying the distances in miles by 1.609 and the elevations in feet by 0.3048 will convert them into kilometers and meters, respectively.

SOURCES OF MATERIAL AND ACKNOWLEDGMENTS

The specimens described in this paper came from institutional and private collections listed below. The initials preceding the names are the abbreviations by which institutions or private collections are referred to in the text.

AMNH: American Museum of Natural History, New York, New York (M. Favreau)
ANSP: Academy of Natural Sciences of Philadelphia, Philadelphia, Pennsylvania (D. C. Rentz)
ASU: Arizona State University, Department of Zoology, Tempe, Arizona (F. F. Hasbrouck)
BMNH: British Museum (Natural History), London, England (C. R. Vardy)
CAS: California Academy of Sciences, San Francisco, California (P. H. Arnaud, Jr., T. J. Zavortink, W. J. Pulawski)
CIS: California Insect Survey, Division of Entomology, University of California, Berkeley, California (H. Daly)
CNC: Canadian National Collections of Insects, Arachnids and Nematodes, Biosystematics Research Institute, Ottawa, Ontario (J. R. Barron)
CSDA: California Department of Food and Agriculture, Sacramento, California (M. S. Wasbauer)
CSU: Colorado State University, Department of Zoology and Entomology, Fort Collins, Colorado (H. E. Evans)
CU: Cornell University, Department of Entomology and Limnology, Ithaca, New York (L. L. Pechuman)
FSCA: Florida State Collections of Arthropods, Gainesville, Florida (E. E. Grissell)
HKT: H. K. Townes, American Entomological Institute, Ann Arbor, Michigan
INHS: Illinois State Natural History Survey, Urbana, Illinois (W. E. LaBerge)
KU: University of Kansas, Snow Entomological Museum, Lawrence, Kansas (G. W. Byers)
KVK: K. V. Krombein, Arlington, Virginia (private collection), now in USNM
LACM: Natural History Museum of Los Angeles County, Los Angeles, California (R. R. Snelling)
MCZ: Museum of Comparative Zoology at Harvard University, Cambridge, Massachusetts (J. Lawrence, J. C. Scott, M. K. Thayer)
MPM: Milwaukee Public Museum, Milwaukee, Wisconsin (J. K. Lawton)
NYSU: New York State University, College of Environmental Sciences and Forestry, Department of Environmental and Forest Biology, Syracuse, New York (F. E. Kurczewski)
OSDA: State of Oregon Department of Agriculture, Salem, Oregon (R. L. Westcott)
OSU: Oregon State University, Department of Entomology, Corvallis, Oregon (P. Oman, G. R. Ferguson)
TG: Terry Griswold, % Bee Biology & Systematics Laboratory, Utah State University, Logan, Utah (private collection)
UAE: University of Alberta, Department of Zoology, Edmonton, Alberta (A. L. Steiner)
UAT: University of Arizona, Department of Entomology, Tucson, Arizona (F. G. Werner)
UCD: University of California, Davis, Department of Entomology, Davis, California (R. M. Bohart, R. O. Schuster)
UCR: University of California, Riverside, Department of Biological Control, Riverside, California (S. Frommer)
UFG: University of Florida, Department of Entomology and Nematology, Gainesville, Florida (B. Saffer)
UGA: University of Georgia, Department of Entomology, Athens, Georgia (R. W. Matthews, C. L. Smith)
UIM: University of Idaho, Department of Entomology, Moscow, Idaho (W. F. Barr)
UMSP: University of Minnesota, Department of Entomology and Zoology, St. Paul, Minnesota (P. J. Clausen)
USNM: United States National Museum of Natural History (Smithsonian Institution), Washington, D.C. (A. S. Menke, K. V. Krombein)
USU: Utah State University, Department of Zoology, Logan, Utah (G. E. Bohart, F. D. Parker, Terry Griswold)
WJP: Wojciech J. Pulawski, % California Academy of Sciences, San Francisco, California (private collection)
WSU: Washington State University, Department of Entomology, Pullman, Washington (M. T. James, R. Zack)

I express my sincere thanks to the curators and other persons who kindly submitted specimens for study. I feel especially indebted to R. M. Bohart, A. S. Menke, K. V. Krombein, and F. F. Kurczewski who helped me in many ways.

SPECIES GROUPS

Sixteen species groups are recognized in *Tachysphex* (see Pulawski 1971, 1974, 1977), but only four of them are represented in North America. They are: the *pompiliformis, terminatus, brullii,* and *julliani* groups. The species described in this paper belong to the *pompiliformis* and *brullii* groups which are defined as follows:

The *pompiliformis* group lacks peculiarities which characterize other groups and thus possibly is a heterogenous assemblage of convenience. The propodeal hindface in this group is inclined, the female pygidial plate is not broadened and without peculiar microsculpture, the preapical bristles on the female gastral segments are not thickened, and the male sterna are pruinose (except in *mirandus*). By comparison, in the *julliani* group the propodeal hindface is vertical or nearly so, male sterna are glabrous or sparsely pruinose, and in the females of most species the preapical bristles of gastral segments IV and V are thickened, and the pygidial plate is broadened or has a peculiar microsculpture. The vertex is simple in the *pompiliformis* group, while in the *terminatus* group a swelling is present behind each hindocellus. Unlike the *brullii* group, the apical female tarsomeres are simple (see that group for details). The *pompiliformis* group is cosmopolitan. Its species prey upon acridid nymphs, but the Palearctic species *fulvitarsis* collects tettigonids. The following new species are members of the *pompiliformis* group: *apricus, arizonac, bohartorum, idiotrichus, irregularis, lamellatus, mirandus, musciventris, occidentalis, papago, solaris, spatulifer, verticalis, yolo,* and *yuma*.

The *brullii* group is characterized by the peculiar apical female tarsomeres: dorsum convex, apicoventral margin produced into a lobe or at least convex, and vertex variously modified (covered with erect setae except glabrous basally, or angulate basally in lateral view, or densely spinose). In other groups the dorsum is scarcely convex, the apicoventral margin is straight or nearly so, and the venter is evenly covered with setae which are usually inclined (but erect in *verticalis*), and it may have a few spines in some species. Furthermore, the propodeal dorsum setae are erect or inclined backwards in most species of the *brullii* group, but only laterally so in *acanthophorus, alayoi, armatus,* many individuals of *mundus,* and some Australian species. Setae are inclined obliquely cephalad in the Australian species *brevicornis* and in most species of other groups. The *brullii* group is widespread throughout all zoogeographic regions. Some species prey upon tettigonids, while others are blattid collectors. The following new species are members of this group: *acanthophorus, armatus, krombeiniellus,* and *menkei*.

Species of the Pompiliformis Group

Tachysphex apricus sp.n.

Etymology.—The specific name *apricus* is a Latin word meaning exposed to the sun.

Diagnosis.—*Tachysphex apricus* differs from other species of the *pompiliformis* group by the setal pattern of its propodeal dorsum: median setae are inclined cephalad, but the lateral setae are directed obliquely backwards and join apicomesally. Some species of the *brullii* group (e.g., *acanthophorus*) have an identical pattern, but the unspecialized apical female tarsomere of *apricus* is distinctive. The male of *apricus* can be distinguished by the compressed femoral notch whose glabrous bottom forms an obtuse, longitudinal crest. *T. idiotrichus* has a similar crest, but unlike that species the body vestiture is short in *apricus*. Unlike most species of the *pompiliformis* group, the propodeal side of *apricus* is alutaceous, shiny, impunctate or minutely punctate.

Geographic Distribution.—Xeric areas between southern Texas, southern Nevada, and southern California, and also Lower California.

Material Examined.—Holotype: ♂, California, San Diego Co., Borrego Valley, 3 May 1956, P. D. Hurd (UCD).

Paratypes: 38 ♀, 60 ♂, 31 Mar. to 3 July, 10 and 31 Aug., 9 Sep. Specimens for which institution is not indicated below are all in UCD.

United States of America

Arizona. **Cochise:** 6 mi. n Apache, collector unknown (1 ♂, NYSU). **Coconino:** 4.5 mi. e Moenkopi, JMD & MAC (1 ♀, ASU). **Maricopa:** 10 mi. e Gila Bend, GDB (2 ♂); 3 mi. sw Wickenburg, PFT & GEB (1 ♂, USU). **Mohave:** 4 mi. w Chloride, PFT, GEB, FDP (1 ♂, USU); 8 mi. e Mesquite (Nevada), FDP & PFT (1 ♀, USU). **Pima:** Organ Pipe Cactus National Monument, J. L. Sperry (1 ♀, 1 ♂); Tucson, W. Benedict (1 ♀, NYSU), Bryant (1 ♀, 1 ♂, CAS), FDP, LAS (1 ♀, 2 ♂; 1 ♀, WJP). **Pinal:** w Stanfield, GDB & FGW (1 ♀). **Yavapai:** Bloody Basin, collector unknown (1 ♀); 10 mi. nw Congress, FDP & LAS (1 ♀).

California. **Imperial:** Glamis, RMB (1 ♀), FDP (1 ♂); Palo Verde, ROS (1 ♀); Pinto Flat, FXW (1 ♂, CAS). **Inyo:** Antelope Springs, HKC (1 ♀, 5 ♂); Big Pine Cr., RMB (1 ♀), FDP (1 ♂); 2 and 5 mi. e Big Pine, EEG (1 ♀, 1 ♂); Little Lake, BV (1 ♀); 3 mi. w Lone Pine, RMB (2 ♂); Tuttle Cr. (2 mi. sw Lone Pine), JAP (1 ♀, CIS). **Kern:** Kernville, T. R. Haig (1 ♂). **Riverside:** 18 mi. w Blythe, RMB (1 ♂); 3.5 and 4 mi. s Palm Desert, MEI, S. Frommer & R. M. Worley (2 ♀, UCR); San Andreas Canyon, RMB (1 ♂); Shavers Summit, MSW (1 ♀, UCD); San Timoteo Canyon, MSW, R. McMaster (1 ♀, CSDA). **San Bernardino:** 1 mi. s Adelanto, MEI (1 ♂); Colton Hills, TG (2 ♀, TG), Kramer, MSW (2 ♀, 3 ♂, CSDA); 3 mi. s Kramer Junction, MEI (1 ♀); sand dunes 7 mi. sw Kelso, MSW & J. S. Wasbauer (1 ♀, CSDA), Mitchells Caverns, TG (1 ♀, TG), 36 road mi. e Twentynine Palms, TG (1 ♂, TG). **San Diego:** Borrego Valley, RMB (4 ♂; 1 ♀, 2 ♂, USNM), JCH (1 ♂), PDH (4 ♂), G. A. Marsh (1 ♀), EIS (2 ♂; 2 ♂, WJP), MSW (1 ♂, CIS), MSW, J. Slansky (1 ♀, 1 ♂, CSDA), FXW (9 ♂, CAS); Scissors Crossing, J. C. Downey (1 ♀), H. & M. Townes (1 ♂, HKT). **Ventura:** Sespe Canyon, R. W. Sporne (1 ♂).

Nevada. **Clark:** Jean, GEB (3 ♂); 30 mi. s Searchlight, PFT, R. Rust, Youssef (1 ♂, USU).

New Mexico. **Dona Ana:** Las Cruces, RMB (1 ♀, UCD). **Otero:** Alamogordo, collector unknown (1 ♀); Alamo Canyon near Alamogordo, MEI (1 ♂, UCR).

Texas. **Brewster:** Big Bend National Park (Nine Point Draw), W. R. M. Mason (1 ♀, CNC).

MEXICO

Lower California. San Ángel, N. Leppla, JMD, J. Bigelow, M. Bentzien, W. Fox, S. William, MAC (1 ♀, ASU); 16 mi. N Puertocitos, MEI (1 ♀, UCR).

Tachysphex arizonac sp.n.

ETYMOLOGY.—The specific name *arizonac* is an Indian word meaning little spring.

DIAGNOSIS.—*Tachysphex arizonac* is characterized by the well-defined mesopleural punctures, median scutal setae transversely oriented, and sternum I with a horizontal depression apically. The females of *arizonac* and *lamellatus* have a peculiar clypeus whose free margin is undulate; they can scarcely be distinguished from each other. A useful character is the hypostomal carina which is low in *arizonac*, but high in many *lamellatus*. Furthermore, in some *arizonac* the middle projection of the clypeal lip is markedly larger than the sublateral one (projections about equal in *lamellatus*). The male of *arizonac* has a peculiar clypeus: bevel semilunate, lobe forecorner prominent (acutely in some specimens), lip usually with obtuse projection mesally. The clypeus is somewhat similar in *texanus*, but in that species setae are appressed or nearly so beneath the mesopleural scrobe (setae suberect in *arizonac*).

GEOGRAPHIC DISTRIBUTION.—Southern Utah, Arizona, and adjacent areas of California; Sonora State in Mexico.

MATERIAL EXAMINED.—HOLOTYPE: ♂, Arizona, Cochise Co., 2 mi. NE Portal, 26 June 1964, J. M. Puckle, M. A. Mortenson, M. A. Cazier (UCD).

PARATYPES: 13 ♀, 17 ♂, 5 May to 17 July.

UNITED STATES OF AMERICA

Arizona. **Cochise:** Huachuca Mts., FXW (1 ♀, CAS; 1 ♀, 3 ♂, UCD). **Maricopa:** 3 mi. SW Wickenburg, PFT & GEB (1 ♀, UCD). **Pima:** Brown Canyon, Baboquivari Mts., K. W. Radford & W. Patterson (1 ♀, 2 ♂, UAT); Sabino Canyon, Santa Catalina Mts., RMB (1 ♂, UCD), collector unknown (1 ♀, WJP).

California. **Imperial:** Experimental Farm and no specific locality, J. C. Bridwell (3 ♀, 1 ♂, USNM; 2 ♀, 1 ♂, WJP). **Inyo:** Big Pine, N. J. Smith (1 ♂, UCD); Deep Springs, H. Nakakihara (1 ♂, UCR). **Riverside:** Upper Deep Canyon at Horsethief Cr., MEI (1 ♂, UCR).

Utah. **Washington:** Leeds Canyon, G. F. Knowlton, W. J. Hanson, T. H. Hsiao (2 ♀, 2 ♂, USU; 1 ♀, WJP); Santa Clara, FDP & PFT (1 ♂, USU); Toquerville, G. F. Knowlton, W. J. Hanson (1 ♂, USU).

MEXICO

Sonora. Cocorit, FDP & LAS (1 ♂, UCD); La Aduana, FDP & LAS (1 ♂, UCD).

Tachysphex bohartorum sp.n.

ETYMOLOGY.—This species is dedicated to Dr. G. E. Bohart (Logan, Utah) and Dr. R. M. Bohart (Davis, California) who have made extensive contributions to our knowledge of North American *Tachysphex*, and who have also helped me in my studies.

DIAGNOSIS.—Like *pechumani*, the female of *bohartorum* has brassy golden frontal vestiture. The frontal vestiture is also golden in *psilocerus* which has a peculiar upper metapleuron. Unlike *pechumani*, the gaster of female *bohartorum* is all red, the flagellum is all black, the clypeal lip is deeply indented laterally (shallowly in *pechumani*), and the mesothoracic venter is peculiar (the posterior, horizontal part is shorter than the anterior, oblique part); the densely punctate-throughout tergum V is a subsidiary recognition feature. *T. bohartorum* is known from California, Oregon, and Nevada, while *pechumani* occurs in New Jersey and Michigan.

The male of *bohartorum* can be recognized by the closely punctate terga (punctures mainly subcontiguous) combined with the apicomesally impunctate and glabrous sterna II–IV.

Supplementary diagnostic characters of both sexes are: propodeum not ridged (at most the hindface has a few, inconspicuous ridges below); propodeal dorsum with setae appressed mesally, oriented obliquely anterad.

GEOGRAPHIC DISTRIBUTION.—Montane areas of southern Oregon and northern California, also Sierra Nevada.

MATERIAL EXAMINED.—HOLOTYPE: ♀, California, Nevada Co., Boca, 11 July 1961, R. M. Bohart (UCD).

PARATYPES: 90 ♀, 231 ♂, 24 Apr., 8 June to 14 Aug., mainly UCD, also BMNH, CAS, CIS, CNC, CSDA, LACM, MCZ, OSU, TG, UCR, USNM, WJP.

California. **Alpine:** Carson Pass, RMB (1 ♂); Hope Valley, PDH (1 ♂), P. C. Hutchinson (1 ♀); 15 mi. NE Red Lake, EIS (2 ♂); Winnemucca Lake, RMB (1 ♀, 2 ♂), N. J. Smith (2 ♀, 1 ♂); Woodfords, W. W. Middlekauf (3 ♂). **Del Norte:** Little Grayback (NE part of county), JAP (4 ♀, 4 ♂, CIS). **Eldorado:** Meyers, RMB (1 ♂); Tahoe, FXW (3 ♀, 3 ♂); Strawberry Valley, E. C. VanDyke (1 ♀); Echo Lake, W. W. Middlekauf (1 ♀, 1 ♂); Echo Portal, P. H. Arnaud (1 ♀); Echo Pass, C. A. Downing (1 ♀). **Humboldt:** Red Cape Lake, TG

(1 ♀, 1 ♂, TG). **Inyo:** Big Pine Cr., 7500 ft, RMB (1 ♀, 1 ♂); near Mono Pass, 12,000 ft, C. D. MacNeill (1 ♀, CIS). **Lassen:** Bridge Cr. Camp, RCB, RMB, G. Schaefers (6 ♀, 1 ♂); Summit Camp, JWMS (1 ♀). **Mariposa:** Sentinel Dome Cutoff (Yosemite National Park), T. N. Seeno (1 ♀). **Modoc:** Cedar Pass in Warner Mts., JWMS (1 ♀, 2 ♂, CIS), 6000 ft, collector unknown (1 ♀); Warner Mts. 2 mi. NNW Fort Bidwell, D. C. Rentz & C. D. MacNeill (1 ♂, CAS). **Mono:** 11 mi. N Bridgeport, RMB, PMM (3 ♂); East Walker R., 13 mi. NE Bridgeport, MSW & J. S. Wasbauer (2 ♂); Leavitt Meadow, R. L. Usinger (1 ♂, CIS). **Nevada:** Boca, RMB, MEI, PMM, WJP (8 ♀, 11 ♂); Sagehen Cr. near Hobart Mills, RMB, R. C. Blaylock, R. L. Brumley, M. A. Chambers, R. H. Goodwin, EEG, D. S. Horning, PDH, MEI, JAP, WJP, G. Schaefers, R. L. Westcott (15 ♀, 98 ♂). **Placer:** Carnelian Bay (Lake Tahoe), RMB, FDP, WJP, BV (3 ♀, 21 ♂); Tahoe, FXW (1 ♂). **Plumas:** Bucks Lake, EIS (1 ♂); Burks, FXW (1 ♀); Lake Almanor, E. G. Linsley (1 ♂); Meadow Valley, W. H. Nelson (1 ♀); 14 mi. W Quincy, W. Turner (1 ♀, 2 ♂, WSU). **Shasta:** Lake Eiler, C. H. Spitzer (1 ♀); Lassen Peak, 7500 ft, JWMS (1 ♀). **Sierra:** Independence Lake, RMB, R. D. Moon (16 ♀, 51 ♂), BV (1 ♀); Kyburz Flat, RMB (1 ♂); Sierra Buttes, F. J. Montgomery (1 ♀); Sierra Valley, RMB (1 ♂); Sierraville, RMB (1 ♂); Yuba Pass, MEI (1 ♂, UCR). **Siskiyou:** McBridge Springs (3 mi. NNE Mt. Shasta City), C. D. MacNeill (3 ♂); Mount Shasta, JAP (2 ♀), 1 mi. SE Salmon Mt., TG (2 ♂, TG). **Trinity:** Coffee Cr. Ranger Sta., A. J. Mueller (1 ♀), JWMS (1 ♀, CIS). **Tuolumne:** Chipmunk Flat, ASM (1 ♀), JWMS (1 ♀, CIS); Dardanelle, EIS (1 ♀); Sonora Pass, 9–10,000 ft, S. M. Kappos, JWMS (1 ♀, 2 ♂).

Nevada. **Douglas:** Spooners Lake N junction Hwy. 28, P. Adams (2 ♂). **Washoe:** Mount Rose, 6500 ft, RMB (1 ♂).

Oregon. **Jackson:** 8 mi. SE Butte Falls, R. L. Westcott (1 ♀, OSDA). **Klamath:** 15 mi. NE Bly, Schuh & Denning (1 ♀, OSU); Eagle Ridge near Klamath Lake, C. L. Fox (1 ♀); Lake of the Woods, H. A. Scullen (2 ♀). **Lake:** Warner Pass, DRM (1 ♂).

Tachysphex idiotrichus sp.n.

Etymology.—The specific name *idiotrichus* is derived from the Greek words *idios*, own, peculiar, and *trix* (tricho-), hair; with reference to the peculiar vestiture.

Diagnosis.—*Tachysphex idiotrichus* differs from other North American species of the *pompiliformis* group by the unusually long setae on the head, thorax, and femora (the vertex setae, for example, equal 2.2–3.0 midocellar diameters); the large punctures on the middle section of the female clypeus (also basally); the presence of graduli on sterna III–V of the female; and sparsely punctate (except apex) male tergum VII. Subsidiary diagnostic characters are: sparsely punctate vertex; and in the male: vertex width more than twice length (like *pechumani*); presence of graduli on sterna III–VI (like *ashmeadii, glabrior, irregularis*, and *verticalis*); and compressed forefemoral notch (as in *apricus*).

Geographic Distribution.—Low mountains of southwestern Texas, New Mexico, southern Arizona, and southern California south to Jalisco State, Mexico.

Material Examined.—Holotype: ♀, Arizona, Cochise Co., Southwest Research Sta., 5 mi. W Portal, 20 Oct. 1962, Vincent Roth (UCD).

Paratypes: 25 ♀, 11 ♂; 19 Feb. to 30 Nov.

United States of America

Arizona. **Cochise:** 3 mi. E Apache, Rozen & Schrammel (1 ♀, UCD); 2 mi. W Chiricahua National Monument, A. L. Steiner (1 ♀, WJP); NW Portal, O. W. Richards (2 ♀, BMNH); 2 mi. SW Portal, A. L. Steiner (1 ♀, UAE); same data as holotype, except 1 ♀, 19 Feb. 1963 (3 ♀; UCD, USNM, WJP); same locality, MAC & Ordway (1 ♂ AMNH); Sulphur Springs Valley, G. Munson (1 ♀, UCD); 14 mi. W Tombstone, RMB (1 ♀, AMNH; 4 ♀, 2 ♂, UCD; 1 ♂, USNM; 1 ♂, WJP); same locality, FDP (1 ♀, 2 ♂, UCD); 1 mi. SE Willcox, G. I. Stage (1 ♀, CAS). **Pima:** Tucson, M. L. Noller (1 ♀, UAT). **Yavapai:** Cottonwood, R. C. Miller (2 ♀, 1 ♂, UCD); 7 mi. N Cottonwood, R. C. Miller (1 ♂, UCD).

California. **San Bernardino:** Mid Hills (9 mi. SSE Cima), 5400–5500 ft, TG (2 ♀, TG).

New Mexico. **Hidalgo:** Rodeo to Road Forks (1 ♀, UCD). **Otero:** Alamogordo, collector unknown (2 ♀, UCD). **Socorro:** 10 mi. W Socorro, U. N. Lanham (1 ♀, CSU).

Texas. **Pecos:** no specific locality, RMB (1 ♂, UCD).

Mexico

Jalisco. Lagos de Moreno, R. C. Bechtel & EIS (1 ♂, UCD).

Tachysphex irregularis sp.n.

Etymology.—The specific name *irregularis* is a Latin word for irregular, with reference to the mesopleural sculpture.

Diagnosis.—*Tachysphex irregularis* differs from other members of the *pompiliformis* group in having a rugose or punctatorugose mesopleuron. The subsidiary recognition features are: the almost impunctate venter of the female trochanters, and in the male: presence of graduli on sterna III–VI, sternal punctures about as large as those on the mesothoracic venter.

Geographic Distribution.—Western U.S., eastwards to Wyoming and New Mexico.

Material Examined.—Holotype: ♀, California, Lassen Co., Hallelujah Junction, 12 July 1954, G. A. Schaefers (UCD).

Paratypes: 41 ♀, 29 ♂; 16 Apr. to 11 Sep.

Arizona. **Cochise:** 8 mi. NE Apache, PDH, E. G. Linsley (1 ♀, 1 ♂, CIS); 14 mi. W Tombstone, FDP (1 ♂, UCD). **Pinal:** 8 mi. SE Olberg, M. A. Mortenson, JMD, MAC (1 ♀, UCD).

California. **Inyo:** Bishop, F. P. VanDuzee (2 ♀, UCD, WJP). **Lassen:** Hallelujah Junction, RMB, J. E. Gillaspy, C. J. Horning, G. A. Schaefers, F. Morishita, EIS, R. H. James,

R. L. Sisson (11 ♀, 10 ♂; AMNH, MCZ, UCD, USNM, WJP). **Modoc:** 5.5 mi. E Cedarville, V. L. Vesterby (1 ♂, UCD); Hot Cr., RMB & GEB (1 ♀, UCD). **Mono:** Benton Crossing, F. G. Andrews (2 ♀, CSDA). **Nevada:** Boca, RMB (5 ♀, 1 ♂, UCD), MEI (1 ♂, UCD); Sagehen Cr., PDH (1 ♂, UCD). **Sierra:** Sattley, RMB (2 ♂, UCD). **Siskiyou:** Macdoel, J. Schuh (2 ♀, UCD), Hatfield, J. Schuh (1 ♂, UCD); Mt. Shasta City, JAP (1 ♀, UCD); Red Rock, J. Schuh (1 ♀, UCD). **Tuolumne:** Sonora Pass, R. W. Thorp (1 ♀, UCD).

Colorado. **Jackson:** 10 mi. N junction of roads 14 & 40, R. & K. Dreisbach (1 ♀, UCD). **Mineral:** South Clear Cr., TG (1 ♀, TG). **Routt:** 7 mi. E Hayden, J. S. Buckett (1 ♂, UCD).

Idaho. **Canyon:** Nampa, GEB (1 ♀, UCD). **Cassia:** 4 mi. SE Malta, R. L. Westcott (1 ♀, UIM); 5 mi. N Malta, R. A. Mackie (1 ♀, UIM). **Custer:** 2 mi. E Leslie, D. S. Horning (1 ♀, UCD). **Elmore:** 4 mi. E Orchard, A. J. Walz (1 ♂, UIM). **Owyhee:** Silver City, A. R. Gittins (1 ♀, UIM); 17 mi. W Silver City, A. R. Gittins (1 ♀, 1 ♂, UIM).

Nevada. **Elko:** Cobb Cr., 6 mi. SW Mountain City, P. H. Baldwin (1 ♀, UCD). **Humboldt:** Orovada, MEI (1 ♂, UCD), FDP (1 ♀, UCD); Paradise City, P. H. Baldwin (1 ♂, UCD); 15 mi. E Paradise City, collector unknown (1 ♂, WJP). **Washoe:** Reno Hot Springs, C. N. Slobodchikoff (1 ♀, CAS), Sky Ranch near Reno, EIS (1 ♂, UCD).

New Mexico. **Dona Ana:** Las Cruces, Arabella Sanchez (1 ♀, UCD). **Hidalgo:** Rodeo, PDH (1 ♂, UCD), H. V. Weems (1 ♂, FSCA).

Oregon. **Klamath:** Lower Klamath Lake, J. Schuh (1 ♀, UCD).

Wyoming. **Fremont:** Shoshoni, GEB & PFT (1 ♂, USU).

Tachysphex lamellatus sp.n.

ETYMOLOGY.—The specific name *lamellatus* is a Latin adjective derived from *lamella,* with reference to the unusually high hypostomal carina.

DIAGNOSIS.—*Tachysphex lamellatus* has a punctate mesopleuron, median scutal setae transversely oriented, and sternum I apically with a horizontal depression. Several other species share these features. Males of *lamellatus* and *sonorensis* have a triangular or subtriangular clypeal lip and a nondentate inner mandibular margin; unlike *sonorensis,* flagellomeres III and IV of *lamellatus* are about equal in length. Females of *lamellatus* and *arizonac* have a peculiar, undulate-free margin of the clypeal lip, but they cannot be distinguished with certainty from each other. The hypostomal carina is unusually high in some females and most males of *lamellatus,* and the gena adjacent to the hypostoma is ridged in most males. Both features are unique to *lamellatus,* and when present, distinguish the species from all other *Tachysphex.*

GEOGRAPHIC DISTRIBUTION.—New Mexico to southern California, north to southwestern Utah, and Mexico.

MATERIAL EXAMINED.—HOLOTYPE: ♂, Mexico, Sonora, Alamos, 25 Feb. 1963, P. H. Arnaud, Jr. (CAS Type No. 13465).

PARATYPES: 76 ♀, 45 ♂, 2 Jan., 25 Feb. to 15 May (Mexico), 10 Mar. to 25 Oct. (USA). Specimens for which institution is not indicated below are kept in UCD.

UNITED STATES OF AMERICA

Arizona. **Cochise:** Paradise, LAS (1 ♀); Portal, JMD (1 ♀); 5 mi. SW Portal, C. W. Sabrosky (1 ♀, USNM); same locality, M. Stathem (1 ♀); 5 mi. W Portal, V. Roth (1 ♂, NYSU); same locality, collector unknown (1 ♂, NYSU); Ramsey Canyon, Huachuca Mts., R. F. Sternitzky (3 ♂, CNC). **Gila:** Gila R. 3 mi. SW Christmas, FGW (1 ♂, UAT). **Pima:** Baboquivari Mts., Bryant (1 ♀, CAS), A. L. Melander (2 ♀, 1 ♂), K. W. Radford & W. Patterson (7 ♀, 2 ♂, UAT); Elkhorn Ranch, Baboquivari Mts., M. L. Noller, K. Roever (2 ♀, UAT); Madera Canyon, 4400 ft, Santa Rita Mts., HKC (1 ♀), ASM & WJP (1 ♀, WJP), FGW (3 ♀, 1 ♂, UAT); Madrona Ranger Sta., Rincon Mts., M. L. Noller, J. C. Bequaert, H. Elton (2 ♀, 1 ♂, UAT); Molino Camp, Santa Catalina Mts., R. S. Beal (1 ♂, CIS); Sabino Canyon, Santa Catalina Mts., RMB (1 ♀), R. H. & L. D. Beamer, W. LaBerge, C. Llang (1 ♀, KU), A. D. Telford (1 ♀, 1 ♂); Santa Catalina Mts., FGW & GDB (1 ♀); Tucson, Bryant (1 ♀, CAS), FGW, Malaise trap (2 ♀, UAT); 5 mi. N Tucson, FGW & GDB (1 ♀). **Pinal:** Superior, Boyce Thompson Arboretum, FGW, J. Bequaert (1 ♂, UAT). **Santa Cruz:** Florida Canyon (Santa Rita Mts.), D. P. Levin (1 ♀, UIM); Madera Canyon (Santa Rita Mts.), D. P. Levin (1 ♂, UIM); Patagonia, FGW & GDB (1 ♀); Sycamore Canyon, Tumacacori Mts., A. & H. Dietrich (1 ♀, NYSU). **Yavapai:** Irving Power Sta., W Strawberry, O. Flint & ASM (1 ♂, USNM). Also Atascasa Mts. [a mistake for Atasco Mts.?], R. H. Crandall (1 ♀, 1 ♂, USNM).

California. **Inyo:** Darwin Falls, JAP (1 ♂, CIS). **Orange:** Laguna Canyon, MEI (1 ♀, UCR). **San Bernardino:** Cajon Pass, J. E. Gillaspy (1 ♀); Mid Hills (9 mi. SSE Cima), TG (2 ♀, 2 ♂, TG).

New Mexico. **Catron:** Glenwood, RMB (1 ♀). **Luna:** 6 mi. NW Florida, J. S. Buckett, M. R. & R. C. Gardner (2 ♀).

Utah. **Washington:** Leeds Canyon, Malaise trap (2 ♀, 1 ♂, USU).

MEXICO

Chihuahua. 6 mi. S Encinillas, MEI (1 ♀, UCR).

Hidalgo. Jackala, L. D. Beamer (1 ♀, KU).

Puebla. 3 mi. NW Petlalcingo, FDP (1 ♂).

Sinaloa. 9 mi. E Chupaderos, FDP, LAS (1 ♀, 2 ♂); 54 mi. S Culiacán, MEI (7 ♀, 2 ♂, UCR).

Sonora. Alamos, same data as holotype (9 ♀, 17 ♂; CAS, UCD, WJP); La Aduana, FDP, LAS (8 ♀, 1 ♂; 4 ♀, UCR), LAS (4 ♂).

Tres Marias Islands. Maria Magdalena I., H. H. Keifer (1 ♀, CAS).

Tachysphex mirandus sp.n.

ETYMOLOGY.—The specific name *mirandus* is a Latin word meaning wonderful, strange, singular.

DIAGNOSIS.—*Tachysphex mirandus* can be recognized by its peculiar sculpture. In both sexes, the punctures are larger on the lateral clypeal section than on the adjacent frons, although the difference is slight in some specimens. The midfemur (also female forefemur) is alutaceous basoventrally, with only a few, sparse punctures. In the female, terga II–V are alutaceous, glabrous (except somewhat pubescent laterally). The male can also be recognized by the mesally nonpubescent, largely glossy and sparsely punctate sterna II–VI combined with the nondentate inner mandibular margin, triangular clypeal lip, and the nonangular clypeal free margin between the lip and the lateral section. Subsidiary recognition features of both sexes are: mesopleural setae suberect (almost as in *semirufus*); horizontal part of mesothoracic venter in most specimens glossy, sparsely punctate, contrasting with dull, strongly microsculptured mesopleuron.

GEOGRAPHIC DISTRIBUTION.—Xeric areas of Nevada, Arizona, southern California, and Lower California.

MATERIAL EXAMINED.—HOLOTYPE: ♀, California, San Bernardino Co., Palm Springs, 11 Feb. 1958, A. Melander (USNM).

PARATYPES: 17 ♀, 6 ♂, 20 Jan. to 14 Apr.

UNITED STATES OF AMERICA

Arizona. **Mohave:** 4 mi. S Hoover Dam, A. R. Gittins (1 ♂, UIM).

California. **Fresno:** Pinoche, 29 Mar. 1930, E. C. VanDyke (1 ♀, UCD). **Imperial:** 9 mi. W Coyote Wells, 26 Mar. 1961, PDH (1 ♂, CIS); Ocotillo, 22 Mar. 1966, PDH (2 ♀, 1 ♂, CIS); Yuha Desert, 15 Feb. 1948, C. D. MacNeill (1 ♀, CAS). **Kern:** 3 mi. NW Indian Wells, 12 Apr. 1954, J. M. Linsley (1 ♀, CIS); Short Canyon (7 mi. NW Inyokern), 15 Mar. 1955, PDH (1 ♂, CIS). **Los Angeles:** Little Rock, 28 Mar. 1971, RMB (1 ♀, UCD), 22 Mar. 1941, Don Wasem (1 ♀, UCD). **Riverside:** Whitewater, 14 Apr. 1958, H. R. Moffitt (1 ♀, UCD). **San Bernardino:** 5 mi. S Essex, 26 Mar. 1970, EEG & R. F. Denno (1 ♀, UCD); 14 mi. E Newberry, A. E. Michelbacher, 31 Mar. 1964 (1 ♀, CIS). **San Diego:** Borrego Valley, 2 & 11 Apr., RMB (2 ♀; UCD, WJP); Borrego Springs, 30 Mar. 1960, MSW (1 ♂, UCD). **San Luis Obispo:** Cuyama Valley, 30 mi. W Maricopa, 21 Mar. 1931, E. P. VanDuzee (1 ♀, UCD). **Tulare:** Kaweah Power House, 20 Jan. 1972, F. G. Andrews (1 ♀, CSDA).

Nevada. **Nye:** Mercury, N. T. S. [collector ?], 24 Apr. 1961 (1 ♀, USNM), 28 Mar. 1962 (1 ♂, USNM).

MEXICO

Baja California Norte. Diablo Canyon, E face of Sierra San Pedro Martír, 6 Apr. 1973, J. Donohoe (1 ♀, CIS); Upper Cantillas Canyon (Sierra Juárez), 19 Mar. 1967, JAP (1 ♀, CIS).

Tachysphex musciventris sp.n.

ETYMOLOGY.—The specific name *musciventris* is derived from the Latin words *muscus*, moss, and *venter*; with reference to the dense pubescence on the female mesothoracic venter and male sterna.

DIAGNOSIS.—The peculiar mesothoracic venter of the female of *musciventris* is unique among *Tachyspex*: the mesothoracic venter is deeply sunken and densely pubescent along the midline on the posterior (horizontal) half. The mesally notched clypeal lip and the usually red hindleg are additional diagnostic characters.

The males of *musciventris* and an undescribed species have a triangular clypeal lip, ill-defined mesopleural punctures, and velvety pubescent sterna III–VI (integument all or largely concealed). Unlike the other species, the vertex width in *musciventris* is 1.6–2.0 times its length, the vestiture is appressed on the hypoepimeral area, and sternum II is velvety pubescent.

GEOGRAPHIC DISTRIBUTION.—California to southwestern Texas, north to southwestern Utah, south to northwestern Mexico.

MATERIAL EXAMINED.—HOLOTYPE: ♀, California, San Diego Co., Borrego, 2 Apr. 1973, R. M. Bohart (UCD).

PARATYPES: 225 ♀, 216 ♂; 25 Mar. to 15 June, and 16–22 Nov.; mostly UCD, but also AMNH, BMNH, CAS, CIS, CNC, CSDA, OSU, TG, UCR, UIM, USNM, USU, WJP.

UNITED STATES OF AMERICA

Arizona. **Cochise:** Dragoon Mts., GDB & FGW (1 ♀). **Gila:** Globe, GEB (1 ♀). **Maricopa:** 8 mi. S Buckeye, MEI (3 ♂, UCR); Gila Bend, GDB & FGW (1 ♀); 18 mi. S Gila Bend, S. A. Gorodenski, JMD, MAC (1 ♀); 5 mi. N Mesa, A. R. Gittins (1 ♀, UIM). **Mohave:** 8 mi. E Mesquite, Nevada, FDP & PFT (3 ♀); 16 mi. N Wikieup, GDB & FGW (1 ♂). **Pinal:** W Stanfield, GDB & FGW (1 ♂). **Santa Cruz:** Tubac, PFT (1 ♂). **Yavapai:** 18 mi. N Aguila, FDP (1 ♀, USU). **Yuma:** Dateland, GDB & FGW (1 ♀); Ligurta, RMB (1 ♀); 15 mi. N Yuma, MEI, FDP (2 ♀); 22 mi. N Yuma, S. A. Gorodenski, JMD, MAC (1 ♀).

California. **Amador:** 5 mi. E Jackson, W. E. Simonds (1 ♂). **Fresno:** 10 mi. W Coalinga, RMB (1 ♂). **Imperial:** Chocolate Mts., Ogilby Road, 3 mi. S junction Hwy. 78, MSW (1 ♀, CSDA); Fish Cr. Mts., D. F. Hardwick (1 ♀); Glamis, RMB, PMM, FDP (4 ♀, 5 ♂); 3 mi. N Glamis, MJW (5 ♀); Palo Verde, MSW & J. S. Wasbauer, PDH (3 ♀); 3 mi. S Palo Verde, G. Tamaki (1 ♀, CIS); 8 mi. S Palo Verde, C. A. Toschi (1 ♂, CIS). **Inyo:** Wildrose Canyon, ASM (1 ♂). **Lake:** Lucerne, D. J. & J. N. Knull (1 ♀). **Kern:** 14 mi. N Blackwells Cor., C. D. MacNeill (2 ♂, CIS); Iron Canyon (El Paso Mts.), C. A. Toschi (1 ♀, CIS); 19 mi. W Shafter, RMB (1 ♀). **Lassen:** Bridge Cr. Camp, J. E. Gillaspy (1 ♂); Summit Camp, PDH, E. G. Linsley (4 ♂). **Los Angeles:** 2.5 mi. Pearblossom, R. W. Brooks (1 ♀); Little Rock, E. P. VanDuzee (1 ♀). **Modoc:**

Cedar Pass, D. L. Dahlsten (1 ♂). **Monterey:** Monterey, FDP (1 ♀). **Riverside:** Boyd Desert Research Center (4 mi. s Palm Desert), C. A. Toschi (2 ♀, CIS); 18 mi. w Blythe, RMB, D. S. Horning, MEI, FDP, ROS (11 ♀, 28 ♂); 10 mi. NW Cottonwood (Joshua Tree National Monument), PDH (1 ♀, CIS); Deep Canyon (3.5 mi. s Palm Desert), JCH (1 ♀, UCR), C. Wilkinson (1 ♀); 5 mi. s Hemet, RMB (1 ♂); Hwy. 74 × Strawberry Cr., EIS (1 ♀, CIS); Hopkins Well, PDH, E. G. Linsley, JAP (6 ♀, 11 ♂); Indio, J. Wilcox (1 ♀, OSU); Keen Camp in San Jacinto Mts., EIS (1 ♂); Millard Canyon, MEI (1 ♂); 7 mi. w North Palm Springs, TG (1 ♂, TG); Palm Canyon, EIS (1 ♂, UCR); Palm Springs, C. Dammers, 11 Nov. (4 ♀); Pinon Flat in San Jacinto Mts., E. S. Ross (1 ♀); Riverside, JCH (1 ♀, UCR), TG (1 ♂, TG); 4 mi. s Riverside, RCB, EIS (2 ♀, 3 ♂); Shavers Summit, MSW (2 ♀); Strawberry Canyon, W. A. Hunt (1 ♀, UCR); Thousand Palms, RMB, EEG, MEI, PMM, DRM, FDP, W. R. Richards (22 ♀, 51 ♂); 10 mi. E Whitewater RMB (1 ♀, 3 ♂). **San Bernardino:** 13 mi. E Amboy, E. G. Linsley, JWMS (13 ♀, 7 ♂); Baker, F. G. Andrews (1 ♀, UCR); 4 mi. s Baker, MSW & J. S. Wasbauer (1 ♀, 1 ♂); 3 mi. w Barstow, Brown & Lundgren (1 ♀, CAS); 2 mi. w Cajon Pass, EIS (1 ♂); Colton, E. P. VanDuzee (1 ♀); 5 mi. SE Hesperia, Rozen & Schrammel (2 ♀); sand dunes 7 mi. SE Kelso, MSW (1 ♂); Needles, JWMS (1 ♂); 2 mi. w Phelan, EIS (1 ♂); Red Mountain, D. F. Hardwick (1 ♀); Vidal Junction, PDH (1 ♀). **San Diego:** Alpine, FXW (1 ♂, CAS); Borrego, RMB, C. Goodpasture, EEG, PDH, H. L. McKenzie, A. L. Melander, FDP, R. Snelling, MSW (97 ♀, 56 ♂); Coyote Cr. (Borrego Valley), FDP (1 ♂); Coronado, F. E. Blaisdell (1 ♀); Scissors Crossing, R. R. Pinger (1 ♂). **San Luis Obispo:** 5 mi. w Nipomo, RMB, C. Goodpasture (5 ♂); 10 mi. w Simmler, PDH, R. W. Thorp, C. A. Toschi (4 ♀, 6 ♂, CIS). **Ventura:** Hungry Valley (5 mi. s Gorman), PDH, JAP (7 ♀, 7 ♂).

Nevada. **Clark:** 20 mi. w Glendale, FDP & PFT (4 ♀).

New Mexico. **Dona Ana:** 4 & 11 mi. N Las Cruces, ♀. W. Richards (2 ♀); Mesilla, GEB (1 ♂, UCD).

Texas. **Hudspeth:** Sierra Blanca, J. O. Martin (1 ♀).

Utah. **Washington:** Santa Clara, FDP & PFT (1 ♀, USU).

MEXICO

Lower California. 7 mi. s Guadalupe, MEI (1 ♂, UCR), San Quintín, FXW (1 ♀, CAS).

Sonora. 60 mi. E San Luis, G. R. Ballmer (1 ♀, UCR), 23 km SW Sonoita, B. & C. Durden (1 ♀, AMNH).

Tachysphex occidentalis sp.n.

ETYMOLOGY.—The specific name *occidentalis* is a Latin adjective meaning western; with reference to the geographic distribution of the species.

DIAGNOSIS.—Sternal punctures of male *occidentalis* are well defined, about as large as those of the mesothoracic venter (sometimes markedly larger). Sternal punctures are similar in some other species (e.g., *irregularis, tarsatus*), but the clypeal lobe of *occidentalis* is contrastingly rounded, nonangulate laterally, and the inner mandibular margin is nondentate (or at most with a rudimentary tooth). The usual presence of a foretarsal rake is an additional recognition feature.

The female of *occidentalis* is less distinctive. It is primarily characterized by the combination of the impunctate mesopleuron, nonridged or only finely ridged propodeal side, the suberect setae on the hypoepimeral area, and the evenly arcuate clypeal lip (neither emarginate mesally nor indented laterally). Females of several other species share these features: *apricus, idiotrichus,* some *krombeini, mirandus,* many *semirufus*. Most of them have various prominent diagnostic features which are absent in *occidentalis*. Furthermore, *occidentalis* and some undescribed species have the clypeal free margin less concave between the lobe and orbit than do the other species. Subsidiary recognition feature of female *occidentalis* is the red hindfemur (partly or all) and hindtibia.

GEOGRAPHIC DISTRIBUTION.—Xeric areas west of the Rocky Mountains, north to Oregon and Idaho, south to Arizona and Lower California.

MATERIAL EXAMINED.—HOLOTYPE: ♂, California, Inyo Co., 12 mi. E Lone Pine, 19 May 1970, R. M. Bohart (UCD).

PARATYPES: 53 ♀, 96 ♂, 4 Apr. to 23 July, 3 Aug., 28 Sep. Specimens for which institution is not indicated below are all in UCD.

UNITED STATES OF AMERICA

Arizona. **Apache:** Lukachukai, L. Burroughs, J. Bigelow, MAC (1 ♀, ASU). **Coconino:** 4.5 mi. E Moenkopi, J. H. & J. M. Davidson, MAC (2 ♀, ASU). **Mohave:** 8 mi. NE Mesquite (in Nevada), FDP & PFT (1 ♀, USU). **Navajo:** Jadito Trade Post, same collectors (2 ♀, ASU).

California. **Fresno:** Jacolitos Canyon, RMB (1 ♂). **Inyo:** Antelope Springs, MEI (1 ♀, UCR), 15 mi. s Big Pine, EEG (1 ♂); Deep Springs, D. Giuliani, MSW & J. S. Wasbauer, MSW & J. Slansky (4 ♀, 13 ♂, CSDA; 1 ♂, WJP); same locality, RMB, BV (6 ♂); Lone Pine, N. W. Frazier (1 ♀); 3 mi. N Lone Pine, JAP (1 ♂, CIS); 7.3 mi. w Lone Pine, Ballmer & Bath (1 ♀); 12 mi. NE Lone Pine, RMB, EEG (1 ♀, 6 ♂). **Kern:** 14 mi. w Shafter, RMB (1 ♀). **Lassen:** Hallelujah Junction, MEI (2 ♂, UCR). **Los Angeles:** 1 mi. w Little Rock, E. G. & J. W. McSwain (1 ♂). **Mono:** Chalfant, BV (1 ♂); 7 mi. SW Lee Vining, A. D. Telford (1 ♀). **Monterey:** Arroyo Seco Camp, PT (1 ♂, USU). **Plumas:** Chilcoot, N. B. & W. M. Elliott (1 ♂, NYSU). **Riverside:** Anza, RMB (1 ♂). **San Bernardino:** Cronise Valley, JAP (1 ♂); Cronise Wash 15 mi. E Baker, WJP (1 ♂, WJP); Four Corners, R. W. Thorp (1 ♀, CIS); Kramer Hills, PDH, G. A. Marsh, ROS (3 ♂; 1 ♂, WJP); Yermo, collector unknown (1 ♀, CAS). **San Diego:** Borrego Valley, RMB (1 ♂), WJP (1 ♀, CAS; 1 ♂, WJP); Borrego State Park, MSW & J. S. Wasbauer (1 ♀, CSDA); Scissors Crossing, F. G. Andrews (1 ♀, UCR). **San Luis Obispo:** 10 mi. w Simmler, PDH (2 ♂, CIS).

Idaho. **Cassia:** 2.5 mi. s Malta, R. L. Westcott (1 ♀, UIM). **Franklin:** Preston, GEB (1 ♂, USU). **Fremont:** 6 mi. NW St.

Anthony, D. S. Horning (1 ♀, 3 ♂, UIM), R. L. Westcott (4 ♂, UIM); St. Anthony Sand Dunes, L. S. Hawkins (1 ♂, UIM), R. L. Westcott (1 ♂, UIM), N. B. & W. M. Elliott (5 ♀, 4 ♂, NYSU; 1 ♀, 1 ♂, WJP). **Lincoln:** 4.5 mi. E Dietrich, R. L. Westcott (1 ♀, UIM); Shoshone, R. W. Haegele (1 ♂, UIM).

Nevada. **Churchill:** 12 mi. NE Stillwater, FDP (3 ♂; 1 ♀, 2 ♂, USNM). **Humboldt:** Orovada, MEI (1 ♂); 10 mi. N Winnemucca, RMB (1 ♀). **Lyon:** Fernley, T. R. Haig (1 ♀); Yerington, R. W. Lauderdale (1 ♀). **Washoe:** Nixon, RMB, R. J. Gill, MEI, FDP, J. E. Slansky (8 ♀, 4 ♂), MEI (1 ♀, UCR), R. L. Westcott (2 ♀, 1 ♂, LACM); Patrick, FDP (1 ♀); 15 mi. E Reno, RMB, MEI, FDP (9 ♂); Wadsworth, FDP (2 ♀, 1 ♂); 2.8 mi. W Wadsworth, G. I. Stage (2 ♂, CAS).

Oregon. **Harney:** 21.5 mi. NW Fields sand dunes, R. L. Westcott (1 ♀, OSDA).

Utah. **Duchesne:** 5.5 mi. W Roosevelt, R. W. Thorp (1 ♂, CIS). **Emery:** Goblin Valley, FDP (2 ♀, USU). **Grand:** 25 mi. S Moab, GEB & R. Brumley (1 ♂; 3 ♂, USU; 1 ♂, WJP). **Millard:** 6 mi. N Delta, S. M. Hogue (1 ♀, UIM); 15 mi. N Delta, PFT (1 ♂, USU); 12 mi. NW Fillmore, FDP & Vincent (2 ♂, USU). **Washington:** Santa Clara, GEB (1 ♀, USU).

Wyoming. **Sweetwater:** 20 mi. W Farson, PFT (1 ♂, USU).

Mexico

Lower California. Punta de Cabras (12 mi. W of km 180 S San Thomas), S. & S. Frommer (1 ♂).

Tachysphex papago sp.n.

Etymology.—Named after the Papago Indians of Arizona.

Diagnosis.—Like *psilocerus, papago* has the punctate mesopleuron, metapleuron, and propodeal side (propodeal side impunctate in some *psilocerus*), apicomesally unsculptured terga I and II (smooth part contrasting with remaining surface), and the largely brown or red female flagellum. Unlike *psilocerus,* the upper metapleuron of *papago* is simple, the metapleural flange is narrow, the malar space is absent, and the hindwing base is broad. The presence of erect setae on the midfemoral venter in *papago* (setae length about 1 DOA) is a subsidiary diagnostic feature.

Geographic Distribution.—Southern Arizona.

Material Examined.—Holotype: ♀, Arizona, Santa Cruz Co., Nogales, Apr. 1937, R. C. L. Perkins (BMNH).

Paratypes: Arizona, same data as holotype (1 ♂, BMNH). **Cochise:** 5 mi. W Portal, 7 May 1977, collector unknown (1 ♂, NYSU); 6 mi. W Portal, 7 & 12 May 1973, A. L. Steiner (2 ♀, UAE, WJP).

Tachysphex solaris sp.n.

Etymology.—The specific name *solaris* is Latin adjective meaning of the sun; it refers to the sunny habitats in which the species occurs.

Diagnosis.—Most *solaris* can be recognized by the uniformly yellowish humeral plate of the forewing base (the median plate is usually contrastingly dark), but in some specimens the plate is partly dark. In other species the humeral plate is all dark or with a dark spot at the middle. Subsidiary diagnostic features of *solaris* are: small size (body length 5–7.5 mm); clypeal free margin shallowly concave between lobe and orbit; vestiture largely concealing mesopleural integument; setae oriented mainly transversely on propodeal dorsum; and densely pubescent male sterna.

Geographic Distribution.—Xeric areas of southern California and adjacent areas of Nevada and Arizona.

Material Examined.—Holotype: ♀, California, San Diego Co., Borrego Valley, 20 Apr. 1957, R. C. Bechtel (UCD).

Paratypes: 59 ♀, 26 ♂, 2 Apr. to 17 June.

Arizona. **Mohave:** 8 mi. E Mesquite (Nevada), FDP & PFT (1 ♀, USU). **Pinal:** 5 mi. NW Coolidge, A. D. Telford (2 ♂, UCD). **Yuma:** 6 mi. SE Parker, S. A. Gorodenski, JMD, MAC (1 ♀, ASU); 8 mi. SE Parker, J. H. & J. M. Davidson, MAC (3 ♀, UCD); 15 mi. E Yuma, PFT, FDP, GEB (1 ♀, USU); 18 mi. NE Yuma, FGW & GDB (1 ♂, UCD).

California. **Imperial:** Glamis, F. G. Andrews (1 ♀, CSDA; 1 ♀, WJP); Pinto Wash, FXW (3 ♂, CAS); Palo Verde, RMB (1 ♂, UCR), MSW (1 ♀, 1 ♂, CSDA; 1 ♂, WJP). **Inyo:** 13 mi. S Death Valley Junction, LAS & ASM (1 ♂, UCD); Lone Pine, RMB (1 ♀, UCD); 2 mi. E Lone Pine, RMB (1 ♂, UCD), 15 mi. S Panamint Springs, PDH (2 ♀, 2 ♂, UCD); S end Owens Lake, M. S. & J. S. Wasbauer (3 ♀, CSDA). **Riverside:** 18 mi. W Blythe, FDP (2 ♀, UCD), WJP (23 ♀, 3 ♂, CAS); Hopkins Well, PDH (1 ♀, UCD); Thousand Palms, FDP (1 ♂, UCD). **San Bernardino:** Bagdad, JAP (2 ♂, CIS); Colton Hills, TG (1 ♀, TG), Cronise Valley, FDP (2 ♀, UCD); Kelso, N. J. Smith (1 ♀, UCD); 7 mi. SW Kelso, M. S. & J. S. Wasbauer (1 ♂, CSDA); 10 mi. E Twentynine Palms, collector unknown (1 ♂, CSDA). **San Diego:** Borrego Valley, RCB, JCH, H. R. Moffitt, EIS (6 ♀, 1 ♂, UCD; 2 ♀, USNM; 2 ♀, 1 ♂, WJP); FXW (2 ♀, 2 ♂, CAS).

Nevada. **Clark:** Glendale, FDP & PFT (1 ♀, 1 ♂, USU); 20 mi. W Glendale, FDP & PFT (1 ♀, USU).

Tachysphex spatulifer sp.n.

Etymology.—The specific name *spatulifer* is a combination of the Latin word *spatula,* a broad, flat tool for stirring or mixing, and the suffix -fer, a bearer; with reference to the female clypeus.

Diagnosis.—The female of *spatulifer* has a distinctive clypeus: the lip is broadened mesally, usually variably, obtusely dentate (including one median tooth). The clypeus is somewhat similar in *crenulatus, musciventris, arizonac,* and *la-*

mellatus, but unlike the former two species the clypeal lip of *spatulifer* is not emarginate mesally, and unlike the latter two the middle scutal setae are oriented posterad and the mesopleuron is impunctate.

The male of *spatulifer* shares with *crenulatus* the following diagnostic combination of characters: clypeal lip triangular, middle scutal setae oriented posterad, mesopleuron impunctate, sterna evenly punctate, with nonvelvety pubescence. Unlike *crenulatus*, the trochanteral punctures of *spatulifer* are subcontiguous, the lip corners are usually closer to the orbit than to each other, and often the propodeal side is coarsely ridged, the gastral apex is black, and the frontal vestiture is golden.

Geographic Distribution.—Washington to California, east to southern Idaho and northern Utah.

Material Examined.—Holotype: ♀, California, Monterey Co., Arroyo Seco Camp, 11 May 1959, A. S. Menke (UCD).

Paratypes: 53 ♀, 85 ♂, 10 Apr. to 25 June (California, Idaho, Oregon), 5–11 Aug. (Utah, Washington). Specimens for which institution is not indicated below are kept in UCD.

California. **Alameda:** 1 mi. E Mission Peak, W. W. Middlekauf (1 ♀, 6 ♂; 1 ♂, CIS). **Amador:** Volcano, RMB (1 ♂). **Contra Costa:** Mt. Diablo, RMB (4 ♂; 1 ♂, WJP), J. G. Rozen (1 ♂), collector unknown (1 ♂; 1 ♂, USU); Las Trampas Ridge (W Danville), FXW (1 ♀, 1 ♂, CAS). **Eldorado:** Placerville, GEB (1 ♀), D. J. Burdick (1 ♂, CIS). **Fresno:** Deer Cove Cr., TG (1 ♀, TG); Watts Valley, B. J. Adelson (1 ♀, CIS). **Kern:** Glennville, RMB (2 ♀); Tejon Canyon, E. C. VanDyke (1 ♀); 1 mi. E Woody, JAP, C. A. Toschi (2 ♂, CIS). **Lake:** N. Fork Cache Cr. × Hwy. 20, MEI (1 ♂). **Mariposa:** El Portal, RMB (1 ♂); Indian Flat, RMB (1 ♀). **Mendocino:** Mendocino, S. F. Cook (1 ♀, CIS). **Monterey:** Arroyo Seco Camp, RCB, RMB, D. J. Burdick, HKC, C. Goodpasture, FDP, LAS, PFT, BV (8 ♀, 21 ♂; 2 ♀, 5 ♂, UCR; 2 ♀, 5 ♂, USNM; 4 ♂, USU; 3 ♀, 3 ♂, WJP); Monterey, FDP (1 ♀, 3 ♂). **Napa:** Samuel Springs, RCB (1 ♂). **Placer:** 4 mi. S Rocklin, MSW, P. Adams (1 ♀, 2 ♂, CSDA). **Riverside:** Pinyon Flat, San Jacinto Mts., E. C. VanDyke (1 ♀). **Sacramento:** Folsom, RMB (1 ♀), MSW (1 ♂, CSDA); 10 mi. NE Folsom, MSW (3 ♂); N Sacramento, PDH (7 ♂, CIS). **San Diego:** Sorrento, JAP (1 ♀, CIS). **San Luis Obispo:** 2.5 mi. Creston, C. A. Toschi (1 ♀, CIS); La Panza Camp, 12 mi. NE Pozo, JAP, R. W. Thorp (2 ♀, CIS); Pozo, PDH, JAP, C. A. Toschi (2 ♀, 2 ♂, CIS); 3 mi. E Pozo, S. W. Thorp (1 ♂, CIS); 5 mi. E Santa Margarita, W. S. & E. S. Ross (1 ♀, CAS). **Santa Clara:** Mt. Hamilton, collector unknown (1 ♀); Los Gatos, J. A. Kusche (1 ♀). **Siskiyou:** Windy Camp, TG (1 ♂, TG). **Solano:** Mix Canyon, R. B. & L. S. Kimsey (1 ♂). **Stanislaus:** 3.2 mi. W Hwy. 120 on Evergreen Road, R. W. Brooks (1 ♀). **Tulare:** Camp Wishon, TG (2 ♀, TG); Sequoia National Park, "Ash Mt. R.," EIS (1 ♂); Tule River Indian Reservation, R. P. Allen (1 ♀, CAS); Wood Lake, N. W. Frazier (1 ♀). **Tuolumne:** 4 mi. E Sonora, J. G. Rozen (1 ♀). **Yolo:** Bear Cr. and Cache Cr. junction, ASM (1 ♀); Davis, FDP, EIS (3 ♀, 1 ♂); Rumsey, ASM (1 ♀).

Idaho. **Oneida:** Black Pine Canyon, Malaise trap (1 ♀, 1 ♂, USU).

Oregon. **Umatilla:** Athena, K. Gray & J. Schuh (1 ♀).

Utah. **Cache:** W. Hodges Canyon, Knowlton & Hanson (1 ♀, USU).

Washington. **Pacific:** Nahcotta, collector unknown (1 ♀, CIS).

Tachysphex verticalis sp.n.

Etymology.—The specific name *verticalis* is derived from vertex, which is unusually narrow in this species.

Diagnosis.—*Tachysphex verticalis* resembles many species of the *brullii* group (such as *belfragei* or *mundus*) in having a longer than wide vertex (as long as wide in some females) and a fine thoracic sculpture. Unlike these species, the propodeal dorsum setae of *verticalis* are inclined obliquely anterad, and the female tarsomere V is simple (apicoventral margin not produced into a lobe, claws short, not prehensile). *T. verticalis* differs from other species of the *pompiliformis* group in having a uniformly microareolate, impunctate mesopleuron and propodeal side, and the contrastingly ridged propodeal hindface. The markedly convex middle clypeal section is also distinctive. Like *crenulatus* and *glabrior*, the lip of the female clypeus has two lateral incisions on each side, but unlike these species the vertex has a shiny, median sulcus which extends posterad from the postocellar impression. The male differs from other species of the group by its longer than wide vertex; like *glabrior*, *idiotrichus*, and *irregularis*, sterna III–VI have graduli.

Geographic Distribution.—Northern Mexico, southern Arizona and southwestern New Mexico, California and adjacent areas of northern Nevada; also isolated in Idaho and Utah.

Material Examined.—Holotype: ♀, California, Riverside Co., 9 mi. W Beaumont, 29 July 1957, J. E. Gillaspy (UCD).

Paratypes: 78 ♀, 165 ♂, 24 May to 5 Oct., mostly UCD, but also AMNH, CAS, CIS, CSDA, HKT, KU, LACM, MCZ, NYSU, UAT, UCR, UIM, USNM, WJP.

United States of America

Arizona. **Cochise:** Box Canyon (Chiricahua Mts.), RMB (1 ♀, 6 ♂); Portal, H. & M. Townes (1 ♂); Skelton Canyon, 6 mi. SE Apache, PDH (1 ♂). **Gila:** Gila R. 3 mi. SW Christmas, FGW (2 ♀, 1 ♂). **Pima:** Baboquivari Mts., O. C. Poling (1 ♂); Gates Pass, D. Graham (1 ♀); 2 mi. E Robles Pass, D.

Graham (2 ♀, 1 ♂); Sabino Canyon, GEB, RMB, FDP, LAS (2 ♀, 5 ♂); Tanque Verde, FGW (1 ♂); Tucson, FDP, LAS (2 ♂).

California. **Alameda:** Tesla, J. E. Gillaspy (3 ♀). **Butte:** 1 mi. NE Pulga, R. L. Langston (2 ♂, CIS). **Inyo:** Antelope Springs (8 mi. SW Deep Springs), RMB, HKC, T. H. Gantenbein, EEG, PMM, JAP (1 ♀, 8 ♂, CAS; 1 ♂, CIS; 1 ♀, 10 ♂), JAP, G. I. Stage (3 ♂, CIS); 3 mi. W Big Pine, LAS (1 ♀); Big Pine Cr., RMB, ROS (2 ♂); 10 mi. N Bishop, RMB (1 ♂); Lone Pine Cr., RMB, EEG (2 ♀), Westgard Pass, H. B. Leech (1 ♂, CAS); 4 mi. W Westgard Pass, H. V. Daly (1 ♀, CIS). **Kern:** 2 mi. W Frazier Park, JAP (1 ♂, CIS); Kernville, D. E. Hardy (1 ♂, KU). **Lassen:** Hallelujah Junction, RMB (1 ♂). **Los Angeles:** Camp Baldy, W. A. McDonald (1 ♂, LACM); Crystal Lake Road, RMB (1 ♂); Elizabeth Canyon, EIS (1 ♂); La Crescenta, RMB (1 ♂); Mount Wilson Road, RMB (1 ♀, 1 ♂); Monrovia, R. Rosay (1 ♀); Sangus, collector unknown (1 ♀, NYSU); Santa Susana Pass, MEI (2 ♂); Tanbark Flat, RMB (3 ♂), FXW (1 ♀, 2 ♂, CAS). **Mariposa:** Jerseydale, P. D. Levin (1 ♂, UIM). **Monterey:** Mill Cr. (Santa Lucia Mts.), EIS (1 ♂); Paraiso Springs, L. S. Slevin (2 ♀); 4 mi. S San Ardo, P. E. Paige (2 ♂); 4 mi. W Soledad, G. R. Ballmer (1 ♀, UCR). **Orange:** Upper Trabuco Canyon, E. M. Fisher (1 ♀). **Placer:** Lake Tahoe, collector unknown (1 ♀). **Riverside:** Anza, RCB (1 ♀); Banning, JCH (1 ♀); 9 mi. W Beaumont, J. E. Gillaspy, JCH, H. R. Moffitt (3 ♀, 9 ♂); Pinyon Flat, P. H. Arnaud (1 ♂, CAS); Riverside, JCH (2 ♀, UCR); San Timoteo Canyon, MSW, R. McMaster, A. Hardy, J. Slansky (5 ♀, 12 ♂); Whitewater, M. J. Stebbins (1 ♂). **San Bernardino:** Cajon, RCB, RMB, H. R. Moffitt (5 ♂); Cajon Junction, D. Burnett (1 ♀); Hole-in-the-Wall (Providence Mts.), TG (1 ♂, TG); Mill Cr. Canyon, JCH (2 ♀); Oak Glen, TG (1 ♀, 1 ♂, TG); Upper Santa Ana R., A. L. Melander (1 ♀); Wildwood Canyon, H. R. Moffitt (1 ♂); 3 mi. SE Yucaipa, TG (1 ♂, TG). **San Diego:** Laguna Mts. road, FXW (1 ♂, CAS); La Jolla, K. Corwin, P. Adams (1 ♀, 2 ♂), J. C. Bridwell (1 ♂); Julian, H. R. Moffitt (2 ♂), FXW (1 ♂, CAS); Poway, F. Blaisdell (1 ♂); San Diego, H. E. & M. A. Evans (2 ♀), H. A. Hill (1 ♂); Scissors Crossing, EIS (1 ♂); Sorrento, JAP (1 ♀, CIS); 9 mi. S Warner Springs, RMB (3 ♂). **San Luis Obispo:** Creston, L. E. Guenther (1 ♂); Nacimiento Dam, JAP (1 ♀, CIS); 3 mi. NW Paso Robles, R. L. Langston (1 ♀, CIS). **Santa Barbara:** Bluff Camp (San Rafael Mts.), PMM, FDP (3 ♂); 3 mi. W Cachuma Lake, RMB, P. E. Paige, FDP, J. R. Russel (4 ♂), W. A. Steffan (2 ♀, CIS); Los Prietos, J. S. Buckett (1 ♂), JAP (1 ♂, CIS); Santa Ynez Mts., RMB, PMM, ASM, FDP (6 ♂). **Santa Clara:** San Antonio Valley, 3.5 mi. N Del Puerto Canyon road, JAP (1 ♀, CIS). **Shasta:** Hat Cr. P.O., E. E. Lindquist (1 ♀, CIS); Redding, T. R. Haig (1 ♂). **Stanislaus:** Del Puerto Canyon, RMB, N. J. Smith (3 ♀, 3 ♂), BV (3 ♀, 4 ♂). **Trinity:** Junction City, T. R. Haig (1 ♀, 1 ♂), 3 mi. W Weaverville, DRM (1 ♂, UCD). **Tulare:** Three Rivers, H. R. Moffitt (1 ♂, UCR). **Ventura:** Foster Park, RMB, ASM (2 ♂); Sespe Canyon, PMM, FDP, RMB (3 ♂), W. A. Steffan (1 ♂, CIS). Also: County unknown, Oak Grove, J. Wilcox (1 ♂, OSU).

Idaho. **Owyhee:** 2 mi. SW Murphy, D. S. Horning, DRM (1 ♂).

Nevada. **Douglas:** 3 mi. S Genoa, RMB (1 ♀, 3 ♂); Minden, RCB, RMB (7 ♀, 1 ♂). **Storey:** Geiger Summit, W. H. Lange (1 ♂). **Washoe:** 54 mi. NW Gerlach, FDP (4 ♂).

New Mexico. **Hidalgo:** Granite Gap, 18 mi. N Rodeo, RMB (2 ♀, 3 ♂, AMNH; 3 ♀, 2 ♂, UCD).

Utah. **Grand:** Moab, GEB (1 ♀). **Washington:** Leeds Canyon, G. F. Knowlton (1 ♀, USU).

MEXICO

Lower California. 10 mi. E Bahía San Quintín, FXW (1 ♀, CAS); 4 mi. S La Rumorosa, MEI (1 ♀, 1 ♂, UCR); 4 mi. WSW Miraflores, J. Slansky, M. K. & C. Wasbauer (1 ♀, 2 ♂); San Quintín, FXW (1 ♂, CAS).

Sonora. Cocorit, FDP (1 ♂, UCD).

Tachysphex yolo sp.n.

ETYMOLOGY.—Named after Yolo County, California, where the holotype was collected.

DIAGNOSIS.—*Tachysphex yolo* is characterized by the transversely oriented middle scutal setae, sternum I with a horizontal depression at apex, and the usually punctate mesopleuron (punctures indistinct in some individuals). Other species share this combination of characters, but the female of *yolo* has a distinctive clypeus and sternum II: the dense clypeal punctation attains the lip base laterally, so that the sparsely punctate, apical area does not extend laterad to the lip corner level (its width is about 0.5–0.8 of the lip foremargin); the micropunctation of sternum II is absent along the midline from the base (or near base) to apex. In the other species, the dense punctation does not attain the lip base, and the sparsely punctate, apical area is as wide as the lip or nearly so; and the micropunctation of sternum II is usually absent only from an apicomedian, triangular area. The male resembles *lamellatus* and *sonorensis* in having nonvelvety sternal pubescence, but unlike these species its clypeal lip is not triangular. Unlike most *lamellatus*, the hypostomal carina of *yolo* is not lamelliform, and unlike the male of *sonorensis*, the flagellomeres III and IV are about equal in length. Subsidiary recognition features are: mesopleural punctures subcontiguous, ridges of propodeal side evanescent in many specimens.

MATERIAL EXAMINED.—HOLOTYPE: ♂, California, Yolo Co., Davis, 4 June 1961, F. D. Parker (UCD).

PARATYPES: 312 ♀, 414 ♂, 1 Apr. to 14 Oct. Specimens for which institution is not indicated are all in UCD.

UNITED STATES OF AMERICA

Arizona. **Cochise:** Bowie, A. D. Telford (3 ♀); Willcox, RMB, PDH, D. D. Linsdale (2 ♀, CIS; 10 ♀, 4 ♂; 2 ♀, USNM); 1 mi. S Willcox, FGW, E. Erickson (1 ♀, UAT); 3.5 mi. S Willcox, E. G. Linsley (1 ♀, CIS). **Coconino:** Moenkopi, RMB (1 ♀); 3 mi. SE Moenkopi, ASM & WJP (1 ♂, WJP); 4.5 mi. E Moenkopi, J. M. & M. A. Davidson & MAC (3 ♀, ASU). **Graham:** S side of San Carlos Reservoir, D. & J. Schuh (1 ♂, OSU). **Maricopa:** Gila Bend, GDB (2 ♀); 5 mi. W Gila

Bend, GDB & FGW (1 ♀); 20 mi. S Gila Bend, R. H. & E. M. Painter (1 ♂, UAT); Sentinel, GDB (3 ♀). **Mohave:** 4 mi. W Chloride, GEB, PFT, FDP (3 ♀, 5 ♂, USU); 9 mi. E Oatman, same collectors (5 ♀, 1 ♂, USU); 16 mi. N Wikieup, FGW & GDB (1 ♂). **Navajo:** Jadito Trade Post, J. H. & J. M. Davidson & MAC (1 ♀, ASU). **Pima:** Tucson, GDB (2 ♀, 1 ♂, UAT), G. & A. Ferguson (1 ♀), R. X. Schick (1 ♀, LACM). **Pinal:** 3 mi. W Oracle, FDW, Bequaert, Holler (1 ♂, UAT); Sacaton, A. D. Telford (1 ♀, 1 ♂). **Yavapai:** 8 mi. N Aguila, FDP (1 ♀, USU). **Yuma:** E Aztec, FGW & GDB (2 ♀); Dateland, GDB & FGW (1 ♂); Parker, J. M. & J. H. Davison (1 ♀, 2 ♂); 8 & 18 mi. SE Parker, J. H. & J. M. Davidson & MAC (3 ♀, ASU); 8 mi. SE Parker, S. A. Gorodenski & JMD (1 ♂, ASU), J. Heddock (1 ♀, CIS); 12 mi. S Parker, MAC & M. A. Mortenson (1 ♀, CIS); NW Vicksburg, FGW & GDB (2 ♀, 1 ♂); Yuma, FGW & GDB (1 ♂); 15 mi. E Yuma, PFT, FDP, GEB (1 ♀, USU); 21 mi. N Yuma, MEI (1 ♀).

California. **Alameda:** Arroyo Valle, W. J. Turner (1 ♀, CIS). **Colusa:** 2 mi. E Colusa, MSW (1 ♀). **Eldorado:** Chile Bar, L. W. Quate (1 ♀). **Fresno:** 25 mi. E Fresno, PFT (2 ♂, USU). **Imperial:** Chocolate Mts., Ogilby road, 3 mi. S junction Hwy. 78, MSW (9 ♀, CSDA); Glamis, FDP (1 ♂); 20 mi. E Glamis, FDP (1 ♀); Palo Verde, RMB, EEG, ROS (3 ♀, 2 ♂), MSW (1 ♀, 1 ♂, CSDA); 3 mi. S Palo Verde, C. A. Toschi (1 ♀, CIS); Pinto Flat, FXW (1 ♀, CAS); Pinto Wash, FXW (1 ♂, CAS); 20 mi. W Yuma, PFT & FDP (1 ♀, USU). **Inyo:** Antelope Springs (8 mi. SW Deep Springs), RMB, HKC, T. H. Gantenbein (6 ♀, 3 ♂; 6 ♀, 11 ♂, CAS), PDH (6 ♀, 13 ♂, CIS), JWMS (1 ♀, CIS), JAP (1 ♂, CIS); Big Pine, C. D. Michener (1 ♂, KU); Darwin Falls, RMB, EEG (1 ♀, 1 ♂); 3.5 mi. S Death Valley Junction, N. L. Rump (1 ♀); 13 mi. S Death Valley Junction, LAS (1 ♂); Deep Springs, RMB, BV (2 ♀, 3 ♂), MSW, MSW & J. Slansky (2 ♀, 13 ♂, CSDA; 1 ♂, WJP); Eureka Valley, D. Giuliani (1 ♀, CSDA); 1 mi. N Lone Pine, MEI (1 ♀, 1 ♂, UCR); 2 mi. E Lone Pine, RMB, EEG (2 ♀, 9 ♂); Owens Lake, MSW & F. G. Andrews (2 ♀, CSDA); Panamint Springs, PMM (1 ♀), FDP (1 ♂); Westgard Pass, H. V. Daly (1 ♂, CIS); Wyman Canyon (White Mts.), HKC (1 ♂, CAS). **Kern:** Johannesburg, EIS (1 ♀); Kernville, T. R. Haig (1 ♀). **Lake:** N. Fork Cache Cr. × Hwy. 20, D. Q. Cavagnaro (1 ♀). **Lassen:** Hallelujah Junction, MEI (2 ♂, UCR). **Los Angeles:** Huntington Park, A. Bauman (1 ♀); 8 mi. N Llano, JCH, EIS (3 ♀). **Mendocino:** Navarro, N. B. & W. M. Elliott (4 ♂, NYSU); Navarro R. × Hwy. 128, Hendy Groves State Park, MSW (9 ♀, 13 ♂, CSDA; 1 ♀, 2 ♂, WJP); Robinson Cr. (4 air mi. SW Ukiah), TG (3 ♂, TG). **Monterey:** Fort Ord, HKC (1 ♂, UCD); Monterey, FDP, L. S. Slevin (3 ♂); Soledad, RMB (3 ♂). **Modoc:** Adin Pass, T. R. Haig (1 ♀, CSDA). **Mono:** Benton Inspection Sta., RMB (1 ♂); Paradise Camp, FDP (1 ♂). **Plumas:** Chilcoot, N. B. & W. M. Elliott (1 ♀, 5 ♂, NYSU); Halsted Campground (E. Branch N. Fork Feather R.), P. H. Arnaud (1 ♀, 1 ♂, CAS). **Riverside:** Andreas Canyon, RMB (2 ♂); Anza, RMB (2 ♀, 2 ♂); 8 mi. E Banning, R. R. Snelling (1 ♂, LACM); 9 mi. W Blythe, JWMS (1 ♀, CIS); 18 mi. W Blythe, RMB, JCH, D. S. Horning, FDP (1 ♀, 4 ♂; 2 ♀, WJP), WJP (1 ♂, CAS); 5 mi. N Desert Center, C. D. MacNeill (2 ♀, CIS); 17 mi. E Desert Center, Rosen & Schrammel (1 ♀); 5 mi. S Hemet, RMB (1 ♀); Indio, PDH (1 ♂), MEI (1 ♀, UCR); Joshua Tree National Monument, PFT (2 ♂, USU); Palm Springs, JWMS (1 ♀); 2 mi. E Palm Springs, EIS (1 ♀); Riverside, JCH (1 ♂), EIS (1 ♂, UCR); Temecula, EIS (1 ♂); Thousand Palms, RMB, EEG, H. R. Moffitt, FDP (3 ♀, 9 ♂), W. R. Richards (1 ♀, CNC); Whitewater, JWMS (1 ♀); Wiley Well, RMB (1 ♂). **Sacramento:** Grand I., MSW (1 ♀, CSDA); Sacramento, RMB, FDP (3 ♂), MSW (4 ♂, CSDA); Sacramento (Sacramento R. Levee), MSW (1 ♂), MSW & F. G. Andrews (2 ♂, CSDA). **San Benito:** Pinnacles, PDH (1 ♂, CIS). **San Bernardino:** 1 mi. S Adelanto, MEI (1 ♂); 10 mi. S Adelanto, J. A. Froebe (1 ♂); Bagdad, JAP (1 ♂, CIS); 4 & 14 mi. S Baker, M. S. & J. S. Wasbauer (2 ♂, CSDA); Cottonwood Wash, TG (2 ♀, TG); Cronise Valley, FDP (1 ♀); Cronise Wash (15 mi. E Baker), WJP (2 ♀, 5 ♂, CAS); 12 mi. SE Ivanpah, PDH (1 ♀, 1 ♂); Joshua Tree National Monument, TG (1 ♂, TG); Kelso Dunes, TG (4 ♀, TG); Kelso Mts., TG (1 ♂, TG); Kramer Hills, G. A. Marsh (1 ♂, CIS), ROS (1 ♀); 3 mi. S Kramer Junction, MEI (2 ♂); 14 mi. S Kramer Junction. JWMS (1 ♀); 20 mi. W Landers, PFT & N. Youssef (1 ♂, USU); 12 mi. ESE Tecopa, MSW, T. Eichlin (1 ♂, CSDA); 22 mi. N Manix, G. A. Marsh (1 ♀); 2 mi. W Phelan, EIS (2 ♂); 14 mi. W Rice, C. D. MacNeill (1 ♂, CIS); Twentynine Palms, R. R. Pinger (1 ♂, CSDA); 32 road mi. E Twentynine Palms, TG (1 ♀, 1 ♂, TG); Vanwinkle Spring, G. E. Wallace (1 ♂); 11 mi. E Yermo, JWMS (1 ♀, CIS). **San Diego:** 8 mi. E Banner, JAP (2 ♂, CIS); Borrego Valley, RMB, EEG, PDH, FDP, EIS, MSW (19 ♀, 29 ♂; 2 ♂, WJP), MEI (2 ♂, UCR), G. A. Marsh (1 ♀, CIS), MSW, J. Slansky, Adams (1 ♀, 4 ♂, CSDA), MSW (1 ♀, 4 ♂, CIS), FXW (2 ♀, 29 ♂, CAS); Del Mar, C. H. Frady (1 ♀, OSU); 1 mi. S Del Mar, PDH (2 ♀, CIS); between Ocotillo & Borrego, A. R. Moldenke (2 ♂, LACM); Scissors Crossing, EIS (2 ♀), MSW (1 ♀, CSDA); Sorrento, JAP (1 ♀, 7 ♂, CIS); 2 mi. N Warner Springs, B. M. Bartosh, RCB (3 ♀, 2 ♂). **San Luis Obispo:** Black Lake Canyon, RMB (1 ♀, 1 ♂); 10 mi. W Simmler, PDH (2 ♂, CIS). **San Mateo:** 10 mi. SW San Francisco, W. Bohart (1 ♂, USU). **Santa Barbara:** 3 mi. W Cachuma Lake, P. E. Paige (1 ♀), Los Prietos, J. S. Buckett (1 ♂), JAP (1 ♀, CIS); 2 mi. E Solvang, JAP (1 ♀, CIS). **Santa Clara:** San Jose, PFT (1 ♀, USU). **Siskiyou:** between Hawkinsville & Lona Gulch, BV (1 ♀, CSDA). **Sutter:** Nicolaus, MSW (1 ♀, 17 ♂, CSDA). **Trinity:** Hayfork Agricultural Inspection Sta., JAP (2 ♂, CIS); Junction City, T. R. Haig (2 ♀, 1 ♂, CSDA). **Ventura:** Foster Park, J. L. Bath (1 ♀, UCR), J. R. Russell (1 ♀); Ventura, J. R. Russell (1 ♀). **Yolo:** Capay, R. E. Rice (1 ♀); Davis, RMB, C. G. Moore, C. R. Kovacic, ASM, L. R. Nault, FDP, WJP, LAS (12 ♀, 28 ♂; 2 ♂, USNM; 2 ♀, 3 ♂, WJP); 3 mi. S Davis, R. R. Snelling (1 ♂, LACM); Putah Canyon, FDP (1 ♀, 2 ♂); Rumsay, RMB (1 ♂), AMS & LAS (1 ♀, 1 ♂, LACM).

Idaho, **Franklin:** Preston (1 ♀, USU). **Fremont:** St. Anthony Sand Dunes, N. B. & W. M. Elliott (1 ♀, 1 ♂, NYSU). **Lincoln:** 6 mi. NE Shoshone, A. R. Gittins (♂, UIM).

Nevada. **Churchill:** 23 mi. E Fallon, E. G. Linsley (1 ♀); 3 mi. W Hazen, ASM (1 ♀), 4 mi. E Hazen, MEI (1 ♂, UCR); Sand Mt. (9 mi. Frenchman), J. Doyen (1 ♀, CIS). **Clark:** Jean, GEB (1 ♂); 9 mi. SW Mesquite, RCB (10 ♀, 6 ♂); 30 mi. S Searchlight, PFT, Rust, Youssef (1 ♂, USU); Valley of Fire, PFT, FDP, GEB (1 ♂, USU). **Humboldt:** 10 mi. N Winnemucca, EEG (1 ♀). **Lyon:** Weeks, FDP (1 ♀). **Mineral:** Luning, R. F. Denno & DRM (2 ♂); 3 mi. SE Schurz, FDP (1 ♂). **Pershing:** Woolsey, T. R. Haig (2 ♀, CSDA). **Washoe:** Nixon, RMB, FDP (1 ♀, 4 ♂), MEI (1 ♂, UCR); Patrick, FDP (1 ♂).

New Mexico. **Dona Ana:** Las Cruces, RMB (1 ♀, 2 ♂), R. H. Beamer (1 ♀, KU); 4 mi. E Mesilla Park, PDH (1 ♂, CIS). **Lincoln:** 5 mi. S Oscuro, R. L. Westcott (1 ♀, UIM). **Otero:** Alamogordo, collector unknown (1 ♀, CU); White Sands National Monument, H. V. Weems (1 ♀, FSCA). **Socorro:** La

Joya, 20 mi. N Socorro, H. E. Evans (6 ♀, 3 ♂, CSU). **Valencia:** Acoma Pueblo, ASM & WJP (1 ♀, WJP).

Oregon. **Deschutes:** Smith Rock State Park, M. B. & W. M. Elliott (8 ♀, 15 ♂, NYSU). **Josephine:** 8 mi. W Grants Pass, R. L. Westcott (1 ♀, ODA). **Klamath:** Bonanza, J. Schuh (1 ♀). **Morrow:** Boardman, G. R. Ferguson (2 ♂). **Umatilla:** Hat Rock State Park, EIS (1 ♀).

Texas. **Hudspeth:** McNary, H. E. Evans (2 ♀, 1 ♂, CSU); Sierra Blanca, RMB (1 ♀). **Presidio:** 5 mi. E Presidio, D. S. Horning (1 ♂).

Utah. **Cache:** Cornish, GEB & PFT (5 ♀, 2 ♂, USU; 2 ♀, WJP). **Emery:** Goblin Valley, FDP (1 ♂, USU), 2 air mi. W Little Gilson Butte, TG (1 ♂, USU). **Juab:** 12 mi. S Eureka, JWMS (1 ♀, CIS); White Sand Dunes (25 mi. SW Eureka), W. F. Barr (1 ♂, UIM). **Millard:** 15 mi. N Delta, PFT (1 ♂, USU); Pahvant (near Flovell), GEB & E. A. Cross (1 ♂, UCD). **San Juan:** 6 mi. S La Sal Junction, R. W. Thorp (1 ♂); 25 mi. S Moab, GEB, R. Brumley (2 ♀, 1 ♂; 1 ♀, USU). **Washington:** Leeds Canyon, G. F. Knowlton, W. J. Hanson, T. H. Hsiao (1 ♀, 2 ♂, USU).

MEXICO

Lower California. 10 mi. E Bahía San Quintín, FXW (1 ♂, CAS); Descanso, RMB (1 ♀); El Pescadero, MSW, J. Slansky (3 ♀, 6 ♂, CSDA); La Paz, FXW (2 ♂, CAS); Los Barriles, MSW (3 ♀, CSDA); 20 mi. N Mesquital, Ross & Bohart (1 ♀); Progreso, Sierra Juárez, FXW (1 ♀, 3 ♂, CAS); 38 km S Rosarito (114°), E. Fischer, R. Westcott (1 ♀, CAS); San Carlos, H. E. Evans, W. Rubink & D. Gwynne (4 ♀, CSU); 3 mi. N San Felipe, MEI (3 ♀, 1 ♂, UCR); 15 mi. N San Ignacio, Ross & Bohart (1 ♀); 10 mi. S San Quintín, J. Slansky, M. & K. Wasbauer (1 ♀, CSDA); San Vicente, C. H. Frady (1 ♀, OSU), JAP (1 ♀, CIS).

Chihuahua. Moctezuma, JWMS (1 ♂, CIS); Samalayuca, RMB (2 ♀).

Sinaloa. 8 mi. S Elota, LAS (1 ♂).

Sonora. Cerro Pinacate, McDougal Crater, GDB (1 ♂, UAT); Guaymas, E. P. VanDuzee (1 ♀); 39 mi. S Puerto Peñasco, M. Leppla, J. Bigelow, MAC, J. Davidson (1 ♀, ASU); "Sonora, 85 km. so.," A. L. Melander (1 ♀, 6 ♂); Tepoca Bay, E. P. VanDuzee (1 ♀).

Tachysphex yuma sp.n.

ETYMOLOGY.—Named after the Yuma Indians of Arizona.

DIAGNOSIS.—*Tachysphex yuma* is characterized by the punctate mesopleuron (punctures shallow), middle scutal setae oriented posterolaterad or (some males) posterad, and sternum I with an apical depression. Several other species share this combination of characters, but they have a uniformly ridged propodeal side (ridges evanescent in many *yolo*). In *yuma*, the propodeal side is either coarsely ridged posteriorly and microridged along the metapleural sulcus; or (most specimens) nonridged along the metapleural sulcus and ridged along the dorsal margin (or dorsal and posterior); or (some males) all nonridged. Furthermore, the flagellum of *yuma* is somewhat longer; for example, the length of flagellomere IV is 3.6–4.2 (female) and 2.0–2.4 (male) times its width, and up to 3.2 and 2.0 times, respectively, in the other species. In the male, the unusually broad clypeal lobe is distinctive (corners markedly closer to orbits than to each other) and the velvety sternal pubescence is an additional recognition feature.

GEOGRAPHIC DISTRIBUTION.—Idaho, Oregon, California, Arizona, southern Texas, northern Mexico (Sonora, Lower California).

MATERIAL EXAMINED.—HOLOTYPE: ♂, Mexico, Baja California Sur, La Paz, 10–12 Oct. 1954, F. X. Williams (CAS Type No. 13966).

PARATYPES: 8 ♀, 25 ♂, 2 Mar. (Sonora), 8 Apr. to 1 June, 14 July (Oregon), 9–15 Oct., 11 Nov.

UNITED STATES OF AMERICA

Arizona. **Cochise:** Canelo, A. & H. Dietrich (1 ♀, NYSU); 5 mi. W Portal, collector unknown (2 ♂, NYSU); 6 mi. W Portal, A. L. Steiner (2 ♂, UAE, WJP). **Maricopa:** Wickenburg, PFT & GEB (1 ♂, WJP). **Coconino:** Grand Canyon National Park, 15 mi. NE Phantom Ranch, J. E. Slansky (1 ♂, UCD).

California. **Imperial:** 20 mi. E Glamis, FDP (1 ♂, UCD). **Inyo:** Darwin Falls, ASM (1 ♂, UCD); Panamint Springs, MEI (1 ♂, UCD); Surprise Canyon, FDP (2 ♂, UCD, WJP). **Riverside:** Boyd Desert Research Center, 4 mi. S Palm Desert, PDH (1 ♀, 1 ♂, CIS; 1 ♀, WJP); Deep Canyon, MEI (3 ♂, UCD, UCR, WJP), EIS (1 ♂, UCD); Salton Beach, A. L. Melander (1 ♀, UCD); Thousand Palms Canyon, RMB (1 ♂, UCD); Whitewater, D. J. R. (1 ♂, CIS). **San Bernardino:** 3 mi. N Crossroads, C. D. MacNeill (1 ♂, CAS). **Shasta:** Redding, DRM (1 ♀, UCD). **Stanislaus:** Empire, E. I. Beamer (1 ♀, KU).

Idaho. **Twin Falls:** Rock Cr. Canyon (19 mi. S Hansen), R. L. Westcott (1 ♀, UIM).

Oregon. **Malheur:** 4 mi. N Juntura, H. A. Scullen (1 ♂, UCD).

Texas. **Brewster:** 20 mi. NNW Marathon, M. Masters (1 ♂, CU).

MEXICO

Baja California Norte. 65 mi. S San Felipe, R. D. Gehring (1 ♂, CIS).

Baja California Sur. 3 mi. S Ignacio, MEI (2 ♂, UCR, WJP), Rancho El Cayote, Maynard & Honey (1 ♂, LACM).

Sonora. Bahía San Carlos, P. H. Arnaud (1 ♀, CAS).

SPECIES OF THE BRULLII GROUP

Tachysphex acanthophorus sp.n.

ETYMOLOGY.—The specific name *acanthophorus* is derived from the Greek words *acanthos*, a spine, and *phorein*, to bear, a spine-bearer; with reference to the tarsal spines.

DIAGNOSIS.—The female of *acanthophorus* has a distinctive tarsal feature: one or two subapical spines on each lateral margin of tarsomere

V, and usually central spines on its venter; unlike *armatus*, the tarsomere V lacks basoventral spines. The lateral, subapical spines on tarsomere V occur also in most western females of *mundus*, but unlike that species the mesopleural vestiture is dense (partly obscuring sculpture) in *acanthophorus*. Tarsomere V is similar in *acanthophorus* and the South American species *spinulosus*, but in the latter the gaster is black and the mid- and hindfemora are red.

The males of *acanthophorus* and *armatus* differ from other species of the *brullii* group in lacking a clypeal bevel and graduli, and in having a very narrow clypeal lip and a transverse sulcus on sterna III–VI (the sulcus is visible only when segments are fully extended). Unlike *armatus* (in which the sternal surface is flat), sternum II of *acanthophorus* is somewhat swollen along the foremargin of the apical depression. Furthermore, the mesopleural sculpture is obscured by vestiture or hardly visible in *acanthophorus*, but easily visible in *armatus*.

Geographic Distribution.—Xeric areas of southwestern U.S. and northern Mexico.

Material Examined.—Holotype: ♀, Arizona, Cochise Co., Willcox, 14 Aug. 1958, P. D. Hurd (UCD).

Paratypes: 134 ♀, 180 ♂, 1 intersex; May to 7 Nov. Specimens for which institution is not indicated are all in UCD.

United States of America

Arizona. No specific locality (1 ♀). **Cochise:** 1 mi. E Apache, J. G. Ehrenberg (2 ♂, AMNH); Bowie, A. D. Telford (1 ♀, WJP); 7 mi. SE Dos Cabezas, D. S. Chandler (1 ♂, UAT); Douglas, G. L. Ballmer (2 ♀); 2 mi. E Douglas, R. W. Brooks (1 ♀); Portal, K. V. Krombein (28 ♀, 22 ♂; BMNH, KVK, WJP); 2 mi. E Portal, J. H. Puckle, M. A. Mortenson & MAC (2 ♂); 2 mi. NE Portal, M. & T. M. Favreau (1 ♂, AMNH); Willcox, RMB (2 ♀, 2 ♂), D. D. Linsdale (1 ♀, 5 ♂; AMNH, UCD), PDH (1 ♀, 2 ♂, CIS; 1 ♀, USNM). **Maricopa:** 5 mi. N Aguila, GEB & PFT (1 ♀, USU); Tempe, collector unknown (1 ♂, MCZ); 5 mi. SE Wickenburg, PDH (1 ♀, CIS). **Pima:** 30 mi. SE Ajo, C. R. Kovacic (1 ♀); Continental, MEI (2 ♂); Sabino Canyon (Santa Catalina Mts.), GDB & FGW (1 ♂, UAT), FDP & LAS (1 ♀); Tucson, C. L. Crow (1 ♀), M. L. Lindsay (1 ♂, UAT), FDP (1 ♂), FDP & LAS (1 ♀). **Pinal:** 5 mi. NW Coolidge, A. D. Telford (1 ♂); Picacho Pass, DRM & J. E. Lauck (1 ♀); collector unknown (1 ♀, UCR); Superior (Boyce Thompson Arboretum), GDB (1 ♂, UAT).

California. **Imperial:** Brawley, GEB (1 ♀). **Inyo:** Antelope Springs (8 mi. SW Deep Springs), HKC (13 ♀, 11 ♂; AMNH, UCD), PMM (3 ♀), DRM (1 ♀, 1 ♂), JAP, G. I. Stage (11 ♀, 48 ♂, CIS); Deep Springs, H. Nakakihara (1 ♀, UCR). **Riverside:** 12 mi. N Blythe (also 18 mi. W), RMB (2 ♀); 20 mi. W Blythe, JWMS (3 ♀, 1 ♂, CIS); Indio, MEI (1 ♂, UCR); 3.5 mi. S Palm Desert, S. Frommer & B. Morley (1 ♀, 1 ♂, UCR). **San Bernardino:** no specific locality, D. W. Coquillett (1 ♂, USNM). **San Diego:** Borrego, A. L. Melander (1 ♀). **Tulare:** Lemon Cove, J. C. Bradley (3 ♀, NYSU; 4 ♂, CU); Three Rivers, collector unknown (1 ♂, CU).

Colorado: **Bent:** Hasty, H. E. Evans (9 ♀, 2 ♂; BMNH, CSU, WJP).

Nevada. **Clark:** Sandy, RCB (1 ♂). **Mineral:** Luning, R. F. Denno & DRM (1 ♀). **Nye:** Mercury (1 ♂, USNM).

New Mexico. **Dona Ana:** Las Cruces, RMB (1 ♀). **Eddy:** 15.5 mi. W Artesia, V. E. Romney (1 ♂, USNM). **Grant:** 25 mi. E Lordsburg, H. A. Scullen (1 ♂). **Hidalgo:** 21 mi. S Animas, J. G. & B. L. Rozen (1 ♀, AMNH); 22 mi. S Animas, J. Rozen & M. Favreau (1 ♂, AMNH); Cienaga Lake, J. H. & J. M. Davidson & MAC (2 ♂); Granite Gap (17 mi. N Rodeo), F. G. Andrews (1 ♀, CSDA); Granite Pass area (20 mi. N Rodeo), Hwy. 80, MSW, J. Slansky & C. Freeberg (1 ♀, CSDA); 1 mi. N Rodeo, J. H. Puckle, M. A. Mortenson & MAC (1 ♂); 4 mi. SW Rodeo, J. G. Rozen (1 ♀, AMNH). **Otero:** White Sands National Monument, RMB (1 ♂). **Socorro:** La Joya (20 mi. N Socorro), W. Rubink (1 ♀, CSU; 2 ♂, USNM). **Quay:** Tucumcari, RMB (2 ♂).

Texas. **Bexar:** no specific locality, H. B. Parks (3 ♀; UCD, WJP). **Brewster:** Big Bend National Park (Nine Point Draw), W. R. M. Mason (4 ♀, 22 ♂; BMNH, CNC, WJP); Big Bend National Park (Boquillas), W. R. M. Mason (1 intersex, CNC); Glenn Spring, F. M. Gaige (1 ♂). **El Paso:** Sierra Blanca, collector unknown (1 ♂, CU). **Hudspeth:** Fort Hancock, CU Exped. (1 ♀, NYSU); McNary, H. E. Evans (1 ♀, 1 ♂; BMNH, CSU). **Presidio:** 3 mi. E Presidio, H. E. Evans (2 ♀, MCZ), J. E. Gillaspy (1 ♀).

Utah. **Garfield:** Shootaring Canyon, D. Vogt (1 ♀, 1 ♂, USU). **Washington:** Leeds Canyon, G. F. Knowlton, W. J. Hanson, T. H. Hsiao (2 ♀, 1 ♂, USU); St. George, GEB (1 ♂); Toquerville, G. F. Knowlton, W. J. Hanson, T. H. Hsiao (2 ♂, USU).

Mexico

Baja California Sur. 4 mi. WSW Miraflores, J. Slansky, M. K. & C. Wasbauer (1 ♀, 4 ♂, CSDA).

Chihuahua. 15 mi. S Chihuahua, H. E. Evans (2 ♀, 4 ♂; BMNH, MCZ, WJP).

Sinaloa. Culiacán, H. E. Evans (1 ♂, CU); S Lorenzo, GEB & RMB (2 ♀, USU); Mazatlán, W. R. M. Mason (1 ♀, CNC); 2.5 mi. N Mazatlán, MSW (1 ♀, CIS); 5 mi. N Mazatlán, MSW & J. Chemsak (1 ♂, CIS). Sonora. Alamos, RMB (1 ♂), W. J. Hanson & T. L. Whitworth (1 ♂, USU); 10 mi. SW Alamos, FDP & LAS (1 ♂); Desemboque, C. & P. Vaurie (1 ♂); 19.4 & 20 mi. S Estación Llano, MEI, EIS, P. A. Rauch (3 ♂, UCR); Guaymas, RMB (1 ♀); 5 mi. S Magdalena, FDP & LAS (1 ♂); Minas Nuevas, C. & P. Vaurie (1 ♂); 10 mi. E Navajoa, W. L. Nutting & FGW (2 ♂, UAT); San Carlos, RMB (1 ♀, 1 ♂).

Tachysphex armatus sp.n.

Etymology.—The specific name *armatus* is a Latin word for armed, with reference to the ventral spines of female hindtarsomere V.

Diagnosis.—The female of *armatus* is unique among the North American *Tachysphex* in having basoventral spines on the tarsomere V. Otherwise it is very similar to *acanthophorus* with which it shares other structures of the tarsomere V: one to several medioventral spines and one or two preapical spines on each lateral margin. The lateral spines are also found in most western specimens of *mundus*.

The male of *armatus* is very similar to *acanthophorus*. See that species for differences.

GEOGRAPHIC DISTRIBUTION.—Desert areas between southwestern Texas and southern California, also Lower California.

MATERIAL EXAMINED.—HOLOTYPE: ♀, Nevada, Clark Co., Sandy, 24 July 1958, R. C. Bechtel (UCD).

PARATYPES: 17 ♀, 9 ♂; May to 5 Sep.

UNITED STATES OF AMERICA

Arizona. **Maricopa:** 10 mi. E Gila Bend, GDB (1 ♀, UCD); Phoenix, R. H. Crandall (1 ♀, UCD); 5 mi. SE Wickenburg, PDH (1 ♀, CIS), P. H. Timberlake (1 ♂, UCR). **Pima:** Tucson, F. M. Carpenter (1 ♀, UCD).

California. **San Diego:** San Diego, F. E. Blaisdell (1 ♀, UCD).

Nevada. **Clark:** Sandy, RCB (1 ♂, WJP). **Lincoln:** Alamo, FDP (1 ♀, WJP).

Texas. **Brewster:** Big Bend National Park, R. W. Strandtmann (1 ♀, 1 ♂; USNM, UCD); Big Bend National Park (Nine Point Draw), W. R. M. Mason (1 ♀, CNC). **Hudspeth:** McNary, H. E. Evans (2 ♀, 3 ♂; CSU, WJP).

Utah. **Washington:** Leeds Canyon, G. F. Knowlton, W. J. Hanson, T. H. Hsiao (1 ♀, 3 ♂, USU).

MEXICO

Lower California. 7 mi. SW La Paz, J. A. Chemsak (1 ♀, CIS), 220 km S Tijuana, FXW (5 ♀, CAS).

Tachysphex krombeiniellus sp.n.

ETYMOLOGY.—Named after K. V. Krombein as a mark of friendship and gratitude.

DIAGNOSIS.—*Tachysphex krombeiniellus* is similar to *belfragei* in having a bicolored gaster and short thoracic vestiture which does not conceal mesopleural sculpture. Unlike that species, the propodeal dorsum of *krombeiniellus* is evenly microareolate, and at least the apical third of the hindfemur is red. It differs from *maurus* and *mundus* by the shape of the clypeus (female lip broadened, male middle section slightly longer than wide). It can also be distinguished from *marurus* and most *mundus* by its basally red gaster combined with the partly or all red hindfemur.

GEOGRAPHIC DISTRIBUTION.—Mainly central U.S. between northern Texas and North Dakota, west to 105th meridian, but also South Carolina, Arkansas, and Florida.

MATERIAL EXAMINED.—HOLOTYPE: ♀, Florida, Levy Co., no specific locality, 3 June 1954, H. V. Weems (USNM).

PARATYPES: 22 ♀, 14 ♂; June to Sep. Specimens for which institution is not given below are all in UCD.

Arkansas. **Mississippi:** no specific locality, J. C. Nickerson (1 ♀).

Colorado. **Yuma:** Yuma, collector unknown (1 ♂; 1 ♂, WJP).

Florida. **Gadsden:** Quincy, Malaise trap (2 ♀, UFG, WJP). **Levy:** no specific locality, H. V. Weems (1 ♀, CU; 2 ♂, FSCA; 1 ♀, 1 ♂, USNM; 2 ♂, WJP).

Kansas. **Graham:** Hill City, RRD (1 ♀). **Pottawatomie:** Blackjack, H. E. & M. A. Evans, C. S. Lin, C. Yoshimoto (2 ♂, MCZ).

Minnesota. **Scott:** Barden (between Savage & Shakopee), C. E. Mickel (1 ♀, UMSP). **Goodhue:** Cannon Falls, C. E. Mickel (1 ♀, UMSP).

Nebraska. **Blaine:** Halsey & Dunning, RRD (2 ♂). **Box Butte:** Alliance, RRD (1 ♀). **Dawson:** Gothenburg, RRD (1 ♂). **Douglas:** Omaha, collector unknown (1 ♀). **Hall:** 6 mi. W Cairo, C. W. Rettenmeyer (1 ♂). **Lancaster:** Lincoln, collector unknown (1 ♀). **Lincoln:** North Platte, R. K. Schwab (1 ♀; 1 ♀, WJP). **Nance:** Genoa, R. M. Barnes (1 ♀, INHS). **Thomas:** Thedford, RRD (3 ♀; 1 ♀, WJP).

North Dakota. **Richland:** 11 mi. W Walcott, J. R. Powers (1 ♀, CIS).

South Carolina. **Aiken:** New Ellenton, A. Hook (1 ♀, UGA).

Texas. **Potter:** 5 mi. N Amarillo, D. R. Miller (1 ♂, USNM).

Wisconsin. **Vernon:** Genoa, collector unknown (2 ♀, MPM).

Tachysphex menkei sp.n.

ETYMOLOGY.—Dedicated to A. S. Menke as a mark of gratitude for his help.

DIAGNOSIS.—*Tachysphex menkei* can be easily recognized by the woolly setae of the head and thorax; the finely, sparsely punctate scutum, scutellum, mesopleuron, and propodeal side; the largely impunctate, red gaster; and glabrous male sterna III–VI.

NATURAL HISTORY.—A female paratype is pinned with her prey, a young nymph of a longhorned decticine grasshopper, probably *Eremopedes* sp., det. A. B. Gurney.

GEOGRAPHIC DISTRIBUTION.—Desert areas from southwestern Texas to southern California.

MATERIAL EXAMINED.—HOLOTYPE: ♀, California, San Diego Co., Borrego Valley, 19 Apr. 1957, R. M. Bohart (UCD).

PARATYPES: 8 ♀, 32 ♂, Apr. to June.

Arizona. **Graham:** 18 mi. E Stafford, FGW & GDB (2 ♂, UCD). **Maricopa:** 30 mi. E Gila Bend, R. F. Smith (1 ♂, UCD). **Yavapai:** 10 mi. NW Congress, FDP & LAS (1 ♀, UCD). **Yuma:** 5 mi. SE Bouse, S. A. Gorodenski, JMD, MAC (1 ♂, ASU).

California. **Imperial:** 30 mi. NE Glamis, R. R. Pinger (2 ♂, CSDA). **San Bernardino:** Adelanto, MEI (1 ♂, UCD). **San Diego:** Borrego Valley, H. R. Moffitt, EIS (2 ♂, UCD). **Riverside:** Palm Springs, RMB (1 ♂, UCD); Andreas Canyon, RMB, HKC (10 ♂, UCD, USNM, WJP).

New Mexico. **Otero:** Alamogordo, collector unknown (1 ♂, ANSP). **Socorro:** Bernardo, A. Apperson (1 ♀, USU).

Texas. **Brewster:** Alpine, J. Gillaspy (1 ♂, MCZ); Big Bend National Park (Nine Point Draw), R. Mason, J. F. McAlpine (3 ♀, 7 ♂; CNC, WJP); Big Bend National Park (Santa Elena Canyon), J. F. McAlpine (1 ♂, CNC); Big Bend National Park (near Doughout Well), B. J. Adelson (2 ♂, UCD). **El Paso:** Tornillo, H. E. Evans & Rubink (1 ♀, WJP). **Hudspeth:** McNary H. E. Evans (1 ♀, CSU). **Presidio:** 3 mi E Presidio, H. E. Evans (1 ♀, MCZ).

LITERATURE CITED

BOHART, R. M., AND A. S. MENKE. 1976. Sphecid wasps of the world. A generic revision. University of California Press, Berkeley, Los Angeles, London. 1 color pl., ix + 695 p.

PULAWSKI, W. J. 1971. Les *Tachysphex* Kohl (Hym., Sphecidae) de la région paléarctique occidentale et centrale. Państwowe Wydawnictwo Naukowe, Wrocław. 464 p.

———. 1974. A revision of the Neotropical *Tachysphex* (Hym., Sphecidae). Polskie Pismo Ent. 44:3–80.

———. 1977. A synopsis of *Tachysphex* Kohl (Hym., Sphecidae) of Australia and Oceania. Polskie Pismo Ent. 47:203–332.

PROCEEDINGS
OF THE
CALIFORNIA ACADEMY OF SCIENCES

Vol. 43, No. 4, pp. 43–58, 27 figs.
November 4, 1982

A REVISION OF THE GRASSHOPPER GENERA *CHROMACRIS* AND *XESTOTRACHELUS* (ORTHOPTERA, ROMALEIDAE, ROMALEINAE)

By

H. Radclyffe Roberts

Department of Entomology, Academy of Natural Sciences,
19th and the Parkway, Philadelphia, Pennsylvania 19103

and

Carlos S. Carbonell*

Museu Nacional, Universidade Federal do Rio de Janeiro,
Quinta da Boavista, 20942 Rio de Janeiro, RJ, Brazil

ABSTRACT: Illustrations, diagnoses, and distributional records are given for 14 species and subspecies of the Neotropical grasshopper genera *Chromacris* and *Xestotrachelus*, of which 1 species, *Chromacris minuta*, and 2 subspecies, *C. trogon intermedia* and *C. psittacus pacificus*, are described as new, and 4 names are newly synonymized. Known information concerning food plants, oviposition, habitat, and predator defense for *Chromacris speciosa* is briefly reviewed. (Orthoptera, Romaleidae, Romaleinae, grasshoppers, Neotropical, new taxa, taxonomic revision)

INTRODUCTION

The grasshopper species of the genus *Chromacris* are of a striking color, usually a glossy green with yellow markings, and red or yellow wings. They occur in the humid areas of the American tropics from Mexico to Argentina. As a general rule, but one species occurs at any one locality. Adults are usually seasonal in their appearance, so that some months of the year a species may appear to be absent from a local fauna. Because most of the taxa of the genus have been poorly defined or understood, the application of a number of their names has been uncertain, and there has been no comprehensive treatment of the genus, a revisionary study appeared to be needed for this common and widespread group of grasshoppers. The monotypic genus *Xestotrachelus* of southern South America is included in this study because of its similarity to *Chromacris* and because it is the only closely related genus.

The subfamily Romaleinae currently includes about 48 genera. Rehn and Grant (1959) erected 16 tribes in this subfamily and proposed the tribe Chromacrini for the genera *Chromacris* and *Xestotrachelus*. Because 10 of their tribes include but one or two genera each, and they give no distinguishing characters for these tribes, it does not appear useful to recognize the tribe Chromacrini and other such tribes of the subfamily.

---

* Bolsista, Conselho Nacional de Desenvolvimento Cientifico e Tecnologico, Brazil.

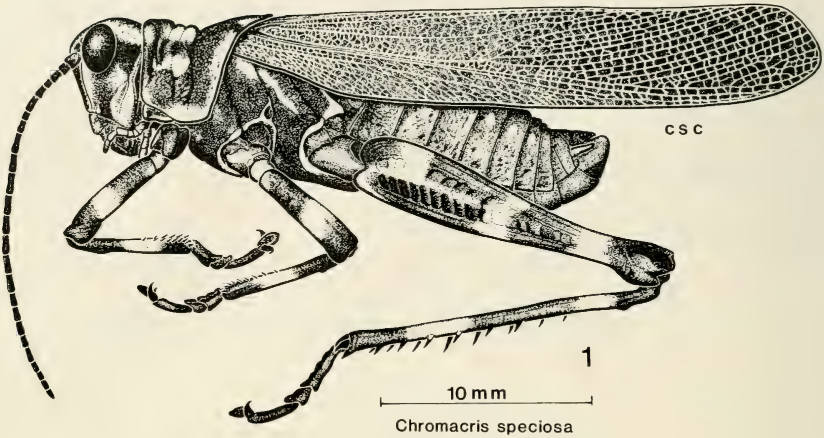


FIGURE 1. *Chromacris speciosa*, Casupa, Florida, Uruguay.

The genus *Chromacris* includes at least eight species, two of which are polytypic, each having two subspecies, and two other species that we tentatively recognize pending further information. One species, *C. minuta*, and two subspecies, *C. trogon intermedia* and *C. psittacus pacificus*, are described as new. There are five junior synonyms, three of which we newly synonymize.

Specimens belonging to various collections are indicated by the following abbreviations: ANSP, Academy of Natural Sciences of Philadelphia; CACS, Dr. C. A. Campos Seabra Collection; CSC, Carlos S. Carbonell Collection, Montevideo, Uruguay; CHFR, C. H. F. Rowell Collection, Zoologisches Institut der Universität, Basel, Switzerland; FCZ, F. Carrasco Collection, Cuzco, Peru; MNHN, Muséum National d'Histoire Naturelle, Paris, France; MZSP, Museu de Zoologia, Universidade São Paulo, Brazil; UMMZ, University of Michigan Museum of Zoology, Ann Arbor, Michigan, U.S.A.

ACKNOWLEDGMENTS

We are grateful to our many friends for their help and advice. We especially thank the following persons and their respective institutions for the loan of specimens. Dr. Irving J. Cantrall, UMMZ; Drs. F. Carrasco and J. A. Escalante, University of Cuzco, Peru; Dr. Marius Descamps and Christiane Amedegnato, MNHN; Dr. Kurt K. Günther, Museum für Naturkunde, Humboldt Universität, Berlin, DDR; and the late Dr. H. Reichardt, MZSP.

SPECIES LIST

In the following list of taxa we have attempted to place similar or related taxa as close to one another as practical. The number assigned to each taxon matches the number in the text. Junior synonyms are given (in italics) below each numbered taxon.

1. **Chromacris colorata** (Serville)
   Rhomalea pedes Pictet and Saussure
2. **Chromacris minuta** n.sp.
3. **Chromacris miles** (Drury)
4. **Chromacris speciosa** (Thunberg)
   Acridium xanthopterum Hahn
   Rhomalea stolli Pictet and Saussure
5. **Chromacris nuptialis** (Gerstaecker)
   Rhomalea latipennis Pictet and Saussure
6. **Chromacris trogon trogon** (Gerstaecker)
7. **Chromacris trogon intermedia** n.subsp.
8. **Chromacris psittacus psittacus** (Gerstaecker)
9. **Chromacris psittacus pacificus** n.subsp.
10. **Chromacris icterus** (Pictet and Saussure)
    Rhomalea opulenta Gerstaecker
11. **Chromacris peruviana** (Pictet and Saussure)
12. **Xestotrachelus robustus** (Bruner)
    Xestotrachelus hasemani Bruner

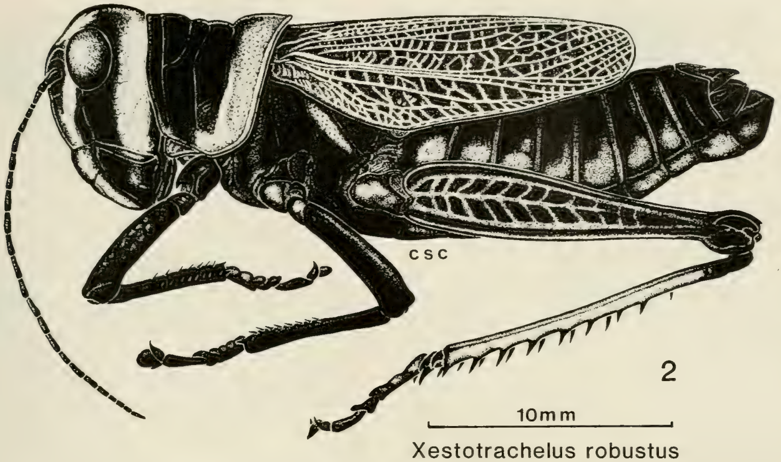


FIGURE 2. *Xestotrachelus robustus,* Chapada dos Guimarães, Mato Grosso, Brazil.

KEY TO SPECIES OF *CHROMACRIS*

1. Exterior of small aedeagus membranous (Figs. 19–20). First two plaits or anterior fold of wings entirely black to base (Figs. 3–6). Colorata group ---- 2

1′. Exterior of aedeagus sclerotized forming a short collarlike structure around the phallotreme opening (Figs. 22–25). First two plaits or anterior fold of wings yellow on basal half (Figs. 7–9), or some black on basal half of first plait (Fig. 10). Trogon group ---------- 6

2(1). Yellow on part of antennae. Stridulating structures weakly developed (Fig. 15) ---------- 3

2′. Antennae entirely black. Stridulating structures well developed (Figs. 16–17) ---------- 4

3(2). Basal portion of antennae yellow (Mexico to Costa Rica) ---- *C. colorata*

3′. Distal portion of antennae yellow (Acapulco, Mexico) ---------- *C. minuta*

4(1′). Membrane of tegmina dark brown to black with strongly contrasting straw-colored veins (inland south central Brazil) ---------- *C. nuptialis*

4′. Not as above ---------- 5

5(4′). Posterior yellow margin of pronotum interrupted by black or green at angle between disc and lateral lobes. Rim of coxal articulation on mesathorax and metathorax entirely or partially yellow (South America) ---------- *C. speciosa*

5′. Posterior yellow margin of pronotum not interrupted at angle between disc and lateral lobes. Rim of coxal articulation on mesathorax and metathorax entirely green (southeastern Mexico) ---------- *C. miles*

6(1′). Antennae entirely black ---------- 7

6′. Antennae with yellow tips ---------- 10

7(6). No bands on hind tibiae ---------- 8

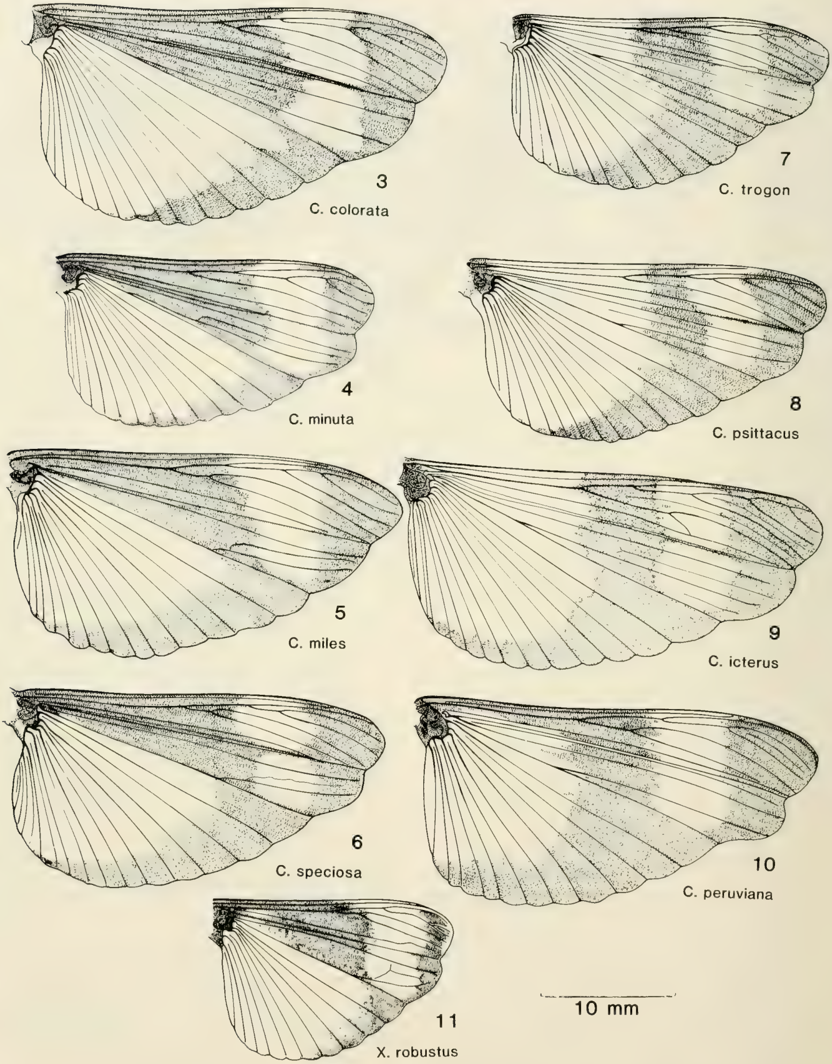
7′. Yellow bands on hind tibiae ---------- 9

8(7). Yellow bands lacking on all legs (Costa Rica) ---------- *C. trogon trogon*

8′. Yellow bands on hind femora (Guatemala, Belize, and Honduras) ---------- *C. trogon intermedia*

9(7′). Proximal yellow band on hind femora interrupted on outer ventral portion (Costa Rica to northern Colombia and Venezuela) ------ *C. psittacus psittacus*

9′. Proximal yellow band on hind femora



FIGURES 3–11. Male hind wings of seven of the eight species of *Chromacris* (3–10) *C. nuptialis* being omitted because of similarity to *C. speciosa* (6), and *Xestotrachelus robustus* (11), all at same scale and from the following localities: (3) *colorata* Medellin de Bravo, Veracruz, Mexico; (4) *minuta* Acapulco, Guerrero, Mexico; (5) *miles* Boloyuc, Quintana Roo, Mexico; (6) *speciosa* Aratinga, Rio Grande do Sul, Brazil; (7) *trogon* San Lorenzo, Alajuela, Costa Rica; (8) *psittacus* Cabima, Panama; (9) *icterus* Tabatinga, Amazonas, Brazil; (10) *peruviana* Satipo, Junín, Peru; (11) *X. robustus* Cerro Corá, Amambay, Paraguay.

entire (western Colombia and western Ecuador) .... *C. psittacus pacificus*

10(6′). Hind tibiae with single, distal, yellow band (southeastern Colombia to northeastern Peru) .... *C. icterus*

10. Hind tibiae with two yellow bands (Peru) .... *C. peruviana*

Chromacris Walker

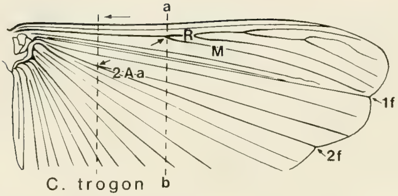
Chromacris Walker, 1870:643. [Type-species *Gryllus speciosus* Thunberg, 1824, by subsequent designation of Rehn 1904:532.]

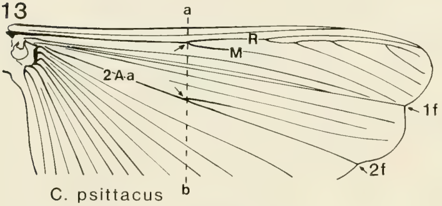
Diagnosis.—Neither pronotal crest nor protruding fastigium present; fully alate (Fig. 1). Medium size, body length of females 33 mm (*C. minuta*) to 55 mm (*C. icterus* and *C. peruviana*). Glossy olive-green to dark green with contrasting yellow or yellow tinged with red markings. These markings may be much reduced as in Peruvian specimens of *C. speciosa*. Hind wings various shades of red, orange, or yellow with contrasting black pattern (Figs. 3–11) characteristic of this genus and *Xestotrachelus*, distinguishing them from all other genera of subfamily. Genitalia (Figs. 19–26) rather uniform throughout the genus. Noteworthy are weakly developed aedeagal valves.

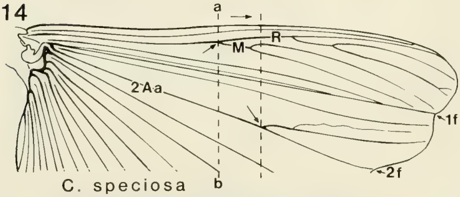
Classification.—Two groups of *Chromacris* can be recognized. One group including *trogon, psittacus, icterus,* and *peruviana* (trogon group) have the proximal half of the first two plaits of the hind wings without black on the anterior portion of first two plaits (Fig. 10). In contrast, first two plaits of group containing *colorata, minuta, miles, speciosa,* and *nuptialis* (colorata group) are entirely black (Figs. 3–6). Aedeagal valves of trogon group are externally sclerotized (Fig. 22–25) whereas those of the colorata group are small membranous lobes (Figs. 19, 20). Trogon group members commonly have yellow wings, occasionally orange, and rarely red. Wings of colorata group members are commonly red, orange in some geographical areas, and frequently yellow in part of Atlantic coastal area of Brazil. In the trogon group, prosternal tubercle small and pointed with concave sides as seen in profile. In contrast, *C. miles, C. speciosa,* and *C. nuptialis* have a large, bluntly pointed tubercle that is variable in form, even intra-specifically. On the other hand, tubercle of *C. colorata* and *C. minuta* more nearly resembles that of the trogon group in its small size, may be pointed, but sides in profile are rarely concave. *C. miles* and its two closely related species, *C. speciosa* and *C. nuptialis,* have a well-developed stridulatory apparatus, as in many other species of the Romaleinae. The serrate cross veins (SV) between the first (1A) and second (2A) anal veins of the second plait (Figs. 16, 17) contact the raised scraper veins on underside of tegmen when wings are folded. Tympanate or fenestrate areas (TA) on either side of these cross veins are well developed as resonators. This stridulatory apparatus is more weakly developed in other species of *Chromacris* and, in many cases, may not be functional. For example, compare the wing of *C. icterus* (Fig. 15) with those in Figures 16 and 17. In summary, the trogon group is distinguished from the colorata group by the aedeagal valves and black pattern of hind wings, and the colorata group is divided into two subgroups by shape of prosternal tubercle and stridulatory apparatus.

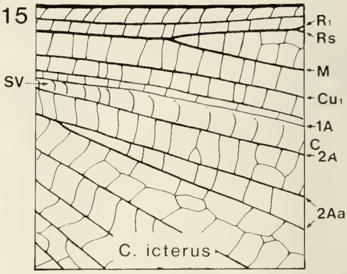
Recognition of species in the genus *Chromacris* has been difficult because of the lack of morphological characters and dependence on color and color pattern. The trogon group of four species, including two subspecies, can be reasonably well defined by a combination of different color-pattern characters (Table 2). The illustrations of the aedeagus of this group (Figs. 22–25) may suggest species differences, but individual variation is such that clear distinctions between species are not evident. The wide-ranging *C. speciosa* of South America has been most puzzling because of the great amount of geographical variation of color and color pattern and variation within a local population. It has been difficult to decide whether we are dealing with species, subspecies, or just color forms. As an example of color forms, about half of the 21 specimens of *C. speciosa* recorded from Floresta de Tijuca near Rio de Janeiro, Brazil, have yellow wings and the other half orange wings, with no intermediates. We have concluded that it is most practical to treat *C. speciosa,* at least for the present, as but one highly variable species. We need more information on *C. miles* and *C. nuptialis* to understand their status as species and their relationship to *C. speciosa*.

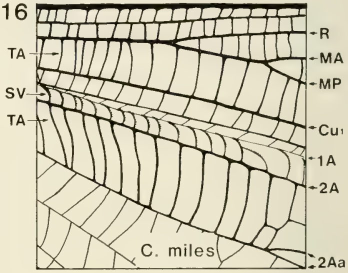
General Observations.—Most of the available data for the genus refer to *C. speciosa*. The biology of this species was studied in Tucumán,

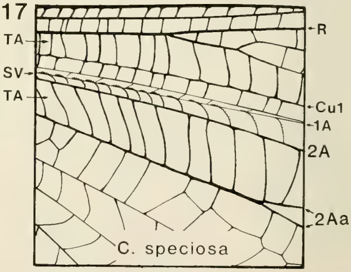
12


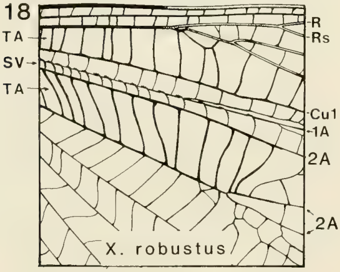
13


14


15


16


17


18


FIGURES 12–14. Male hind wings of three species of *Chromacris* showing relative position of radius (R) median (M) fork to the second anal accessory (2Aa) fork. The 2Aa fork is more distant from the base of wing than the R-M fork in *C. speciosa* (Fig. 14) and its related species, *C. miles* and *C. nuptialis,* whereas in *C. trogon* and *C. psittacus* (Figs. 12 and 13) and all other species of the genus, the 2Aa fork is equidistant or closer to base of wing than the R-M fork. The 1f is the first and the 2f is the second fold line of wing.

FIGURES 15–18. Details of stridulatory area of male hind wings of three species of *Chromacris* (Figs. 15–17) and *Xestotrachelus robustus* (Fig. 18). Note well-developed tympanate areas (TA) in Figs. 16–18. Terminology of wing venation follows Ragge (1955). SV, serrate veinlets or cross veins; TA, tympanate or fenestrate areas; R, radial vein; Rs, radial sector; Cu1, first cubital vein; 1A, first anal vein; 2A, second anal vein.

Argentina, by Barrera and Turk (1977). Data on the biology of *C. colorata* have been reported from Monterrey, Mexico, by Pretto-Malca (1968), at the other extreme for the distribution of the genus. Some data on the food of other species exist, mainly in papers of applied entomology. Some aspects of the general biology of the species of the genus, such as their general preference for solanaceous and composite plants and the gregariousness of their juveniles, are generally known by all entomologists who have collected these insects in the field.

Oviposition and Development.—Eggs of *C. speciosa* are laid in the soil, the top of the egg-pod 10 to 20 mm under the surface. Eggs are cemented together in the pods, but not embedded in the frothy secretion which covers the egg-pods of other acridoids. This secretion just forms the upper half of the pod, while the egg-mass is bare and usually 15 mm long, 8.5 mm wide. The number of eggs in each pod varies between 61 and 70, with a mean of 66 eggs (Barrera and Turk 1977). This species grows from hatching to imago, under the Tucumán climate, in 30 to 60 days, passing through five instars in the male and six instars in the female. Nymphs are black with red and some white markings. Sexual maturity is attained 10 days after the last molt. Adults mate repeatedly and females lay at least two pods. The insects usually disperse after reaching the imaginal stage (Turk and Barrera 1976). Pretto-Malca (1968) stated that egg-pods of *C. colorata* contain an average of 35 eggs and that the insect reaches the imaginal stage through six nymphal instars, and sexual maturity about 18 days later. Nymphs of this species are highly gregarious.

Food Plants.—*Chromacris speciosa* prefers solanaceous plants. Turk and Barrera (1976) reported its feeding on *Cestrum parqui, C. strigillatum, C. lorentziana, Lycium cestroides, Solanum argentinum* and *S. verbascifolium* (Solanaceae), and also on *Verbesina encelioides* (Compositae) and alfalfa (*Medicago sativa*, Leguminosae). They bred to maturity nymphs of this species found on alfalfa, using only this plant for food, and development was normal. They reported that in laboratory breedings nymphs which were first fed on *Lycium cestroides* readily changed to other species of *Lycium*, but would starve to death rather than accept *Solanum* or genera of other plants. Conversely, nymphs started on *Solanum* would not accept *Lycium*. Thus, food plants, at the generic level, are determined by the first food of the newly hatched nymphs. The same feeding experiments demonstrated that this species would not eat species of the grass family (Turk and Barrera 1976). Carrasco (1962), however, reported *C. speciosa* and another unidentified species (evidently *C. peruviana* according to Carrasco's description) feeding on rice plants and doing considerable damage to this crop in Peru. Guagliumi (1973) mentioned *C. speciosa* as feeding on sugar cane in northeastern Brazil. Astacio-Cabrera (1975) reported *C. colorata* in Nicaragua on the composite *Baltimora recta*, and Pretto-Malca (1968) has stated that this species in Mexico usually feeds, and has been bred on, *Solanum elaeagnifolium*. Rowell (1978) reported the Solanaceae as the preferred food of *C. trogon* in Costa Rica.

Behavior.—The gregarious stages of *Chromacris*, which are usually seen forming large groups on the tops of their food plants, together with their bright and contrasting coloration suggest that they are unpalatable or poisonous to predators and that their coloration is premonitory. One of us (H.R.R.) recently observed 20 to 30 conspicuous nymphs on top of a tussock of grass two or three meters from a small solanaceous shrub stripped of its leaves, which suggests that the gregarious behavior is a part of the premonitory defense. After reaching the imaginal stage, these insects tend to disperse. Adults are very visible during flight, but once they alight on vegetation, they seem to disappear after the display of their colorful wings suddenly ceases.

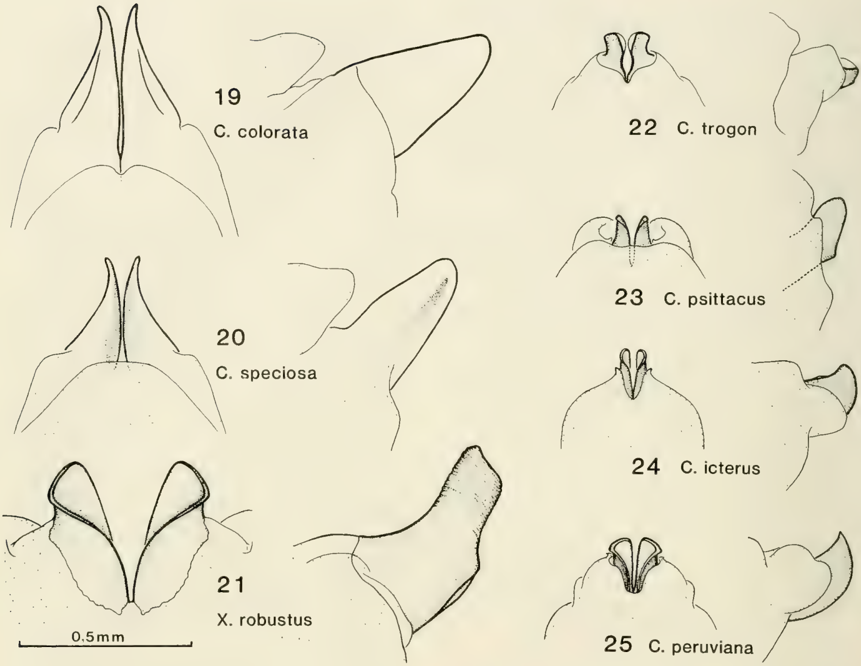
Habitat.—The species of this genus are usually found at forest edges and clearings, roadsides, edges of cultivated fields, and nearly all places where herbaceous solanaceous and composite plants occur. They seem to avoid heavy forest and prairie habitats.

1. **Chromacris colorata** (Serville)

Acridium coloratum Serville, 1839:674. [Holotype, MNHN, no longer extant, said to come from South Carolina, USA, obviously in error. Mention of the 8–10 basal segments of the antennae as yellow and others black clearly indicates that it is the Mexican species.]

Rhomalea pedes Saussure, 1859:392. [Lectotype, ♂, Geneva Museum; Mexico. So labelled by C.S.C. and here designated.]

Diagnosis.—Eight to 12 proximal segments of antennae yellow, distal segments black—a unique color pattern for the genus. Posterior margin of the pronotum yellow, but no yellow patches on midportion of lateral lobes, as is usual in *C. speciosa*. Three yellow bands on hind femur and only one distal band on hind tibia. Middle leg with one band on tibia, femur, and



FIGURES 19–25. Dorsal and lateral views of aedeagi. Figs. 19 and 20 are examples of *colorata-miles* group. Figs. 22–25 are examples of *trogon* group. Fig. 21. *Xestotrachelus robustus* from Cerro Corá, Amambay, Paraguay. Fig. 19. *Chromacris colorata* from Medellin de Bravo, Veracruz, Mexico. Fig. 20. *C. speciosa* from Resistencia, Chaco, Argentina. Fig. 22. *C. trogon* from San Lorenzo, Aulajuela, Costa Rica. Fig. 23. *C. psittacus* from Las Pavas, Santa Marta Mts., Colombia. Fig. 24. *C. icterus* from Villavicencio, Colombia. Fig. 25. *C. peruviana* from Aucayacu, Huánuco, Peru.

trochanter. Fore legs with one band on tibia. Hind wings rich cherry-red, with black pattern (Fig. 3) similar to that in *C. speciosa*. Prosternal tubercle tapers to a narrow point, much as in *C. psittacus* and other yellow-winged species. The small, short aedeagus formed by a pair of papillose, flattened lobes (Fig. 19) slightly sclerotized internally. Aedeagus similar to others of the colorata group.

DISTRIBUTION.—Tropical humid areas of Mexico south to Costa Rica. Of common occurrence July to September.

SPECIMENS.—**Mexico.** States of Nuevo León, Tamaulipas, San Luis Potosí, Veracruz, Oaxaca, Guerrero, Morelos, Jalisco, Nayarit, Sinaloa, and Yucatán.

Guatamala. EL PETÉN: 3 mi [4.8 km] S Tikal, 16 Aug. 1974 (J. C. Lee), 6♂, 3♀. 22 mi. [35 km] NW Poptun, 15 Jul. 1974 (J. C. Lee), 1♂, 3♀.

Belize. Río Grande, Aug. 1931 (J. J. White), 3♀.

Nicaragua. MANAGUA: Sep. 1955 (E. Morales-Agacino), 2♂, 1♀, CSC.

Costa Rica. GUANACASTE: Cañas, Sep. 1965 (C. H. F. Rowell), 1♂, 1♀, CHFR.

COMMENTS.—Specimens from Volcán Colima (Jalisco, Mexico) and Guanacaste (Costa Rica) agree with Serville's description of *Acridium coloratum* in lacking any banding on fore and middle legs and on hind tibia, and much reduced banding on hind femora. The type-specimen of *Rhomalea pedes* has fully banded legs, as have most Mexican specimens. Costa Rican specimens show small yellow marks on the prozonal part of the lateral lobes of the pronotum, as is also true of some specimens of *C. speciosa*. These Costa Rican specimens also have 12 segments of the antennal flagellum yellow, the following 4 segments part black and part yellow, and only the tip of the antennae entirely black. The Costa Rican specimen has no yellow on posterior margin of pronotum.

2. **Chromacris minuta** n.sp.

DIAGNOSIS.—Six to eight apical antennal segments yellow, other segments black. Hind wings orange-red rather than cherry-red as in *C. colorata*. Body color pale olive-green with greatly reduced yellow markings. No yellow bands on legs except weakly developed proximal and median bands on hind femur. Prosternal tubercle short and conical. End of aedeagus much as in *C. colorata*. Body size small for the genus, males 26–31 mm, females 35–39 mm from fastigium to end of wings.

SPECIMENS.—**Holotype:** ♂, ANSP, Acapulco, Guerrero, Mexico, 13 Aug. 1935 (H. R. Roberts, E. R. Helwig).

Paratypes: Mexico. GUERRERO: 5 mi. [8 km] N Acapulco, 15 Sep. 1940 (C. Bolivar, H. R. Roberts), 7♂, 1♀. Same data as for holotype, 6♂, 8♀, 3 juv.

COMMENTS.—This species is most similar to *C. colorata*. It should be looked for elsewhere along the Pacific coast of Mexico. A female of *C. colorata* from between Tierra Colorada and Río Papagayo, about 40 km north of Acapulco, shows some reduction of yellow banding of the legs as occurs in *C. minuta*, but in other respects is typical of *C. colorata*.

3. **Chromacris miles** (Drury)

Gryllus locusta miles DRURY, 1773:79, pl. 42, fig. 2. [Holotype, ♀, not found in British Museum or Oxford collections, but excellent figure should suffice; "Bay of Honduras."]

DIAGNOSIS.—Red wing pattern (Fig. 5) similar to that in *C. colorata* and others of the colorata group. Resembles *C. colorata* in lacking yellow in middle area of lateral lobe of pronotum. This condition occurs rarely in *C. speciosa*. Similar to *C. speciosa* in having entirely black antennae and two yellow bands rather than one on hind tibiae, but differs in having yellow on hind margin of pronotum interrupted by black or green only on midline, whereas in *C. speciosa* it is interrupted on midline and both sides at the angles that limit disc from lateral lobes of metazona. Also, in *C. miles* rim of coxal articulation on mesathorax and metathorax green, whereas it is entirely or partially yellow in *C. speciosa*.

SPECIMENS.—**Mexico.** QUINTANA ROO: 5 mi. [8 km] SE Polyuc (Boloyuc), 28 Jul. 1960 (P. M. Litchfield), 1♂, UMMZ. VERACRUZ: Laguna Verde, Aug. 1974 (M. Descamps), a small series of males and females, MNHN.

COMMENTS.—It has been thought that Drury's name should be applied to Thunberg's South American species, *C. speciosa*. Finding specimens from Veracruz and the peninsula of Yucatán which closely match Drury's figure supports the existence of a distinct species in the Bay of Honduras region. Based on the black pattern of the hind wings, this species belongs to the colorata group and is closest to *C. speciosa* in the strong development of the stridulatory areas on the hind wing. Its color pattern is also more similar. *C. speciosa*, however, does not occur north of Colombia, and *C. miles* occurs within the range of *C. colorata*. More information on the distribution of the genus in this region is needed to clarify our understanding of Drury's species.

4. **Chromacris speciosa** (Thunberg)

Gryllus speciosus THUNBERG, 1824:404. [Lectotype, ♀, so labelled by C.S.C. and here designated; two male syntypes also examined; Uppsala Museum; Brazil].

Acridium xanthopterum HAHN, 1835, table A, fig. 2. [Holotype unknown; Brazil. Hahn attributes the name to Perty in "Ins. nov bras.," but no such reference has been found. Black pattern of hind wing shown in illustration identifies it as the yellow-winged form of this species. New synonym.]

Rhomalea stolli PICTET AND SAUSSURE, 1887:351. [Lectotype, ♂, so labelled by C.S.C. and here designated; Geneva Museum; Bahia, Brazil. Synonym by Kirby 1910:373.]

DIAGNOSIS.—Varies geographically and locally. Red winged over most of its range, but in lowland coastal area from Bahia, Brazil, to Uruguay, wings are frequently orange or yellow, and tegmina tend to be green rather than green tinged with red. Yellow-winged individuals readily distinguished from the typically yellow-winged species of the trogon group by entirely black basal half of the first two plaits (anterior or first paired fold of wing) (Fig. 6). In Paraguay, Argentina, and Uruguay wings tend to be orange-red, and yellow markings are tinged with red. In Bolivia, Peru, and Ecuador reduction and variation in leg banding evident. Elsewhere, hind femur almost always has three pale bands and the hind tibia two pale bands. Specimens from Ecuador and Peru lack hind tibial bands,

TABLE 1. VARIATION IN BANDING OF HIND FEMUR OF *Chromacris speciosa* (22 specimens from Ecuador and Peru, 60 specimens from Santa Cruz, Bolivia).

	Banding of hind femur					
	Ecuador, Peru			Bolivia		
	Strong	Weak	Absent	Strong	Weak	Absent
Proximal	17	5	—	40	20	0
Median	—	10	12	5	37	18
Distal	—	1	21	27	3	30

and hind femur usually has a strong proximal band, median band may be weak or absent, and distal band nearly always absent. Some 60 specimens from city of Santa Cruz region of eastern Bolivia show great variation in presence or absence of various bands. Hind tibia may have a distal band or none. Hind femur usually has strong proximal band; it is never absent; median band usually weakly developed; distal band may be strongly developed (Table 1). Also, in the Andean region north to Ecuador, body color and tegmina darker.

SPECIMENS.—Unless otherwise noted all specimens have red hind wings, three yellow bands on hind femur, two yellow bands on hind tibia, and tegmen tinged with red.

Colombia. MAGDALENA: Aracataca, 4–10 Aug. 1920 (Rehn, Hebard), 8♂, 3♀; (3 lack proximal tibial band).

Venezuela. CARABOBO: San Esteban, Nov.–Dec. 1939 (P. Van Duse), 6♂, 7♀. COJEDES: 26 km S jct. Rts. 8 and 13 on Rt. 8, forest, 13 Jul. 1981 (Otte et al.), 1♂, 3♀.

Guyana. Bartica, Dec. 1912 (H. S. Parish), 30♂, 35♀.

Brazil. AMAPÁ: Rio Puxacá, Mazagão, Feb. 1961 (J. C. M. Carvalho), 3♀, UMMZ. Eighteen specimens from Belém, Santarém, Obidos, and Manaus on the Amazon are similar to the Guyana series. PARÁ: Jacareacanga, 6°16′S, 57°44′W, Dec. 1968 (Alvarenga), 3♂, 9♀, UMMZ. BAHIA: 100 km NW Feira de Santana, 13 Mar. 1981 (Roppa, Carbonell, Roberts), 2♂, 2♀; Itabuna, research center, 22 Nov. 1974, cacão forest (Roberts, Carbonell), 1♀; Mucurí, Aug. 1977 (Roppa, Becker), 2♂ (one yellow wings, other orange wings). ESPÍRITO SANTO: Itapemirim falls, 1–6 km E BR. 101, edge of forest and marsh, 5 Dec. 1974 (Roberts, Carbonell), 4♀ (lack usual yellow median spots on lateral lobe of pronotum); 3 km S Linhares, cacão forest, 1 Dec. 1974 (Roberts, Carbonell), 2♂, 1♀ (lack usual yellow spots on lateral lobe of pronotum). RIO DE JANEIRO: Floresta de Tijuca, Jan. 1981, 4♂, 6♀ (yellow wings), 5♂, 6♀ (orange wings); BR. 101, 1 Feb. 1974 (D. Otte), 2♂ (yellow wings, tegmina lack red tinge); Petropolis, 12 Apr. 1913 (M. Burr), 2♂ (yellow wings, tegmina lack red tinge). MINAS GERAIS: Viçosa, 9 Aug. 1938 (B. T. Snipez), 2♀ (yellow wings, tegmina lack yellow tinge); 46 km SE Itajuba, 1400 m, 21 Mar. 1980 (Roppa, Carbonell, Roberts), 3♂, 3♀. GOIÁS: betw. São Simão and Jataí, 5 Mar. 1980 (Roppa, Carbonell, Roberts), 1♂, 2♀; 15–30 km E Mineiros, 7–9 Mar. 1980 (Roppa, Carbonell, Roberts), 1♀. SÃO PAULO: 10 km W São João de Boa Vista, 19 Mar. 1980 (Roppa, Carbonell, Roberts), 30♂; Franca, Jan. 1911 (E. Garbe), 1♂, 1♀; Salto Grande, Feb. 1911 (H. Luderwaldt), 1♂; Cubatão (Alin), 2♂, 1♀ (orange wings, tegmina lack red tinge); Piracicaba, 1♂ (orange wings). PARANÁ: 24°38′S, 54°07′W, 500 m, Mar. 1965, "virgin deciduous forest (no Araucaria) with many palms (Euterpe etc.), no grass, under growth of ferns and other plants" (F. Plaumann), 4°, 19♀, UMMZ; Curitiba, 13 Feb. 1941 (J. R. Bailey), 1♂, 1♀, UMMZ (male has orange wings, lacks red tinge on tegmina). SANTA CATARINA: Nova Teutonia, 27°11′S, 52°23′W, 6 km SW Seara, 300–500 m, 1961–1964 (F. Plaumann), 6♂, 5♀, UMMZ; Corupa, Jan.–Mar. 1956–1962 (Anton Maller), 3♂, 9♀, UMMZ (1♂, 5♀ have red wings, 2♂ lack red tinge on tegmina, 2♂, 4♀ have orange-yellow wings and lack red tinge on tegmina); Rio Capivari, 1889 (Fruhstorfer), 2♀ [gift of Dr. H. Saussure, ANSP, labelled *R. miles* Drury and *Rhomalea speciosa*, probably what Pictet and Saussure considered to be *R. miles* Var. C, as it has yellow wings; there are two Rio Capivari's in eastern lowlands of Santa Catarina]; Pinhal 700 m, Apr. 1959 (Anton Maller), 1♀ (yellow wings, lacks red tinge on tegmina). RIO GRANDE DO SUL: Aratinga, Feb. 1964 (Carbonell, Mesa, Monné), 1♂ (yellow wings). MATO GROSSO: 40 km E Rodonópolis, 11 Mar. 1980 (Roppa, Carbonell, Roberts) 1♂; 30 km NW Alto Araguaya, 750 m, 10 Mar. 1980 (Roppa, Carbonell, Roberts) 1♂; Chapada near Cuiabá, 4♂, 3♀ (1♂ lacks distal band on hind femur); Corumbá, Urucum, 22–29 Dec. 1919 (R. G. Harris), 12♂, 12♀ (proximal median bands weak, distal band strong on hind femur, proximal tibial band usually absent); Tres Lagos, 6–10 Dec. 1919 (Harris), 4♀ (hind legs fully banded, and one of these with yellow markings strongly tinged with red), 1♀ (distal band on hind femur and hind tibia only). MATO GROSSO SUL: 30–60 km E Aquidauana, 16 Mar. 1981 (Roppa, Carbonell, Roberts), 2♂.

Uruguay. Whole country, Dec.–Apr., large series, CSC (yellow markings tinged with red).

Ecuador. Balzapamba (R. Haensch), 1♂ (weak proximal band on hind femur). Putumayo Dist., La Sombra to El Encanto, 23 Aug. 1920, 1♂ (strong proximal and weak median band on hind femur).

Peru. JUNÍN: Satipo, 15 Nov. 1945 (P. Paprzycki), 1♂, 8♀; Satipo, 650 m, Jul. 1940 (Schunke) 1♀; Col. Perené, El Campamento, 22 Jul. 1920, 2♀; Chanchamayo, 1♂, 1♀; Vilcanota, 1♀; Puerto Yessup, Feb. 1930 (M. A. Carriker), 1♀. CUZCO: Valle de Urubamba, Sahayaco, 800 m, 7 Dec. 1947 (Weyrauch), 4♂; Prov. La Convención, Sangobatea, Jan. 1976 (J. S. Escalante), 3♂, 3♀, JAE; Prov. Paucartambo, Salvación, Oct. 1968 (F. Carrasco), 1♀, FCZ. All Peruvian specimens have moderate to well-developed proximal bands, weak to no median bands, and no distal bands on hind femur; no bands on hind tibia and other legs.

Bolivia. SANTA CRUZ: Province of Sara, 450 m, Jan. 1918 (J. Steinbach), 19♂, 27♀ (35 had no tibial banding, 11 had weak distal yellow bands; on hind femur all had weak to strong proximal bands, 14 had no median bands, 22 had weak to strong distal bands, and 24 had no distal bands) [Note: this previously recognized Province of Sara, bounded in part by the Río Grande or Guapay and the Río Mamoré or Ichilo, is the region where Steinbach did much of his collecting, and included the town of Buena Vista (where his relatives lived and where a niece presently operates a small restaurant, store, and inn), Portachuelo, and the city of Santa Cruz, that is, Santa Cruz de la Sierra.]; Buena Vista, May 1917 (Steinbach), 2♂, 1♀; between Buena Vista and San Carlos, 350 m, cacão forest, 21 Feb. 1976 (Ronderos, Roberts) 2♂, 1♀; between Buena Vista and Portachuelo, 20 Feb. 1976, 1♀ (specimens from last three localities similar in variation to those from

Prov. of Sara; Santa Cruz de la Sierra, Feb. 1922 (J. Steinbach), 5♂, 6♀; 18 km sw Santa Cruz, 400 m, 16 Feb. 1976 (Ronderos, Roberts), 3♂, 2♀ (of last 16 specimens, 15 had a strong distal band on hind femur, 1♂ lacked this band); Prov. of Nuflo de Chávez, Ascención, 15°42′S, 63°05′W, 500 m, Nov. 1963 (Walz), 4♂, 5♀ (5 had distal and 4 had no distal band on hind femur). See Table 1 for a summary of this banding.

Paraguay. 26 specimens from Villa Rica, Jan., Feb.; Sapucay, Jan.–Apr.; Horqueta, Dec., Jan. (yellow markings strongly tinged with red; hind femur with three bands, hind tibia with two bands).

Argentina. 102 specimens from 24 localities in the provinces of Jujuy, Feb.; Salta, Mar.; Chaco, Feb.; Misiones, Dec., Feb.; Tucumán, Mar.; Catamarca, Mar.; Córdoba, Mar.; Entre Ríos, Mar.; La Rioja, Feb.; Mendoza Feb.–Apr.; San Luis, Jan.; Buenos Aires, Feb. As in Paraguay and Uruguay, yellow markings are strongly tinged with red; hind femur with three bands, hind tibia two bands. Adults may be found December to April.

COMMENTS.—Unlike other species of the genus, no consistent differences have been found to distinguish various geographical developments. Comparing specimens, for example, from Carabobo, Venezuela, with those from Santa Cruz, Bolivia, or Corupá, Brazil, it is evident that considerable geographic differentiation occurs, but it does not seem possible or practical with our present evidence to recognize subspecific elements of the species.

5. **Chromacris nuptialis** (Gerstaecker)

Rhomalea nuptialis GERSTAECKER, 1873:185. [Holotype, ♂, bearing label with number 2008, and ♀ allotype, Berlin Museum; Saltogrande (Sellow). The locality of Salto Grande of Sellow is uncertain. Sellow visited Salto Grande on the Uruguay River (Department of Salto, Uruguay), but none of the species he labelled Saltogrande has ever been found in Uruguay or the adjacent Brazilian state of Rio Grande do Sul. Sellow's Saltogrande is very probably that on the Paranapanema River in the state of São Paulo. Types examined.]

Rhomalea latipennis PICTET AND SAUSSURE, 1887:351. [Holotype, ♂, Geneva Museum; Brazil. It does not have a locality label but bears the number 477-56, which in the museum records corresponds to Brazil, collected by Ferrier circa 1856. We have been unable to trace the collector's route in Brazil. Holotype examined. New synonym.]

DIAGNOSIS.—Coloration highly variable, including individuals with pale yellow and pale red wings. Body and legs with yellow or red markings (irrespective of wing color). Antennae black. Pattern of hind wings as in *C. speciosa*. Tegmina very characteristic, membrane dark brown to black, strongly contrasting straw-colored veins. Fore and middle legs without transverse bands, ground color variable from greenish yellow to reddish brown; longitudinal series of black spots, sometimes coalescing into black streaks. Hind femora black to dark brown, with longitudinal carinae and fishbone pattern of a lighter color, variable from reddish brown to straw-yellow; transverse bands absent or very slightly marked, only exceptionally, plainly visible, proximal one on upper half only, median one may be complete, distal one always absent. Proximal and median bands always visible on inner and lower surfaces of hind femur as conspicuous yellow or red areas, no trace of distal one. Hind tibia generally dark colored, especially on inner side, transverse bands generally absent, sometimes faintly marked, the distal one, proximal one, or both may be visible in different specimens. Prosternal tubercle relatively slender, long, and curved rearwards.

DISTRIBUTION.—Inland south-central Brazil, including southern Goiás, western Minas Gerais, western São Paulo, and northwestern Paraná.

SPECIMENS.—**Brazil.** D.F.: Brasília, Nov. 1963 (N. Tangerini), 2♂ (yellow wings), CACS. GOIÁS: rodovia Anapolis–Brasília, km 63, 17 Feb. 1964 (H. M. Canter), 1♂ (yellow wings), MZSP; betw. São Simão and Jataí, 5 Mar. 1980 (Roppa, Carbonell, Roberts), 1♀ (red wings), CACS; Minieros, Feb. 1975 (Roppa, Silva), 1♀ (red wings), CACS. MINAS GERAIS: Uberaba, Feb. 1979 (Roppa, Silva), 1♂ (red wings), CACS; Diamantina, Mar. 1956 (D. Albuquerque), 1♀ (red wings), CACS; Lagoa Santa, Jul. 1965 (M. S. Morgante), 1♂ (yellow wings), MZSP. PARANÁ: Vila Velha, Jan. 1975 (C. Valle), 1♂, 1♀ (yellow wings), MZSP.

COMMENTS.—Individuals of this species are highly variable in color, and therefore difficult to identify. However, the only other species known from the area is *C. speciosa*, from which it can be separated by the peculiar coloration of its tegmina, the very different color on pronotum and legs, and the form of its pronotal tubercle. The species appears to be uncommon, being always represented by one or two specimens from each locality, which is unusual for species of this genus. Possibly, this taxon is a highly aberrant variation of *C. speciosa* in the middle of whose territory it occurs, but the constancy of some of its characters seems to indicate that it is a distinct species.

6. **Chromacris trogon trogon** (Gerstaecker)

Rhomalea trogon GERSTAECKER, 1873:186. [Holotype, 1♀, Berlin Museum; Costa Rica. (Gerstaecker noted that hind legs were lacking. A bright yellow marked leg was later attached and now removed. Holotype examined.]

DIAGNOSIS.—Hind wings yellow to orange-yellow, and lack black on anterior basal half of first two plaits (Fig. 7). Antennae entirely black. No yellow banding on legs, although often faint pale green bands present on hind femora (Table

TABLE 2. DIAGNOSTIC CHARACTERS FOR THE SPECIES AND SUBSPECIES OF THE TROGON GROUP OF GENUS *Chromacris*. A band that does not extend entirely around the hind femur is listed as a half band.

Name	Range	Antenna	Basal ½ of wing	Pronotal metazona	Hind femur	Hind tibia
t. intermedia	N Guatemala to Honduras	all black	all yellow	no yellow	3 half bands	no bands
t. trogon	Costa Rica	all black	all yellow	no yellow	no bands	no bands
p. psittacus	Costa Rica to N Colombia, N Venezuela	all black	all yellow	no yellow	2 and ½ bands	2 bands
p. pacificus	W Colombia, W Ecuador	all black	all yellow	no yellow	3 bands	2 bands
icterus	E Colombia to NE Peru, NW Brazil	tip yellow	all yellow	yellow patches	3 bands	1 band
peruviana	Peru	tip yellow	plait 1 black	yellow patches	3 bands	2 bands

2). Reproductive structures and prosternal tubercle similar to those in *C. psittacus* and other yellow-winged species of the trogon group.

DISTRIBUTION.—Costa Rica and questionably Nicaragua.

SPECIMENS.—**Costa Rica.** Pozo Azul, Río Perris or Parrita (forested foothills of Pacific coastal plain), May 1902 (M. A. Carriker), 2♂, 1♀; 22 Aug. 1927 (Lankester and Rehn), 3♂, 1♀. Between La Unión and Buenos Aires, Terraba Valley, 5500 ft. [1670 m], May 1935 (Lankaster), 1♀. Juan Viñas, 3300 ft. [1000 m], Mar. 1902 (L. Beamer), 1♂, 1♀; 27 Jun. 1909 (P. P. Calvert), 1♂, 1♀. Peralta, 8 Aug. 1909 (Calvert), 1♂; May 1923 (Lankester), 1♂. La Emelia near Guapiles, Aug. 1923, Sep. 1927 (Rehn), 4♂. Cariblanca, 600 m (Lankester), 1♀. Parisimina, 5 m, 26 Jul. 1928 (M. Valerio), 1♀. PUNTARENAS: Río Cataratas, near Brujo, Sep. 1979 (Rowell), 1♂, 1♀. ALAJUELA: 5 km S San Lorenzo, Sep. 1979 (Rowell), 1♂, 1♀, CHFR.

Nicaragua. CHONTALES: (Janson), 1♂, 1♀ (poorly preserved but appears to be this species).

COMMENTS.—Although we have no records of *C. trogon trogon* and *C. psittacus* occurring together, it seems possible that they do. For example, we have this species from near Guapiles and *C. psittacus* from Siquirres about 30 km distant in similar lowland forest country.

7. **Chromacris trogon intermedia** n.subsp.

DIAGNOSIS.—Wing orange with no black on basal half of first two plaits, or first paired fold as in *C. colorata*. Antennal segments all black. Hind femur with yellow bands that may be weakly or strongly developed. Hind tibia with no bands. Prominent wide yellow stripe along ventral margin of lateral lobe of pronotum that extends onto cheek of head. Prosternal tubercle short, tapering rapidly to a point. Distinguished from *C. psittacus* by lack of banding on hind tibia, and from the nominate subspecies of *C. trogon* by banding on hind femur (Table 2).

DISTRIBUTION.—Northern Guatemala, Belize, and Honduras.

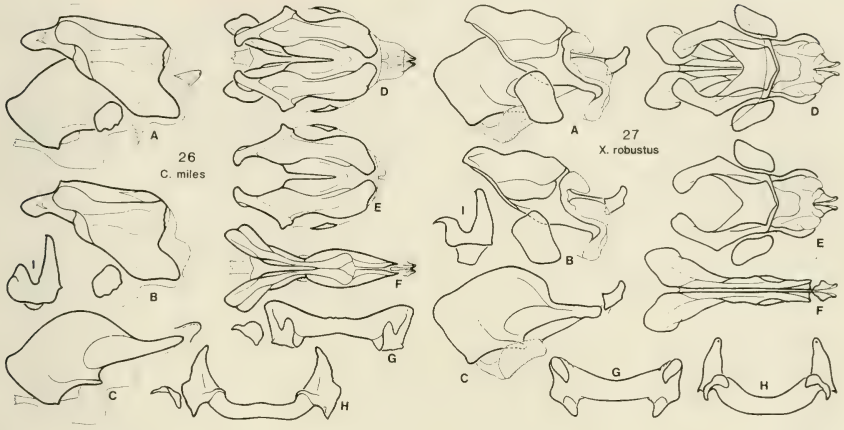
SPECIMENS.—**Holotype:** ♂, ANSP; Honduras, Lancertilla near Tela, Dept. Atlantica, 100–800 ft. (30–250 m), rain forest, 8 Nov. 1930.

Paratypes: Same data as for holotype, 3♀. **Belize.** 50 mi. [80 km] S El Cajo, Mountain Pine Ridge road, 17 Aug. 1960 (P. N. Litchfield), 1♂, 2♀, UMMZ. **Guatemala.** Piedras Negras, 600–800 ft. [180–240 m], 30 Jun. 1933 (D. W. Amran), 1♀.

COMMENTS.—This subspecies is intermediate between *C. trogon trogon* and *C. psittacus* in the reduction in banding of the hind leg, which might suggest that they should be treated as three subspecies, but *C. trogon trogon* and *C. psittacus* occur close together in Costa Rica, though as noted under the subspecies, *C. trogon trogon,* they have not been recorded from the same locality. Specimens from Nicaragua and Honduras are needed to help clarify the problem.

8. **Chromacris psittacus psittacus** (Gerstaecker)

Romalea psittacus GERSTAECKER, 1873:185. [Lectotype, ♂, among four male syntypes with same data, one marked "typus" and here designated; Berlin Museum; Bogotá, Colombia. Species of *Chromacris* probably do not occur in the vicinity of Bogotá. ANSP has specimens of *C. icterus* also labelled Bogotá, and this species actually occurs at lower elevations on the eastern slopes of the Andes.]



FIGURES 26 and 27. Internal male genitalia of *Chromacris miles* from Quintana Roo, Mexico (Fig. 26), and *Xestotrachelus robustus* from Ihú, Caaguazú, Paraguay (Fig. 27). *A*, phallus, lateral; *B*, cingulum, lateral; *C*, endophallus, lateral; *D*, phallus, dorsal; *E*, cingulum, dorsal; *F*, endophallus, dorsal; *G*, epiphallus, dorsal; *H*, epiphallus, frontal; *I*, epiphallus, lateral, left side.

DIAGNOSIS.—Wings yellow to orange-yellow, lacking black on anterior basal half (Fig. 8). Antennae all black. No yellow on dorsum of metazona of pronotum. Hind femur with three yellow bands, but proximal band not entire. Hind tibia with two bands. For comparison with other species see Table 2.

SPECIMENS.—**Costa Rica.** Siquirres, 3 Jul. 1903 (M. A. Carriker), 7♂, 1♀. Ujarass de Terraba, 10 Sep. 1907, 1♂. Monte Verde, "summer," 1928 (F. G. Wallace), 1♂, 1♀. Castilla Farm, lower Río Reventazon, 29 Jul. 1936 (C. W. Dodge), 1♂.

Panama. Gatún, Jul.–Aug. 1916 (D. E. Harower), 8♂, 3♀. Cabima, 24 May 1911 (August Busck), 2♂, 1 juv. Barro Colorado Island, C.Z., 22 Jul. 1933 (H. H. Hood), 1♀.

Colombia. CUNDINAMARCA: Las Mesitas, Sep. 1915 (A. Maria), 1♂, 3♀.

Venezuela. ZULIA: Kasmera, Río Yasa, Sierra de Perija, 250 m, 19 Sep. 1961, 2♂, 3♀, Universidad Central, Instituto de Zoologia Agricola, Maracay.

COMMENTS.—Evidently seasonal. One of us (H.R.R.) visiting Costa Rica for several years in the Pacific and Caribbean lowlands during February and March never encountered this species or *C. trogon*. Most of our records suggest that it occurs commonly May to September.

9. **Chromacris psittacus pacificus** n.subsp.

DIAGNOSIS.—Similar to *C. psittacus psittacus* except proximal yellow band on lower portion of hind femur entire rather than interrupted. See Figure 1 and Table 2.

SPECIMENS.—**Holotype:** ♂, ANSP; Ecuador, Dos Puentes, below Naranjapata along the Guayaquil-Quito railway in Chanchan River valley, 1750 ft. [530 m], 15 Mar. 1931 (W. J. Coxey). [Additional information on location of Dos Puentes is added here from Coxey 1927:10.]

Paratypes: Colombia. EL VALLE: Jiménez, 1600 ft. [486 m], 19 Mar. 1907 (M. G. Palmer), 2♂, 1♀; Choco (M. G. Palmer), 1♀. ANTIOQUIA: Andagoya, 1♀; Cordillére, "vers occid. Río Yurumaqui," 1933 (E. Aubert de la Rue), 1♂, 1♀, MNHN. NARIÑO; "entre Guayacana et el Diviso," 80 m, Nov. 1968 (M. Descamps), 1♂.

Ecuador. CHIMBORAZO: Dos Puentes, 1750 ft. [533 m], 11 Jan. 1921 and 15 Mar. 1931 (W. J. Coxey), 5♂, 2♀; Ventura, 1400 ft. [469 m], 10–13 Apr. 1922, 3♂, 3♀. GUAYAS: Bucay, 900 ft. [274 m], 19 Mar. 1922 (G. H. Tate), 1♀. TUNGURAHUA: Ambato, 1♂, MNHN; Balzapamba, near Ambato (R. Haensch S.), 1♂, Berlin Museum.

COMMENTS.—The slight but consistent difference in the form of the proximal yellow band on the hind femur of these specimens warrants subspecific recognition.

10. **Chromacris icterus** (Pictet and Saussure)

Rhomalea icterus PICTET AND SAUSSURE, 1887:353. [Lectotype, ♀, so labelled and here designated, Geneva Museum; Quito, Ecuador.]

Rhomalea opulenta GERSTAECKER, 1889:32. [Holotype, ♀, Zoological Museum, University of Greifswald; São Paulo de Olivença, Amazonas, Brazil. Holotype examined. New synonym.]

Diagnosis.—Tip of antenna yellow. Anterior, basal portion of hind wing entirely yellow (Fig. 9). Yellow patches on dorsum of metazona of pronotum. Three yellow bands on hind femur. Single proximal band on hind tibia distinguishes species from all others (see Table 2). A large species with relatively long wings; males 30–38 mm, females 40–55 mm from fastigium to wing tips.

Distribution.—Southeastern Colombia, eastern Ecuador, northwestern Brazil and northeastern Peru.

Specimens.—**Colombia.** Bogotá: (so labelled but probably in error) (A. Maria), 2♂, 4♀. Cundinamarca: Susumuco, Feb., Sep. 1916, 1917 (A. Maria), 3♂, 2♀. Meta: Villavicencio, May, Jun. 1919 (A. Maria), 2♂, 2♀. Putumayo: "bord riviére Mocoa," 800 m, Nov. 1968 (M. Descamps), 1♂, MNHN.

Ecuador. Morona-Santiago Prov.: s of Méndez, 800 m, 19–21 Oct. 1977 (L. E. Peña), 1♀.

Peru. Loreto: Putumayo District, La Chorrera to La Sombra, 21 Aug. 1920, 1♀; Iquitos, 8 Jan. 1920 (H. S. Parish), 1♀.

Brazil. Amazonas: "Hyntanahan" probably Huitanaa, Rio Purus, Jan. 1922 (S. M. Klages), 1♀; Tabatinga, Sep.–Dec. 1977 (L. C. Pereira, B. Silva), long series both sexes, CACS; Eirunepe, Jun. 1950 (J. C. Carvalho), 2♂, 1♀, CACS; Atalaya do Norte, Nov. 1977 (B. Silva), long series, CACS.

11. **Chromacris peruviana** (Pictet and Saussure)

Rhomalea peruviana Pictet and Saussure, 1887:352. [Lectotype, ♀, so labelled by C.S.C. and here designated from among 1♂ and 3♀ syntypes, Geneva Museum; Peru.]

Diagnosis.—Similar to *C. icterus* in having yellow wings and yellow antennal tips, but differs by having two yellow bands on hind tibiae rather than one (Table 2); differs from all other yellow-winged species by having the black on anterior portion of first plait of hind wings extend to base of wing (Fig. 10). Tegmina relatively long, narrow, and greatly surpassing ends of hind femora; anterior and posterior margins bordered by yellowish or pale green areas. This tegminal coloration is unique for genus.

Specimens.—**Peru.** Junín: Chanchamayo, a district around La Merced in valley below Tarma, 2000–3000 ft. (610–914 m), 1♂; Satipo, near Huancayo, 1650 m, Jul. 1844 (Schunke), 1♂; Mar., Jun. 1944 (P. Paprzycki), 3♀; Puerto Yessup, Feb. 1930 (M. A. Carriker), 1♀. Huánuco: Leonpampa, 110 km e Huánuco, Dec. 1937 (Felix Woytkowski), 3♂, 1♀; Tingo María, 670 m, Sep. 1946 (Weyrauch), 3♀; same locality, 2 Dec. 1954 (E. D. Schlinger, E. S. Ross), 1♀; Divisoria, Cordillera Azul, 1500 m, 1♂, 1♀. Loreto: Río Aguaytia, between Tingo María and Pucallpa, 400 m, Feb. 1961, 1♂, 2♀. San Martin: Prov. Huallaga, Río Mixiollo, 1200 m, 7 Aug. 1900 (C. A. Baer), 1♀. Cuzco: Paucartambo, Pilcopata, Nov. 1968 (F. Carrasco), 1♂, 1♀; Paucartambo, Atalaya, May 1976 (Descamps, Carbonell), 1♂, 1♀, CACS.

Venezuela. Aragua: Nov. 1942, 3♀.

Comments.—The Venezuelan specimens are undoubtedly this species. However, *C. icterus* occurs between this and the Peruvian localities, suggesting the need to confirm the correctness of the locality.

Xestotrachelus Bruner

Xestotrachelus Bruner, 1913:469. [Type-species *Xestotrachelus hasemani* Bruner (=*X. robustus*) by original designation.]

Diagnosis.—Red and black pattern of hind wings (Fig. 11) closely resembles red-wing species of *Chromacris*, but head and thorax are much more robust, and tegmina may extend well short of, or only slightly beyond, end of hind femora (Fig. 2). Head, pronotum, and other parts of body and appendages may be contrastingly marked with black, pale olive-yellow, and red. Hind tibiae usually red. Phallic structures described under *X. robustus*.

Distribution.—Known from Maranhão in northeastern Brazil, Bahia, Espírito Santo, Mato Grosso; Paraguay; and eastern Bolivia.

12. **Xestotrachelus robustus** (Bruner)

Zoniopoda robusta Bruner, 1911:60. [Lectotype, ♂, here designated, ANSP; Chapada dos Guimarães, Mato Grosso, Brazil. The type-series consisted of a male and female, each labelled as the type.]

Xestotrachelus hasemani Bruner, 1913:470. [Holotype, ♀, ANSP; labelled as from Galhão, not Calhão as reported by Bruner, Rio Sapão, western Bahia, Brazil. Actually Galhão, 10°35′S, 46°15′W, is in Goiás on the Rio Galhão, and the Rio Sapão is nearby in Bahia. New synonym.]

Diagnosis.—See diagnosis of genus. Extent of black on prozona and mesozona of pronotum variable, may be entirely black, or divided to form two black transverse bands. Extent of red on sides and undersides of abdomen also variable. Easily distinguished from species of *Chromacris* by red hind tibia and lack of banding on hind femur.

Phallic structures generally similar to those in *Chromacris*. Aedeagal valves (Fig. 21) strongly sclerotized, much larger, and sculptured. Rami of cingulum (Fig. 27*B*) narrow, partly surrounding base of aedeagus, strongly bent inward and ventrad near their end, and outer surface at bend covered with small spines. Epiphallus (Fig.

27*G–I*) similar to that in *Chromacris* except that the ancorae are well developed.

Distribution.—See distribution of genus.

Specimens.—**Brazil.** Maranhão: Barra do Corda, Feb. 1955, 1♀, CACS. Bahia: Maracás, Feb. 1963 (F. M. Oliveria), 3♀, CACS. Espírito Santo: Linhares, Mar. 1981 (B. Silva), 1♂, CACS. Goiás: in addition to the type-locality of *X. hasemani*, 60 km w Mineiros, 10 Mar. 1980 (Roppa, Carbonell, Roberts), 1♂. Mato Grosso: in addition to the type of *X. robustus*, Corumbá, Urucum, 23–29 Dec. 1919 (R. G. Harris), 4 juv., 18♂, 14♀. Mato Grosso Sul: 30–60 km E Aquidauana, 16 Mar. 1980 (Roppa, Carbonell, Roberts), 1♂.

Bolivia. Santa Cruz: prov. of Sara, 450 m, Jan.–Feb. 1922 (J. Steinbach), 8♂, 16♀; Buena Vista, 500 m, 3 Feb. 1922 (J. Steinbach), 1♀.

Paraguay. Caaguazú: near Ihú, Mar. 1965 (Carbonell, Mesa, Monne), 1♂, 2♀, CACS. Amambay: Cerro Corá, Jan. 1972 (Descamps, Ronderos, Carbonell), 8♂, 5♀, 1 last instar nymph, CSC.

Comments.—Individual geographic variation in relative tegminal length is evident. In the series recorded from eastern Bolivia, tegmen shorter than or about as long as hind femur. In the series from Corumbá, tegmen slightly or decidedly longer than femur. Tegmen of male from near Aquidauana 19 mm and hind femur 15.5 mm in length, whereas in the male from Mineiros, Goiás, tegmen 16 mm and femur 17 mm. Tegmen of female holotype of *X. hasemani* is 26 mm, hind femur 18 mm. This specimen has a decidedly longer tegmen in proportion to the hind femur than do specimens to the south. It seems possible, however, that populations to be found between this type-locality and those presently observed to the south will be intermediate in relative tegminal length. The aedeagus of the male from Espiríto Santo is relatively shorter and therefore appears to be somewhat broader in lateral view than others examined. The red patch near the end of the hind wing in the longer-winged specimens from Linhares and Maranhão connects narrowly with the large red field of the wing. Conceivably, this modification is the result of the lengthened wing. With more evidence the longer-winged *hasemani* form might be recognized as a subspecies.

Noteworthy is the last instar nymph from Cerro Corá, Paraguay, recorded above, the color of which is well preserved and matches the color pattern of the adult. Unlike the species of *Chromacris* which have a bright but relatively cryptic coloration in the adult stage, *X. robustus* has a much more striking coloration in the adult, which may well serve as a warning to predators. Assuming this is correct, then there would be no need to develop a different coloration in the nymphal stages as in *Chromacris*.

Literature Cited

Amedegnato, C. 1974. Les genres d'acridiens néotropicaux, leur classification par familles, sous-familles et tribus. Acrida 3:193–204.

Astacio-Cabrera, O. 1975. Notas sobre algunas acridioideos de Nicaragua. Organismo Internacional Regional Sanidad Agropecuaria, Managua, Nicaragua. 41 p.

Barrera, M., and S. Z. Turk. 1977. Acridios del NOA. II. Contribución al conocimiento de huevos, desoves y hábitos de postura de algunas especies de tucuras (Orthoptera, Acrididae) de la Provincia de Tucumán. Acta Zoological Lilloana 32(9):167–188.

Bruner, L. 1911. South American Acridoidea. Annals of the Carnegie Museum 8(1):5–147.

———. 1913. South American locusts (Acridoidea) II. Annals of the Carnegie Museum 8(3–4):423–506.

Carrasco-Z, F. 1962. Observaciones sobre algunas plagas de interés para la zona del Cuzco. Revista Peruana Entomologia Agrícola 5:97–100.

Coxey, W. J. 1927. Impressions of Ecuador. Year Book (1926) Academy of Natural Sciences of Philadelphia: 5–20.

Drury, D. 1773. Illustrations of natural history, wherein are exhibited upwards of two hundred and twenty figures of exotic insects, etc., vol. II. London. 92 p., 50 pl.

Gaugliumi, P. 1973. Pragas de cana-de-acucar, nordeste do Brazil. M.I.C. Instituto do Açucar e do Álcool. Coleção Canavieira, no. 10. Rio de Janeiro, v + 622 p.

Gerstaecker, A. 1873. Acridiodea nonulla nova insigniora. Entomologische Zeitung, Stettin 34(1–3):185–197.

———. 1889. Charakteristik einer Reihe bemerkenswerther Orthopteren. Mittheilungen aus dem naturwissenschaftlichen Verein Neu-Pommern und Rügen in (Greifswald) Berlin 20:1–58.

Hahn, C. W. 1835. Icones Orthoptorum. Nurnberg. 3 p., 4 pl.

Kirby, W. F. 1910. A synonymic catalogue, Orthoptera Saltatoria. British Museum, London 3(2):1–674.

Pictet, A., and H. de Saussure. 1887. Catalogue d'Acridiens. Bulletin de la Société Entomologique Suisse 7(9):331–376.

Pretto-Malca, R. 1968. Estudios del ciclo biológica, morfometría y etiología de *Chromacris colorata* (Serville), (Orthoptera, Acridoidea). Instituto Tecnologia, Monterrey, mimeographed report:83–87.

Ragge, D. R. 1955. The wing-venation of the Orthoptera Saltatoria. British Museum (Natural History) London. 159 p.

Rehn, J. A. G. 1904. Notes on Orthoptera from northern and central Mexico. Proceedings of the Academy of Natural Sciences of Philadelphia 31:513–548.

———, and H. J. Grant. 1959. An analysis of the tribes of the Romaleinae with special reference to their internal genitalia (Orthoptera: Acrididae). Transactions of the American Entomological Society 85:233–271.

Rowell, H. F. 1978. Food plant specificity in neotropical rain-forest acridids. Entomologie Experimentia et Applicata 24:451–462.

Saussure, H. de. 1859. Orthoptera nova Americana. Revue Magazin Zoologie (2)11:390–394.

Serville, M. A. 1839. Histoire Naturelle des Insects Orthopteres, Paris: 1–776.

Thunberg, C. P. 1824. Grylli Monographia, illustrata.—Mémoirs de l'Academie Imperiale des Sciences de St. Petersbourg 9:390–430.

Turk, S. Z., and M. Barrera. 1976. Acridios del NOA. I. Estudios biológicos, morfométricos y aspectos ecológicos de *Chromacris speciosa* (Thunberg) (Acrididae, Romaleinae). Acta Zoologica Lilloana 32(6):121–146.

Walker, F. 1870. Catalogue of the specimens of Dermaptera Saltatoria in the collection of the British Museum 4:605–809.

CALIFORNIA ACADEMY OF SCIENCES
Golden Gate Park
San Francisco, California 94118

PROCEEDINGS
OF THE
CALIFORNIA ACADEMY OF SCIENCES

Vol. 43, No. 5, pp. 59–66, 5 figs., 1 table.

November 4, 1982

A NEW GENUS AND TWO NEW SPECIES OF REMARKABLE PACIFIC WORM EELS (OPHICHTHIDAE, SUBFAMILY MYROPHINAE)

By
John E. McCosker
Steinhart Aquarium, California Academy of Sciences, Golden Gate Park,
San Francisco, California 94118

Abstract: *Glenoglossa wassi* gen. et sp.nov., described from Samoa, differs from all other myrophine ophichthids in its elongate tongue decorated with a lure, and in certain osteological and cephalic pore conditions. *Neenchelys daedalus* sp.nov., is described from midwater-captured juveniles and adults from off New Guinea and the central Pacific and represents the second known midwater worm eel; it differs from its congeners in its extreme elongation and vertebral number. The status of the species of *Pseudomyrophis* and *Neenchelys* is discussed. An analytical key to the genera of the ophichthid subfamily Myrophinae is provided.

Introduction

The snake eels and worm eels of the family Ophichthidae are the most diverse and inventive of true eels. The more than 220 species distributed among more than 53 genera inhabit all tropical and subtropical oceans and seas, and have invaded the intertidal zone, coral reefs, shallow substrates, and even the midwater realm. To this array of astounding evolutionary forays, I add two remarkable new western Pacific species, one representing a distinct new genus of worm eels, of the subfamily Myrophinae (sensu McCosker 1977). The first, *Glenoglossa wassi* gen. et sp.nov., is unique among eels in having modified its glossohyal into a lure, not unlike that of a uranoscopid stargazer or an antennariid. The other, *Neenchelys daedalus* sp.nov., represents a second, independent invasion of the midwater realm by an ophichthid.

Materials and Methods

Measurements are straight-line, made either with a 300 mm ruler with 0.5 mm gradations (for total length [TL], trunk length, and tail length) recorded to the nearest 0.5 mm, or with dial calipers (all other measurements) and recorded to the nearest 0.1 mm. Body length comprises head and trunk lengths. Head length (HL) is measured from the snout tip to the posterodorsal margin of the gill opening; trunk length is taken from the end of the head to mid-anus; maximum body depth does not include the median fins. Vertebral counts, which include the hypural, were taken from radiographs. Stained and cleared specimens were prepared using the Taylor (1967) trypsin technique. Institutional abbreviations of material examined are explained in the Acknowledgments.

Analytical Key to the Genera of Ophichthidae, Subfamily Myrophinae

1a. All branchiostegal rays originate either in association with hyoid or before level of epihyal tips; free rays, when present, fewer than attached; tail tip a hard or fleshy finless point; gill opening midlateral to entirely ventral, unconstricted .... subfamily Ophichthinae

1b. Accessory branchiostegal rays originate behind ends of epihyal, free rays more numerous than attached; caudal fin rays conspicuous, confluent with dorsal and anal, tail tip flexible; gill openings midlateral, a constricted opening (subfamily Myrophinae) 2

2a. Anterior nostril non-tubular, posterior nostril before eye; eye large, ca. 6 times in head length; pectoral fin moderately developed .... *Benthenchelys* Fowler, 1934

2b. Anterior nostril tubular, posterior nostril either before eye, along upper lip, or within mouth; eye smaller, 10 or more in head; pectoral fin may be absent 3

3a. Posterior nostril before eye, above the lip and not covered by a flap; pectoral fin present, but may be reduced to a small, barely noticeable flap in posterodorsal corner of gill opening 4

3b. Posterior nostril labial, either within lip and opening into mouth, or along lip and covered by a flap; pectoral fin either present and well developed or absent 5

4a. Dorsal fin origin in anterior trunk region; snout conical; pectoral fin well developed, $\cong$ snout; third preoperculomandibular pore (pop^3) absent .... *Neenchelys* Bamber, 1915

4b. Dorsal fin origin in posterior trunk region; snout broad, tumid; pectoral fin minute, $\leq$ eye; pop^3 present .... *Pseudomyrophis* Wade, 1946

5a. Pectoral fin well developed; pleural ribs absent behind 15th–20th vertebrae 6

5b. Pectoral fin absent; pleural ribs present on all trunk vertebrae 7

6a. Dorsal fin origin above or behind anus; maxilla stout, not tapering posteriorly, and abutting pterygoid; vomerine teeth absent .... *Ahlia* Jordan and Davis, 1891

6b. Dorsal fin origin anterior to mid-trunk region; maxilla thin and tapering posteriorly, not closely associated with pterygoid; vomerine teeth present .... *Myrophis* Lütken, 1851

7a. Tongue elongate, extending well beyond mouth and decorated with a fleshy appendage; inner edge of lips and palate decorated with fleshy lappets; teeth conical and uniserial .... *Glenoglossa* novum

7b. Tongue not elongate, not extending outside of mouth, lacking a fleshy appendage at its tip; inner edge of lips and palate smooth; teeth either conical or blunt, uniserial or multiserial 8

8a. A prominent median toothed groove on ventral side of snout, bordered by dermal folds, extends anteriorly to anterior nostrils; anterior nostrils elongated tubes equal to eye in length .... *Schismorhynchus* McCosker, 1970

8b. Ventral side of snout without a prominent median groove bordered by dermal folds; anterior nostrils less than eye in length 9

9a. Teeth absent on vomer, absent or embedded on intermaxillary, those on maxillary and dentary minute or villiform; dorsal fin origin behind anus .... *Schultzidia* Gosline, 1951

9b. Teeth present on intermaxillary, maxillary, dentary, and vomer; dorsal fin origin either before or behind anus .... *Muraenichthys* Bleeker, 1853

Glenoglossa McCosker, gen.nov.

Type-species.—*Glenoglossa wassi* McCosker, sp.nov.

Diagnosis.—Body moderately elongate, laterally compressed posteriorly; snout conical, grooved on underside; anterior nostril within a tube, posterior nostril within a short tube at outer edge of lip, directed ventrally; dorsal fin origin slightly before anus; pectoral fin absent; pop^3 absent; tongue elongate, extends beyond mouth, decorated with fleshy appendage; inner edge of lips and palate decorated with fleshy lappets; teeth conical, uniserial, absent on vomer; gill arches reduced, third hypobranchial and second infrapharyngobranchial absent, third and fourth upper pharyngobranchial tooth plates weakly fused; suspensorium nearly vertical, pterygoid slender

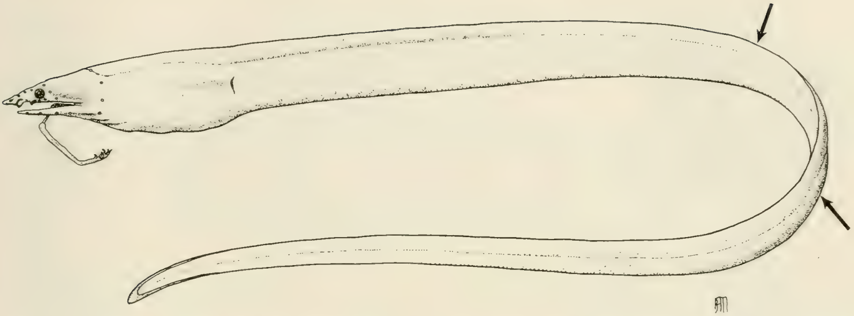


FIGURE 1. Holotype of *Glenoglossa wassi* McCosker, sp.nov., CAS 47049, 153.5 mm TL. Arrows indicate origin of dorsal and anal fins.

and reduced; cleithrum and supracleithrum reduced to thin slivers. Other characters those of the single species.

ETYMOLOGY.—From the Greek *γλη̄̃νοσ* (*glenos*), a thing to stare at, and *γλῶσσα* (*glossa*, feminine), tongue.

Glenoglossa wassi McCosker, sp.nov.

(Figures 1–3)

HOLOTYPE.—CAS 47049, 153.5 mm TL, collected using rotenone over sand at base of large coral head, 40 m depth, Larsen Bay, Tutuila Island, American Samoa; R. Wass and G. Yamasaki, 18 Nov. 1975.

PARATYPE.—CAS 47048, 88.8 mm TL, collected using rotenone along sloping sand bottom at base of coral and lava cliff, 40 m depth, Steps Point, Tutuila Island, American Samoa; R. Wass and R. Lubbock, on 4 Mar. 1975. This specimen was cleared and stained.

COUNTS AND MEASUREMENTS.—The condition of the holotype is parenthetically followed by that of the paratype: TL 153.5(88.8); head length 20.8(12.8); trunk length 54.7(30.0); tail length 78.0(46.0); body depth at gill openings 5.6(3.7); body width at gill openings 3.0(1.9); origin of dorsal fin 67.1(39.6); snout length 3.5(2.3); upper jaw length 6.7(4.4); eye diameter 1.1(0.7); interorbital distance 2.0(1.0). Total vertebrae 127(126), preanal vertebrae 54(53).

DESCRIPTION.—Body moderately elongate, depth at gill oepnings 24–26.5 in TL, tapering and laterally compressed posteriorly. Head and trunk 2.03–2.07 and head 6.9–7.4 in TL. Snout acute; lower jaw included, tip slightly in advance of anterior nostril base. Anterior nostril tubular; posterior nostril at edge of lip, entirely outside of mouth, within small tube. Eye slightly in advance of midpoint of upper jaw. Gill opening mid-lateral, a constricted opening.

Median fins low, lying partially within a groove, meeting each other and extending noticeably beyond caudal tip. Dorsal fin arises less than a head length in advance of anus.

Head pores minute, difficult to discern. Single temporal and interorbital pores. Four pores along mandible. Two preoperculomandibular pores. Lateral line pores difficult to identify in preserved specimens; approximately 11 pores before the gill opening.

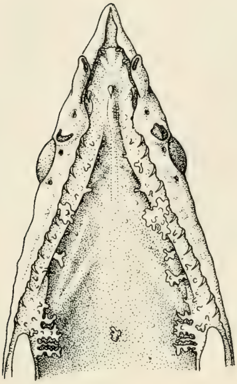
Tongue extends from mouth. A fleshy appendage, differing slightly in each specimen (Figs. 2–3), extends beyond the slender glossohyal. The inner edge of lips, floor of mouth, and palate flanked by fleshy tissue (Fig. 2).

Teeth small, conical, uniserial in jaws. An intermaxillary chevron of four teeth, followed by two medial teeth. Vomerine teeth absent. Nine teeth along maxilla, 14 along mandible.

Body color in isopropyl alcohol uniformly tan. Numerous, minute brown punctations in mouth, along head and dorsal body surface. Fins pale. Base of lure has a dark spot. Eyes dark blue. Color of paratype in life, recorded by R. Wass, "light greenish-yellow with tiny purple brown specks. Lure transparent with black 'eye.'"

ETYMOLOGY.—Named in honor of Richard C. Wass, collector of these and many other important fishes from Samoa.

REMARKS.—This myrophine is remarkable in the development of its tongue which, because of its length and appearance, serves as a lure to attract small fish. It is the only eel known to use



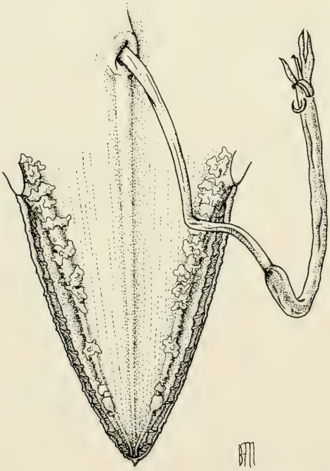


FIGURE 2. Open mouth of holotype of *Glenoglossa wassi* McCosker, sp.nov., CAS 47049.

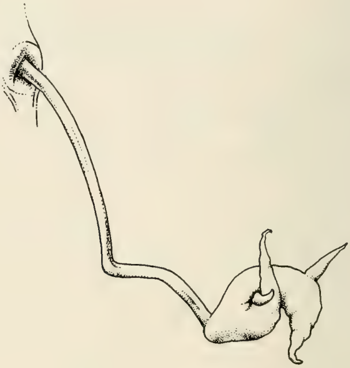


FIGURE 3. Tongue lure of paratype of *Glenoglossa wassi* McCosker, sp.nov., CAS 47048.

such a feeding strategy, and is certainly no less remarkable than those of certain uranoscopids, ceratioids, or the alligator snapping turtle. The "eyes" and appendages of the lure would indicate that it resembles a small crustacean. In the stomach of the holotype was a partially digested goby-like fish nearly 2 cm in length. The other oral decoration provided by the fleshy labial lappets suggests that the eel lies buried in the sand with its head exposed, luring prey by flicking its glossohyal.

Glenoglossa wassi is most closely related to species of *Muraenichthys* and *Schismorhynchus*. It is easily separable from them on the basis of its tongue development, its absence of vomerine teeth, and certain other osteological characters. It is most like *Schismorhynchus* in its general facies, the development of its snout groove, reduced pterygoid, and gill arch reductions, conditions which probably relate to the feeding behavior of the species involved. It is clearly a specialized worm eel whose ancestry is in the sharp-snouted, conical-toothed species group of *Muraenichthys* (sensu McCosker 1977) that gave rise to *Schismorhynchus* and may have shared a common ancestor with it.

Neenchelys Bamber, 1915

TYPE-SPECIES.—*Neenchelys microtretus* Bamber, 1915.

DIAGNOSIS.—Body moderately to extremely elongate, laterally compressed behind head; tail much longer than head and trunk; snout conical, anterior nostril in a tube, posterior nostril an elongate slit entirely before eye; eye moderate; dorsal fin origin mid-trunk; pectoral fin moderately developed, girdle limited to reduced cleithrum and supracleithrum; gill opening reduced, a constricted hole; pop^3 absent; teeth few, conical and slender, uniserial on jaws and vomer; maxillary attachment at mid-vomer; gill arches reduced; suspensorium nearly vertical, slightly

FIGURE 4. Holotype of *Neenchelys daedalus* McCosker, sp.nov., AMS I.19690-012, 341.5 mm TL.

inclined anteriorly; pterygoid slender and reduced; neurocranium rounded, lacking a crest; color uniform.

Neenchelys daedalus McCosker, sp.nov.
(Figures 4–5)

HOLOTYPE.—AMS I.19690-012 (field no. JP 69-29), held in trust for Papua New Guinea National Fish Collection, 341.5 mm TL, a female with eggs, captured in Astrolobe Bay, s of Madang, Papua New Guinea (5°24′S, 145°52.5′E), 6-ft Isaacs-Kidd midwater trawl (IKMT), 0–140 fms [0–256m] over a "rough peak 500+ fms" bottom, 1850–2100 h, 7 Oct. 1969. In that same collection were numerous myctophids, gonostomatids, and chauliodontids.

PARATYPE.—CAS 50708, 272.9 mm TL, collected with the holotype.

COUNTS AND MEASUREMENTS (in mm).—The condition of the holotype is parenthetically followed by that of the paratype: TL 341.5(272.9); head length 23.5(21.4); trunk length 65(53.5); tail length 253(198); body depth at gill openings 6.6(5.9); body width at gill openings 4.7(4.0); body depth at anus 6.2(5.0); body width at anus 4.2(3.5); origin of dorsal fin 49.5(42); length of pectoral fin 5.2(5.0); snout length 3.9(3.8); upper jaw length 6.2(5.2); eye diameter 1.2(1.2); interorbital distance 2.05(1.8). Total vertebrae 235(225); preanal vertebrae 59(58).

DESCRIPTION.—Body extremely elongate, depth at gill opening 46.3–51.7 in TL, tapering slightly and laterally compressed posteriorly. Tail much longer than head and trunk, 1.34–1.38 in TL. Head and trunk 3.64–3.86 and head 12.8–14.7 in TL. Snout moderately acute; lower jaw included, its tip extends to anterior base of anterior nostril. Top and sides of snout and edge of lower jaw covered with numerous small papillae (presumably sensory in function), slightly smaller than cephalic pores. Anterior nostril tubular, directed ca. 45° laterally, posterior nostril an elongate slit above upper lip, nearly as wide as orbit. Eye begins behind midpoint of jaw, moderate in size, 4.3–5.2 in jaw length. Gill openings low on side, each a constricted opening.

Pectoral fin well developed, nearly as long as gape. Median fins well developed and obvious, not lying in a groove as in most myrophines. Anal fin larger than dorsal, nearly as deep as body. Dorsal fin arises about mid-trunk, the predorsal distance 6.49–6.89 in TL.

Head pores small but apparent (Fig. 5). Single temporal and interorbital pores. Five mandibular pores, and two over preopercle. Two postorbital pores. Lateral line pores small but obvious; 14 on head, 61 before anal opening, not discernible in posterior tail region.

Teeth few, slender, conical, of moderate size for a myrophine. A single premaxillary tooth, flanked by a pair of retrorse teeth, followed by two medial teeth, then a pair of teeth, at which point the maxillae attach, each possessing 6–7 uniserial teeth. Vomer has three teeth that end about midway along toothed portion of maxilla. Lower jaw teeth uniserial, 17–18 on each side.

Gill arches reduced; first basibranchial absent, third and fourth infrapharyngobranchial tooth plates weakly fused. Branchiostegal rays numerous, unbranched; eight attached to hyoid (1 along the ceratohyal, 7 along the epihyal), 25 unattached, on each side.

Body color in isopropyl alcohol uniform tan, except belly which is dark brown to black. Fins colorless. Eye dark blue.

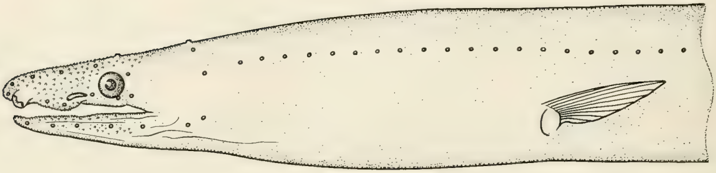


FIGURE 5. Head of holotype of *Neenchelys daedalus* McCosker, sp. nov., AMS I.19690-012.

ETYMOLOGY.—Named *daedalus*, a noun in apposition, in honor of the Greek artisan who escaped from his Earth-bound prison and ascended into heaven.

REMARKS.—All specimens of *Neenchelys daedalus* have come from midwater. It therefore seems likely that it is a midwater eel, although the possibility exists that juvenile and subadult specimens were merely transformed leptocephali that were captured just prior to settlement, and/or the adults were benthic eels that were captured en route to a surface spawning event. Both possibilities are unlikely in that the size range of the specimens is too great and their condition is too "uniform" to have been captured during transformation, and none appear to have retained larval conditions. Furthermore, the morphometric changes in eye size undergone by surface-migrating benthic myrophines, such as *Ahlia egmontis* (see Cohen and Dean 1970, and McCosker 1977), are absent. Further evidence for a midwater habitat is provided by the partially digested crustacean material in the gut of the cleared-and-stained specimen (which suggests that it had fed prior to capture and not while in the net) as well as the darkened vent and presence of sensory papillae on the snout.

The evidence thus suggests that *N. daedalus* is the second ophichthid known to have left the substrate to adopt a midwater life style. This adaptation has been independently achieved, however, in that its closest relatives are benthic, fossorial species. The other midwater ophichthid, *Benthenchelys cartieri* Fowler, lives pelagically at 100–250 m over deep water in the central Indo-Pacific (Castle 1972) and displays many similar adaptations, such as enlarged median fins, sensory papillae, an elongate tail, and slender teeth.

The new species is more similar in appearance, owing to its extreme elongation, to the Atlantic species of *Pseudomyrophis* than to its congeners. However, its osteology, pore condition, and fin size and placement are in agreement with *Neenchelys microtretus* Bamber, 1915, *N. buitendijki* Weber and de Beaufort, 1916, and the sketchily described *N. parvipectoralis* Chu, Wu, and Jin, 1981. Castle (1980) has illustrated the larvae of *Neenchelys* and commented upon their distribution. The new species may be separated from its congeners using the characters in Table 1.

In an earlier publication (McCosker 1977), I cautiously recognized the generic distinction between *Neenchelys* and *Pseudomyrophis*. My subsequent examination of additional osteological preparations of *Neenchelys* spp. and *Pseudomyrophis* spp. have further substantiated those

TABLE 1. VERTEBRAE AND BODY PROPORTIONS (in thousandths of TL) OF THE SPECIES OF *NEENCHELYS*.

	Head length	Tail length	Body depth	Total vertebrae
N. microtretus	114[1]	580	38[1]	151[2]
N. buitendijki	117–127[1]	565–643	31–51[1]	142–148[2]
N. parvipectoralis	~95[3]	~615[3]	~60[3]	—
N. daedalus	68–78	725–746	19–22	225–235

[1] From Nelson 1966.

[2] From Castle 1980.

[3] Calculated from Chu, Wu, and Jin 1981.

differences. In an independent study, Mark M. Leiby (in litt., Florida Dept. of Natural Resources, 14 Jan. 1982) has compared the leptocephali of species of those genera and concluded that they are trenchantly different. The two *Pseudomyrophis* species that are similar in body elongation to *Neenchelys daedalus, P. nimius* Böhlke, 1960, and *P. atlanticus* Blache, 1975, inhabit mud and sand substrates in deep water. Dean (1972) and Mark Leiby (in litt.) have concluded that *Myrophis frio* Jordan and Davis, 1891, and an undescribed Atlantic species are congeners of *Pseudomyrophis nimius.* Two species are known from the eastern Pacific: *P. micropinna* Wade, 1946, the type-species; and an undescribed species ranging from Costa Rica to Baja California.

Eleven other Pacific specimens, captured by midwater trawls, were tentatively identified as *Neenchelys daedalus.* They are all smaller specimens and appear identical in proportions to the new species. They differ considerably, however, in total vertebrae numbers: the holotype and paratype have 235 and 225, respectively, whereas eight of the others had 251–274 ($\bar{x} = 266.8$) vertebrae. I am unable to account for such a large mean difference and broad range in vertebral number for conspecifics in such close geographical proximity, and therefore have not made them type-specimens.

COMPARATIVE MATERIAL.—*Neenchelys daedalus* (non-paratypes): AMS I.19707-017 (field no. JP 69-53), 5(172–187), Manus Island, Papua New Guinea, 4°15′S, 145°11′E, 6-ft IKMT, 0–125 m, over 750+ m depth, John E. Paxton aboard FRV TAGULA, 0120–0320 h, 22 Oct. 1969. (Many gonostomatids and myctophids were captured in the same collection.) From the same collection: CAS 50709, 2(187–225); CAS 50710, 1(190, cleared and stained); and ANSP 149295, 2(175–185). SIO 77-171 1(144), Banda Sea, 105 km sw of Buru Is., 04°30.5′S, 125°34.6′E, 0–1500 m over 3600 m, Jim Coatsworth, 26 Aug. 1976.

Neenchelys buitendijki: ZMA.102.171, 1(218), syntype, "probably from Moluccos," Indonesia. UH uncat., 2(118–123, specimens dissected), Bombay City, India (specimens from Mohamed 1958, reported on by Nelson 1966).

Neenchelys microtretus: BMNH 1915.10.25.1, 1(183), holotype, Red Sea.

Pseudomyrophis micropinna: LACM 21557, 1(139), holotype, Isla Ladrones, Gulf of Chiriquí, Panama. SIO 60-72, head and trunk only, cleared and stained.

Pseudomyrophis nimius: USNM 186274, 1(319), holotype, Gulf of Mexico. ANSP 110150, 1(350, cleared and stained), Gulf of Mexico.

Pseudomyrophis atlanticus: MNHN 1971-40, 1(259) holotype, Pointe-Noire. MNHN 1971-41, 1(241), paratype, Pointe-Noire.

ACKNOWLEDGMENTS

Specimens and assistance were generously provided by the staffs of many institutions. In particular, I thank: John Paxton and Doug Hoese, Australian Museum, Sydney (AMS); Eugenia Böhlke and the late James Böhlke, Academy of Natural Sciences of Philadelphia (ANSP); the staff of the British Museum (Natural History) (BMNH); John E. Randall, Bernice P. Bishop Museum (BPBM); William N. Eschmeyer and staff, California Academy of Sciences (CAS); Robert Lavenberg, Natural History Museum of Los Angeles County (LACM); Jacques Blache and Marie-Louise Bauchot, Muséum National d'Histoire Naturelle, Paris (MNHN); Richard H. Rosenblatt, Scripps Institution of Oceanography (SIO); William Bussing, University of Costa Rica (UCR); Leighton R. Taylor, Jr., Waikiki Aquarium and University of Hawaii (UH); the staff of the United States National Museum of Natural History (USNM); and Hans Nijssen, Zoölogisch Museum Amsterdam (ZMA). I also thank: Beth A. Meinhard for the preparation of Figures 1–3; Kathy Smith for the preparation of Figures 4–5; Michael Hearne for the preparation of radiographs; Lillian Dempster for nomenclatural assistance; and Mark Leiby, Peter Castle, and Eugenia Böhlke for their stimulating discussions concerning the relationships of worm eels.

LITERATURE CITED

BAMBER, R. C. 1915. Reports on the marine biology of the Sudanese Red Sea, from collections made by Cyril Crossland. XXII. The Fishes. J. Linn. Soc. London 31:477–485.

BLACHE, J. 1975. Contribution à la connaissance des Poissons Anguilliformes de la côte occidentale d'Afrique. 15^e note: compléments aux familles des Muraenidae, des Heterenchelyidae et des Ophichthidae. Bull. Inst. Fr. Afr. Noire 37(3):708–740.

BLEEKER, P. 1853. Diagnostische beschrivnigen van nieuwe of wenig bekende wisschsoorten van Batavia. Tintal I–VI, Nat. Tijdschr. Neder.-Indie 4:451–516.

BÖHLKE, J. E. 1960. A new ophichthid eel of the genus *Pseudomyrophis* from the Gulf of Mexico. Not. Nat. (Phila.) 329: 1–8.

CASTLE, P. H. J. 1972. The eel genus *Benthenchelys* (fam. Ophichthidae) in the Indo-Pacific. Dana Rep. 82:1–32.

———. 1980. Larvae of the ophichthid eel genus *Neenchelys* in the Indo-Pacific. Pac. Sci. 34(2):165–171.

CHU, Y. T., H. WU, AND X. JIN. 1981. Four new species of the families Ophichthyidae and Neenchelidae. J. Fish. China 5(1):21–27.

COHEN, D. M., AND D. DEAN. 1970. Sexual maturity and migratory behaviour of the tropical eel, *Ahlia egmontis.* Nature 227(5254):189–190.

Dean, D. M. 1972. Osteology and systematics of the echeline worm eels of the Atlantic Ocean (Pisces, Anguilliformes). Ph.D. Thesis. Univ. of Miami, Miami, Florida. 88 p.

Fowler, H. W. 1934. Descriptions of new fishes obtained 1907 to 1910, chiefly in the Philippine Islands and adjacent seas. Proc. Acad. Nat. Sci. Philadelphia 85:233–267.

Gosline, W. A. 1951. The osteology and classification of the ophichthid eels of the Hawaiian Islands. Pac. Sci. 5(4):298–320.

Jordan, D. S., and B. M. Davis. 1891. A preliminary review of the apodal fishes or eels inhabiting the waters of America and Europe. Rep. U.S. Comm. Fish. Fish. (1888) Pt. 16: 581–677.

Lütken, C. F. 1851. Nogle bemaerkinger om naeseborenes . . . aalefamilien. Vidensk. Meddel. Naturhist. Foren. Kjobenjavn. 21 p.

McCosker, J. E. 1970. A review of the eel genera *Leptenchelys* and *Muraenichthys,* with the description of a new genus, *Schismorhynchus,* and a new species, *Muraenichthys chilensis.* Pac. Sci. 24(4):506–516.

———. 1977. The osteology, classification and relationships of the eel family Ophichthidae. Proc. Calif. Acad. Sci., ser. 4, 41:1–123.

Mohamed, K. H. 1958. On the occurrence of the eel *Neenchelys buitendijki* Weber & deBeaufort in Indian waters. J. Bombay Nat. Hist. Soc. 55:511–517.

Nelson, G. J. 1966. Osteology and relationships of the eel *Neenchelys buitendijki.* Copeia 1966:321–324.

Taylor, W. R. 1967. An enzyme method of clearing and staining small vertebrates. Proc. U.S. Natl. Mus. 122(3596): 1–17.

Wade, C. B. 1946. Two new genera and five new species of apodal fishes from the eastern Pacific. Allan Hancock Pac. Exped. 9(7):181–213.

Weber, M., and L. F. deBeaufort. 1916. The fishes of the Indo-Australian Archipelago. III. Ostariophysi: II Cyprinoidea, Apodes, Synbranchi. E. J. Brill, Leiden. 455 p.

CALIFORNIA ACADEMY OF SCIENCES
Golden Gate Park
San Francisco, California 94118

PROCEEDINGS
OF THE
CALIFORNIA ACADEMY OF SCIENCES

Vol. 43, No. 6, pp. 67-76, 3 figs., 3 tables. July 6, 1983

PSILORHYNCHUS GRACILIS, A NEW CYPRINOID FISH FROM THE GANGETIC LOWLANDS

By
Walter J. Rainboth
Department of Biology, University of California, Los Angeles,
Los Angeles, California 90024

ABSTRACT: *Psilorhynchus gracilis* is described from 147 specimens collected at 10 lowland localities in Bangladesh. Of the four previously described species of *Psilorhynchus* (*balitora, homaloptera, pseudecheneis,* and *sucatio*), the new species resembles *P. balitora* most closely. The new species is compared with *P. balitora* and *P. sucatio,* both of which are syntopic species of the Gangetic plains. *P. sucatio* may be distinguished from *P. balitora* and the new species by its reduced dorsal ray count and numerous shape and coloration differences. *P. balitora* differs from the new species in lateral line and circumferential scale counts, number of unbranched pectoral rays, coloration, and shape of the head and mouth parts. The preferred habitat and distribution of the three lowland species are compared, and a key to the genus *Psilorhynchus* is provided.

INTRODUCTION

Fishes of the genus *Psilorhynchus* McClelland are known to occur primarily in the Gangetic drainage of southern Asia, where four described (Menon 1974) and one undescribed species are found. Most ichthyologists (following Hora 1925) have recognized *Psilorhynchus* as the sole genus in the family Psilorhynchidae. A recent re-analysis of the relationships of *Psilorhynchus* has been published by Chen (1980), who believes the genus to belong to the Cyprinidae. I have not located a copy of that publication and must reserve comment at this time.

Of the five known species, two (*Psilorhynchus homaloptera* Hora and Mukerji, 1925, and *P. pseudecheneis* Menon and Datta, 1964) have relatively smaller scales and greater numbers of simple pectoral rays than the remaining three species. These small-scaled species also prefer high-gradient streams located in the eastern Nepalese Himalayas (*P. pseudecheneis*) and the Naga Hills of the Assam-Burma border (*P. homaloptera*). The subspecies *P. homaloptera rowleyi* Hora and Misra, 1941, of the Chindwin River (Irrawaddy) is one of the two species of this genus from Burma (Fig. 1). These taxa from high-gradient streams are not known to present any taxonomic problems.

Two species from easily accessible lowland areas were described by Hamilton in 1822 as *Cyprinus sucatio* and *C. balitora.* While collecting in the People's Republic of Bangladesh in 1977 and 1978, I obtained three species from Gangetic lowland streams. Two of the species were those described by Hamilton and one is described, herein, as new.

Hamilton's (1822) somewhat brief original descriptions of two lowland species now referred to *Psilorhynchus* were not accompanied by figures, although he had prepared figures for them during his stay in India. Hamilton's figures are of prime importance because he kept no pre-

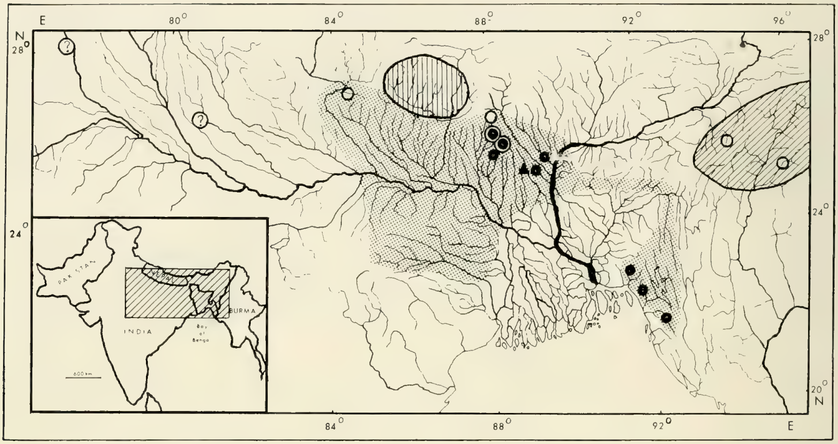


FIGURE 1. Distribution of the known species of *Psilorhynchus*. Inset map indicates region displayed. Darkened circles represent *P. gracilis* localities, with triangle marking the type-locality. Open circles are localities for *P. balitora*, with question marks in outlying non-verified reports. Two localities have both *P. gracilis* and *P. balitora*. Vertical hatching covers the range of *P. pseudecheneis*. Diagonal hatching shows the range of *P. homaloptera*. Stippling highlights the known range of *P. sucatio*.

served material. However, only half of the figures (and neither of the *Psilorhynchus* figures) were published in Hamilton's original monograph. The remaining figures were published subsequently by several authors including McClelland (1839), who published Hamilton's figures of *Psilorhynchus*. The reasons for this were explained partially by McClelland (1839) and more fully documented by Gudger (1924) and Hora (1929). Although he had seen but a single individual of one of the species, McClelland placed both species in the new genus *Psilorhynchus* and presumed that his single specimen was *P. balitora* (Hamilton), for which he coined a new specific name, *variegatus*, to replace *balitora*—a local term meaning sand-digger. McClelland preferred the use of classical Latin or Greek to the use of local dialects; for example, he changed the homalopterid generic name *Balitora* Gray, 1834, to *Platycara*. Such replacement of names is inadmissible under the present rules of nomenclature.

In Hamilton's figures (McClelland 1839:pl. 50), *Psilorhynchus sucatio* is easily recognized; however, I collected two species which resemble the illustration of *P. balitora*. Because McClelland's *P. variegatus* refers to an individual of a *balitora*-like species, the possibility that his species may have been distinct from Hamilton's will also be explored.

MATERIALS AND METHODS

Measurements were made to the nearest 0.1 mm with dial calipers. Standard length was measured from the snout tip to the base of the caudal fin. All pre-fin lengths extend from the tip of the snout to the base of the first unbranched ray at fin origin. Dorsal and anal fin lengths are measures of the longest simple ray, whereas the paired fins are depressed and measured from insertion to posteriormost extension. Caudal fin length is measured from the posterior end of the urocentrum to the tip of the normally spread upper fork. Body depth is measured from dorsal fin origin to pelvic fin insertion. The snout to occiput length (head length = HL) is the distance to the posterior margin of the supraoccipital bone. The snout to preopercle length is taken on a horizontal. Snout to maxilla length is measured to the posterior end of the maxilla. Orbital measurements are taken to the bony margin. Mandible length is distance from the symphysis to articulation with the quadrate. Gape width is the distance between the two articulation points of upper and lower jaw.

Fin-ray counts are expressed with lower case Roman numerals signifying unbranched rays and Arabic numerals for branched rays. The deeply divided final branched ray in both the dorsal and anal fin is counted as one. Caudal counts list procurrent rays of the upper fork as Roman numerals with Arabic numerals for principal rays of the upper/lower forks followed by Roman numerals giving lower-fork procurrent rays. Lateral line scales were counted for the body and tallied separately from those on the caudal fin base. Lateral transverse counts include the median scale at the dorsal fin origin, record the lateral line with a slash (/), and include the median ventral row before the anal fin. Circumferential counts encircle the body on the scale row immediately anterior to the dorsal and pelvic fins. Circumpeduncular counts include all scales around the peduncle at its narrowest region. The number of anal scales refers to median scale rows between the anus and anal fin. Belly scale rows include all complete, free-edged midventral scale rows crossing anterior to the pelvic fin insertion. Counts given for lateral blotches include all distinct midlateral blotches whether or not they are perfectly bisected by the lateral line.

Body measurements are summarized as percent standard length (% SL), head measurements as percent head length (% HL).

Most of the material was collected by the author and is housed at the Museum of Zoology, The University of Michigan, Ann Arbor (UMMZ) or at the Chandpur Freshwater Fisheries Research Station, Chandpur, Bangladesh (CFRS). Other specimens are from the American Museum of Natural History, New York (AMNH), and the Stanford University (SU) collection now housed at the California Academy of Sciences, San Francisco. Paratypes of the new species have been deposited at all aforementioned institutions plus the Field Musuem of Natural History, Chicago (FMNH), the Academy of Natural Sciences of Philadelphia (ANSP), and the United States National Museum, Washington, D.C. (USNM).

Distribution maps are part of drainage maps of the southern half of the Asian continent drafted by the author from the most recent world-wide series of 1:5,000,000-scale topographic maps prepared by the U.S. Defense Mapping Agency.

Psilorhynchus McClelland

Psilorhynchus McClelland, 1839:300, 428 (type-species *Cyprinus sucatio* Hamilton, by subsequent designation of Jordan 1919).

Diagnosis.—Body arched dorsally and flattened ventrally. Anteriorly depressed, becoming cylindrical with lateral compression posteriorly. Ventral surface of head markedly flattened. Mouth small, inferior, and transverse with a projecting snout; devoid of barbels. Pharyngeal teeth uniserial. Gill membranes joined broadly to isthmus with aperture extending ventrally to base of pectoral fin. Paired fins inserted horizontally. Breast naked. Scales moderate to large, 31 to 50 pored scales on the complete lateral line. Fin-ray counts: D ii–iii/7–9; A ii–iii/5; P_1 iv–x/9–12; P_2ii/7. Anus very close to pelvic fin; at least 8 scale rows separate anus from anal fin.

Key to the Species of *Psilorhynchus*

1a. Branched dorsal fin rays 7 2
1b. Branched dorsal rays 8 (or 9) 4

2a. Abdomen fully scaled; simple pectoral rays 4 .... *sucatio* (Hamilton)
2b. Abdomen naked; simple pectoral rays 7–10 3

3a. Total lateral line scales 42–44; simple pectoral rays 7 or 8; abdomen smooth .... *homaloptera* Hora and Mukerji
3b. Total lateral line scales 48–50; simple pectoral rays 10; abdomen with three transverse folds of skin .... *pseudecheneis* Menon and Datta

4a. Gape width greater than mandible length; simple pectoral rays 6–7 (rarely 5) or more; circumferential scales 18 .... *balitora* (Hamilton)
4b. Gape width much less than mandible length; simple pectoral rays 4–5; circumferential scales 16 .... *gracilis* sp.nov.

Psilorhynchus gracilis sp.nov.

(Figures 2 and 3)

Holotype.—UMMZ 205342 (adult female, 50.5 mm SL), Jabuneswari River at Badarganj, Rangpur Dist., Bangladesh, 3 Apr. 1978.

Paratypes (all from Bangladesh).—UMMZ 205343 (26 specimens, 29.4–49.9 mm SL), and CFRS uncat. (9 spec.) same collection data as holotype. UMMZ 205337 (2 spec., 25.7–29.7), Sangu River at Bandarban, Chittagong Hill Tracts, 25 Dec. 1977; UMMZ 205345 (8, 34.1–40.7), Ghaghat River at Rangpur, Rangpur Dist., 3 Apr. 1978; UMMZ 205348 (31, 26.6–51.2), USNM 231693 (5), AMNH 43097 (5), CAS 50011 (5), and ANSP 148729 (5), and FMNH 94285 (5), Mahananda River at Tetulia, Dinajpur Dist., 5 Apr. 1978; UMMZ 205351 (15, 27.6–46.4), Keratoya River at Bhajanpur, Dinajpur Dist., 6 Apr. 1978; UMMZ 205353 (2, 34.3–39.0), Tangam River at Thakurgaon, Dinajpur Dist., 6 Apr. 1978.

Other Material Examined (all from Bangladesh).—UMMZ

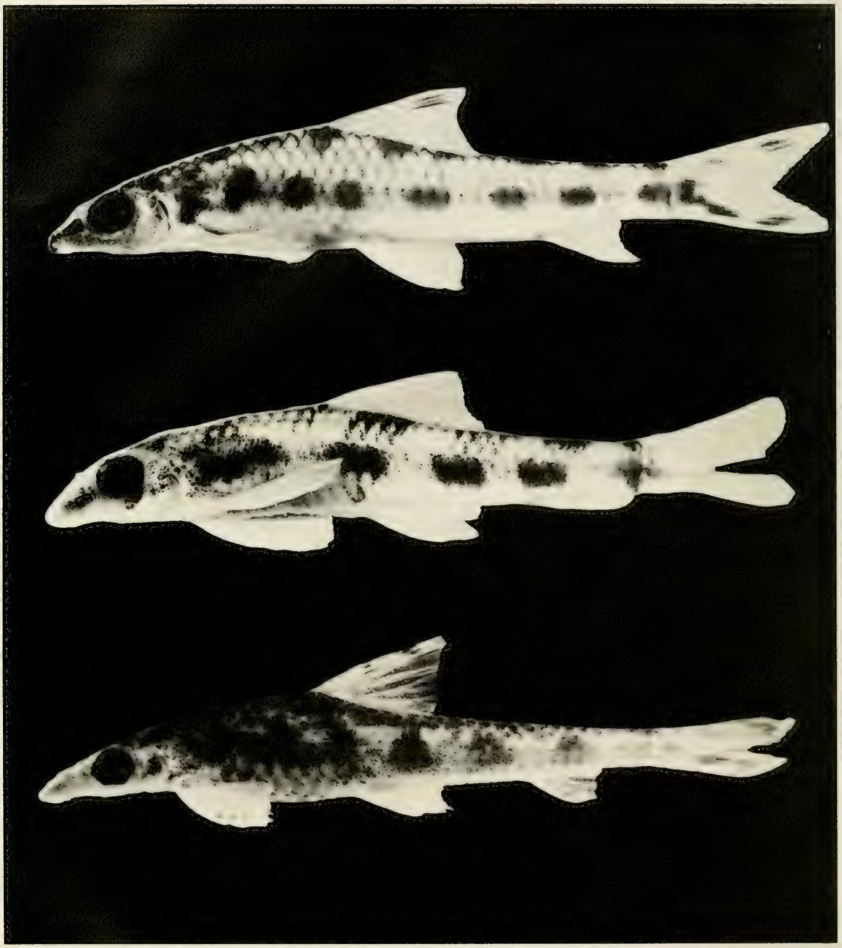


FIGURE 2. Young specimens of three lowland species of *Psilorhynchus* from Bangladesh. (*top*) *P. gracilis,* 34 mm SL, Jabuneswari River. (*middle*) *P. balitora,* 20 mm SL, Mahananda River. (*bottom*) *P. sucatio,* 64 mm SL, Rangapani Creek.

205340 (18, 10.4–19.0), Dharla River at Kurigram, Rangpur Dist., 2 Apr. 1978; CFRS uncat. (3, 33.8–35.4), Muhuri River, 10 km NE of Feni, Noakhali Dist., 2 Feb. 1978; CFRS uncat. (1, 40), Halda River at Daulatpur, 40 km N of Chittagong, Chittagong Dist., 24 Feb. 1978; CFRS uncat. (6) Halda Creek at Khaia Bazaar, 53 km N of Chittagong, Chittagong Dist., 24 Feb. 1978.

DIAGNOSIS.—Lateral line scales 33 to 36 on body plus 1 or 2 pored scales on caudal fin, totalling 35 to 37; pectoral fin with 4 or 5 simple rays; branched dorsal rays 8 (rarely 9); 2 distinct dorsal spots anterior to dorsal fin origin with a third at the origin; midventral region scaleless anteriorly, with 2 to 5 complete, free-edged scale rows immediately anterior to pelvic fin insertion; pectoral fin short, extending beneath dorsal fin origin, but never reaching pelvic insertion; eye

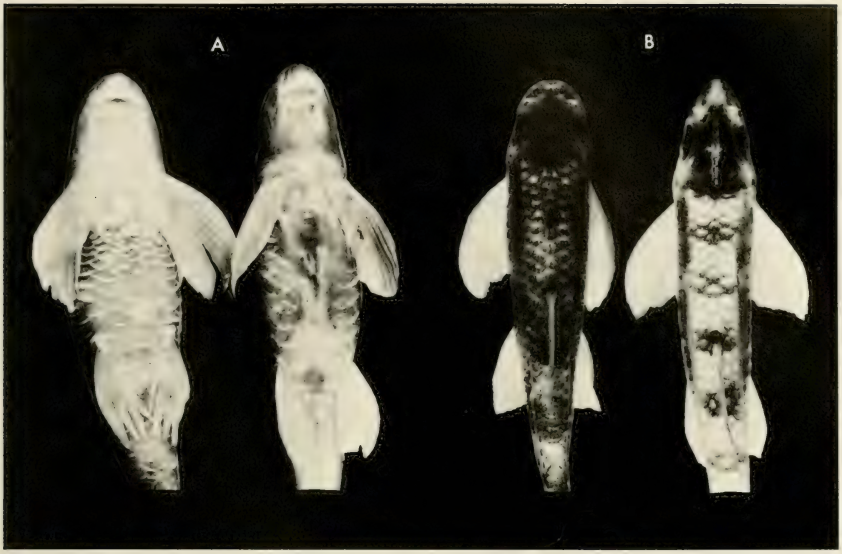


FIGURE 3. Comparison of ventral (*A*) and dorsal (*B*) aspects in *Psilorhynchus balitora* and *P. gracilis*. In each pair, left is *P. balitora*, and right is *P. gracilis*. In ventral aspect (*A*), *P. balitora*, 39 mm SL, Siliguri, and *P. gracilis*, 47 mm SL, Jabuneswari River. In dorsal aspect (*B*), *P. balitora*, 27 mm SL, Mahananda River, and *P. gracilis*, 32 mm SL, Jabuneswari River.

in upper part of head, not visible from below; no spots on anal or paired fins, although membrane between first 5 pectoral rays slightly darkened in some adults.

DESCRIPTION.—Predorsal scales 10 or 11; circumferential scales 16 (rarely 15 or 17); circumpeduncular scales 10; lateral transverse scale-rows 4/3; scale rows between anus and anal fin 8 or 9. Scales one row above lateral line immediately posterior to dorsal fin have 6 or 7 radii in adults of 50 mm SL.

Paired fins inserted horizontally; pectoral with 4 or 5 unbranched rays and 9–12 branched rays, totalling 14–17 elements, extending as far as dorsal fin origin when depressed, with distal margin separated from pelvic fin insertion by at least 2 scale rows; pelvic fin inserted slightly posterior to dorsal fin origin, with 2 simple and 7 branched rays. Dorsal fin closer to snout tip than to caudal base, with 3 simple and 8 (rarely 9) branched rays. Anterior and posterior rays of equal extension in depressed dorsal fin, which when normally expanded has an oblique and concave posterior margin. Anal fin short and somewhat falcate, its posterior margin well in advance of caudal fin, with 3 simple and 5 branched rays. Caudal fin deeply and evenly forked, possessing 19 (10/9) principal rays preceded by 6 or 7 procurrent rays above and 5 or 6 below. Body elongate, arched above and generally flat below; greatest depth at dorsal fin origin and greatest width at pectoral fin insertion; shape somewhat depressed anteriorly, gradually becoming cylindrical, then compressed posteriorly.

Head depressed, ventral mouth small and transverse. Upper lip separate from upper jaw by a deep groove and from snout by a shallow groove. Ventral surface of snout separated from lateral surfaces by deep rostral grooves. Upper lip joined to lower lip at corner of mouth by a fairly prominent flap of skin. Lower lip thick and followed on chin by a number of large, globular papillae which decrease in size posteriorly. Lower jaw long, its length much greater than width of gape. Gill membranes broadly joined to isthmus; gill aperture extends dorsally from pectoral fin base. Eye large, upper margin level with flat interorbital space; width of orbit approximating interorbital width. Tip of snout somewhat pointed if viewed from dorsal aspect.

Nuptial tubercles evident on large males, randomly distributed on head. Heaviest tubercle accumulation below eye on lower part of cheek where eruption takes form of tight clusters rather than usual single pattern. Anterior body scales have tubercles bordering their free margins. Tubercle distribution on body progressively sparser posteriorly. Pectoral fins on breeding males show single row of tubercles ornamenting dorsal surface of each ray, with tubercles on anterior rays largest. Pelvic fins with same pattern but with smaller tubercles. Large females have same tubercle distribution as males but with slight differences. Females have lower tubercle density than males, lack tubercles on paired fins, and do not display tubercles in the clumped suborbital pattern of males.

COLORATION.—Generally recognizable in specimens greater than 15 mm SL, although variable. Laterally, a series of 7–10 dark blotches with posteriormost extending onto caudal fin. First lateral blotch midway between lateral line and base of pectoral fin in small specimens. This spot enlarges with age, to cover lateral line. Lateral line always bisects remaining large lateral spots. Middorsal spots discontinuous with lateral spots; dorsal spots on same transverse scale rows as lateral blotches, having identical counts on all specimens. Where fish has unequal lateral spot counts, some dorsal spots obliquely cross middorsal line, and on each side are still on same scale rows as lateral spots. Two distinct dorsal spots anterior to dorsal fin origin, with another at origin and a fourth under posterior dorsal fin rays. Four or five spots between dorsal fin and caudal fin. All scales of back and upper side have marginal melanophores connecting to create network ventrally to just below lateral line. Network darkens with age, but always distinct. Head dark dorsally with light median-longitudinal streak flecked with large discrete melanophores from snout to posterior edge of occiput. A dark band projects from each nostril to coalesce anteriorly at tip of snout. Pigment lacking on fins of small specimens, appearing gradually at 30 mm SL and increasing substantially with size. Caudal fin ultimately has 2 black blotches per lobe, with proximal spot often joining median spot at caudal base. Dorsal fin has apical spot which runs along anterior 2 or 3 rays. No blotches on paired fins, although large specimens have darkened membranes between first 4 or 5 pectoral rays. Peritoneum dense black dorsally, becoming an irregular medium to dark gray below.

ETYMOLOGY.—The Latin adjective *gracilis* (gender masculine) was chosen because of the fish's slender shape, which immediately distinguishes the new species from *Psilorhynchus balitora,* the most similar species.

COMPARISON OF SPECIES

Several counts aid in distinguishing the three lowland species. The diagnostic counts (Table 1) demonstrate resemblances between *P. gracilis* and *P. balitora* in dorsal rays and total pectoral fin elements. However, lateral line and circumferential counts are closest between *P. gracilis* and *P. sucatio.* Belly squamation is distinctive in *P. gracilis,* which never has more than two to five midventral scale rows anterior to the pelvic fins. *P. sucatio* always has a fully scaled belly and sympatric specimens of *P. balitora* never exhibit fewer than eight midventral prepelvic scale rows. Specimens from the Chindwin River, Burma, and the Rapti River, Nepal have naked breasts and bellies, but are typical *P. balitora* in all other respects. Both *P. homaloptera* and *P. pseudecheneis* have scaleless bellies. Two AMNH 15767 paratypes of *P. homaloptera* from the Naga Hills were incorrectly identified. One is *P. balitora* with typical counts and measurements which have been included in all four tables. The other specimen is a loach (genus *Noemacheilus*).

Several proportional measurements show notable differences. However, overlap in proportional measurements may occur when juveniles are included, even though adult proportions display pronounced differences. For instance, of seven measured *P. balitora,* four adults were over 40 mm SL and three juveniles were less than 30 mm SL. The robust adults have a body depth of 25.5% SL, whereas the juveniles have a body depth of 19.4% SL (Table 2). Juvenile proportions of *P. balitora* overlap with those of adults of the other two species. Other proportions distinguishing *P. gracilis* from *P. balitora* at any size are those for the anal, pectoral, and pelvic fins. Proportions (taken as % HL) differing consistently in these two species are interorbital width, gape width, and mandible length (Table 2). A single perfectly discriminating character is gape width, which is considerably less than the man-

TABLE 1. DIAGNOSTIC COUNTS FOR THE THREE LOWLAND SPECIES OF *PSILORHYNCHUS*. Number counted in parentheses.

	P. balitora	*P. gracilis*	*P. sucatio*
Dorsal fin rays	iii/8 (17)	iii/8–9 (18)	ii/7 (18)
Pectoral fin rays	v–viii/7–9 (41)	iv–v/9–12 (60)	iv/8–9 (18)
Caudal fin rays	v–vi, 9/8, iv–v (10)	vi–vii, 10/9, v–vi (18)	iii–iv, 9/9, iii (18)
Lateral line scales	30–34 + 1 or 2 (41)	33–36 + 1 or 2 (60)	34–35 + 1 or 2 (18)
Circumferential scales	17–20 (41)	15–17 (60)	16–18 (18)
Anal scales	9–10 (17)	8–9 (18)	8–11 (13)

dible length in *P. gracilis,* whereas the size relationship is reversed in *P. balitora.*

Psilorhynchus gracilis differs from *P. sucatio* in the depth of the caudal peduncle and several head-measurement proportions, most notably the interorbital width: approximating the orbital width in *P. gracilis* and nearly doubling the orbital width in *P. sucatio.* Also, in *P. sucatio* the anterior dorsal rays show greater extension when depressed, whereas *P. gracilis* and *P. balitora* have equal or greater posterior extension of the last rays.

Color patterns are most similar between *P. gracilis* and *P. balitora* in younger specimens. Therefore, sub-adults have been illustrated (Fig. 2). Juveniles of *P. sucatio* have a continuous black midlateral stripe extending from opercle to caudal fin. The stripe fades with age, and gradual coalescence of blotches gives the adult color pattern. Remnants of the stripe can be seen on the figured specimen as discrete melanophores between the lateral spots. Dorsally, *P. sucatio* exhibits darkening of entire scales rather than the reticulated network found in *P. gracilis* and *P. balitora.* Both *P. gracilis* and *P. balitora* always have a series of lateral blotches with smaller and more numerous spots on *P. gracilis* (Table 3). The lateral spots on *P. gracilis* and *P. balitora* are on the same diagonal scale rows as the dorsal spots. On *P. gracilis* dorsal and lateral spots are totally distinct, whereas *P. balitora* exhibits a faint continuous band between the lateral and dorsal spots. The predorsal spot pattern (Fig. 3) for *P. gracilis* is two distinct blotches with a third at the dorsal fin origin, and for *P. balitora* a single blotch, with a second beginning at the dorsal origin. In adult *P. balitora* the dorsum gradually darkens causing the pattern to become somewhat obscure, although it still persists. *P. gracilis* retains a distinct reticulated pattern throughout adult life.

A recently described taxon *Psilorhynchus*

TABLE 2. PROPORTIONAL MEASUREMENTS FOR THREE SPECIES OF *PSILORHYNCHUS*. Characters 2 through 9 expressed as %SL. Characters 10 through 15 expressed as %HL (snout to occiput).

	P. balitora		*P. gracilis*		*P. sucatio*	
	Range (mm)	$\bar{x}$ ± SD	Range (mm)	$\bar{x}$ ± SD	Range (mm)	$\bar{x}$ ± SD
1. Standard length	22.7–47.8	(n = 7)	28.2–51.2	(n = 10)	26.4–64.3	(n = 13)
2. Snout to dorsal fin	48.1–52.8	50.3 ± 2.1	44.6–47.9	46.8 ± 1.1	43.9–48.9	46.3 ± 1.6
3. Snout to pectoral fin	22.4–23.9	23.2 ± 0.5	18.8–22.7	20.1 ± 1.3	19.7–23.1	21.0 ± 1.1
4. Body depth	18.5–26.9	22.9 ± 3.5	18.0–21.4	19.7 ± 1.3	15.7–21.4	18.3 ± 1.9
5. Peduncle depth	8.2–9.4	8.9 ± 0.4	7.5–8.4	8.0 ± 0.3	6.1–7.3	7.0 ± 0.4
6. Pectoral fin length	25.9–28.7	27.4 ± 1.0	21.0–23.4	22.4 ± 0.8	17.3–22.7	20.6 ± 1.6
7. Pelvic fin length	20.7–22.9	21.5 ± 0.3	16.9–19.9	18.4 ± 1.0	16.4–19.3	18.4 ± 1.0
8. Anal fin height	15.4–18.0	17.0 ± 0.9	14.2–15.2	14.8 ± 0.4	12.1–14.4	13.0 ± 0.9
9. Snout to occiput	23.0–24.8	24.1 ± 0.6	20.3–24.0	22.0 ± 1.3	20.4–23.9	21.5 ± 1.0
10. Snout to maxilla	32.3–35.6	33.6 ± 1.3	23.6–31.0	27.8 ± 2.4	25.5–32.2	31.0 ± 0.9
11. Orbit width	31.3–35.4	33.4 ± 1.5	30.3–33.8	31.8 ± 1.0	25.2–30.5	27.7 ± 1.7
12. Interorbital width	36.5–41.6	38.6 ± 2.0	29.8–36.3	33.7 ± 2.0	42.8–56.5	50.0 ± 4.7
13. Gape width	26.8–31.6	28.4 ± 2.0	19.1–24.7	22.1 ± 1.6	23.3–28.2	25.6 ± 1.9
14. Mandible length	19.6–23.6	21.4 ± 1.5	29.4–42.5	33.9 ± 4.1	25.0–32.7	27.3 ± 2.3
15. Head depth at pupil	46.4–55.3	51.0 ± 3.1	39.4–47.3	43.8 ± 2.8	33.6–42.0	38.6 ± 2.7

TABLE 3. DISTRIBUTION OF VALUES FOR CHARACTERS DISTINGUISHING *PSILORHYNCHUS GRACILIS* AND *P. BALITORA*. Counts for *P. gracilis* holotype are underlined.

Total lateral line scales	32	33	34	35	36	37
P. gracilis	0	0	0	40	19	1
P. balitora	3	21	12	4	1	0
Simple pectoral rays	4	5	6	7	8	
P. gracilis	32	28	0	0	0	
P. balitora	0	5	19	16	1	
Circumferential scales	15	16	17	18	19	20
P. gracilis	3	55	2	0	0	0
P. balitora	0	0	4	26	3	8
Lateral blotches	5	6	7	8	9	10
P. gracilis	0	0	16	33	9	2
P. balitora	23	16	2	0	0	0

sucatio var. *damodarai* David, 1953, appears to be a local race of *P. sucatio* with slightly larger pectoral fins than those found on individuals from Bangladesh. The Damodar River variety is also listed as having "8" branched dorsal rays as opposed to "7–8" for Gangetic specimens. I have not seen any specimens with eight branched dorsal rays, although the deeply divided last ray could be erroneously counted as such.

DISCUSSION

Of the characteristics given for identification in Hamilton's description (1822), few would be of use in distinguishing species as similar as *P. gracilis* and *P. balitora*. However, Hamilton does state that there are approximately 12 rays in each pectoral fin. This count is closer to what I found for *P. balitora* (minimum 13) and fewer than in the new species (Table 3).

Hamilton's figure of the dorsal aspect reproduced in McClelland (1839) shows six simple rays in each pectoral fin, and anterior-dorsum and head color patterns identical to my observations for *P. balitora*. Hamilton's figure displays the anterior part of the dorsum on *P. balitora* with one blotch midway between the occiput and the dorsal fin, and another at the dorsal fin origin on both lateral and dorsal views. The dorsal coloration of the head has two black spots separated by a transverse white line in the interorbital space. There is no longitudinal white streak from the snout to occiput as on the new species (Fig. 3). There are 34 total scale rows in longitudinal series, which better describes *P. balitora* (Table 3). Although the lateral blotches on Hamilton's illustration of the lateral aspect might correspond to the new species, six lateral spots are commonly seen in *P. balitora*, which also exhibits a lengthened anterior blotch similar to that in Hamilton's figure. The total dorsal spots illustrated in dorsal aspect might be high for *P. balitora*, however, even though both lateral and dorsal views are presumably taken from the same fish, the blotches do not match (the lateral view has one fewer dorsal spot on the peduncle). Because the lateral view shows an equal number of lateral and dorsal blotches, that would presumably be a better indicator of the dorsal spot pattern on the caudal peduncle than the illustrated dorsal aspect. From these characters it would seem that Hamilton's *Cyprinus balitora* is synonymous with my *Psilorhynchus balitora* rather than with the new species.

Psilorhynchus variegatus McClelland remains as a potential name for the new species. McClelland (1839:430) stated that his single specimen differed little from Hamilton's *balitora* except for a few features. McClelland listed 17 rays in the pectoral fins and 33 scales in the lateral line. The total of 17 pectoral fin elements occurs in both species as a maximum, but 33 lateral line scales is the mode for *P. balitora* and two scales below the minimum total count found in *P. gracilis* (Table 3). Therefore, it appears that *P. variegatus* McClelland is indeed a synonym of *P. balitora* (Hamilton) and that *P. gracilis* is a new species.

Other accounts in Day (1878) and Shaw and Shebbeare (1937) apply to *P. balitora*. No published account appears to have included the new species under the name *P. balitora*, which is rather surprising in view of its abundance and apparently widespread occurrence in the Gangetic lowlands.

DISTRIBUTION AND HABITAT PREFERENCE

Thus far the new species has been collected only in Bangladesh. However, the extent of its preferred habitat would suggest a much wider distribution throughout the lower reaches of the Ganges and Brahmaputra rivers. The southernmost collections of *Psilorhynchus gracilis* in Bangladesh are from rivers that currently have independent exits into the Bay of Bengal (Fig. 1). The species is also fairly common in sandy streams of northwest Bangladesh. *Psilorhynchus gracilis* was taken in the same collections with *P. balitora* and *P. sucatio* in the Mahananda River at Tetulia and the Keratoya River at Bhajanpur, both in Dinajpur District. *P. sucatio* was taken at each of my collection localities for *P. gracilis* except one site from the Muhuri River (Feni River drainage) of Noakhali District in southeast Bangladesh. However, *P. sucatio* was taken in two other collections from the Feni River drainage.

Psilorhynchus gracilis is found over small pebbles in shallow running waters where the bottom is primarily sand. In this regard it resembles *P. balitora* which is sometimes found in the same habitat but which is always closely associated with hard substrates. *P. gracilis* is generally free-swimming and occasionally rests on its spread paired fins. *P. balitora* prefers to maintain close fin contact with the substrate, often not moving unless strongly disturbed. *Psilorhynchus gracilis* may be caught easily on pebble outcrops having both species present because of its greater tendency to leave the bottom. A seine pulled under or through the gravel of the same outcrop catches *P. balitora,* which will be taken out along with the substratum. *P. sucatio* differs from the other lowland species in being taken primarily along the edges of sandy streams, and seems to be most abundant near emergent or overhanging vegetation. I have not observed *Psilorhynchus* burrowing, although several species of loaches were seen to burrow into sand within inches of *Psilorhynchus* under observation. Attempts to elicit burrowing by disturbing the fishes were not successful.

The *P. balitora* taken at the same localities as *P. gracilis* were all small, about half to two-thirds adult size. This possibly indicates that fully grown individuals occur upstream in areas of higher gradient. It is also consistent with the physical and behavioral characteristics of the species. *P. balitora* has much larger pectoral fins with more simple rays, and a wider and higher body predorsally. It depresses its head when positioned in an area of strong current, and is forced down onto its fins. This shape is common among Asian hillstream fishes which attach themselves to hard substrata in high-gradient streams (e.g., *Garra, Homaloptera, Gastromyzon*). This somewhat passive posturing for increased friction is a much more efficient method than constant swimming for maintaining position in the current of torrential streams. Thus, it would appear that northern Bangladesh may be the southernmost region of the Gangetic plain occupied by *P. balitora,* a species adapted to higher gradients than either *P. gracilis* or *P. sucatio.*

COMPARATIVE MATERIAL EXAMINED

Psilorhynchus balitora—INDIA: SU 28701 (2 specimens, 42.8–45.2 mm SL), Siliguri, North Bengal, no date given; SU 32627 (1, 40.2) Siliguri, North Bengal, Apr. 1937; AMNH 15767 (1, 47.8), Keleki Stream at Emilioni, Naga Hills, Assam (paratype of *Psilorhynchus homaloptera* Hora and Mukerji). NEPAL: UMMZ 207678 (7, 33.1–37.2), Rapti River at Chitawan Valley, Apr.–May 1975. BURMA: AMNH 13811 (14, 32.5–42.8), Upper Burma, Chindwin drainage. BANGLADESH: UMMZ 205347 (19, 15.6–26.7) Mahananda River at Tetulia, Dinajpur Dist., 5 Apr. 1978; CFRS uncat. (15) same data; UMMZ 205350 (11, 14.1–18.6), Keratoya River at Bhajanpur, Dinajpur Dist., 6 Apr. 1978.

Psilorhynchus sucatio—BANGLADESH: UMMZ 205338 (5 specimens, 20.2–22.6 mm SL), Sangu River at Bandarban, Chittagong Hill Tracts, 25 Dec. 1977; UMMZ 205339 (32, 46.3–73.3), Rangapani Creek, 6 km NNW of Jaintapur, Sylhet Dist., 19 Feb. 1978; UMMZ 205341 (5, 12.5–17.5) Dharla River at Kurigram, Rangpur Dist., 2 Apr. 1978; UMMZ 205344 (5, 15.5–55.6), Jabuneswari River at Badarganj, Rangpur Dist., 3 Apr. 1978; UMMZ 205346 (57, 13.8–58.8), Ghaghat River at Rangpur, Rangpur Dist., 3 Apr. 1978; UMMZ 205349 (42, 15.7–41.8), Mahananda River at Tetulia, Dinajpur Dist., 5 Apr. 1978; UMMZ 205352 (22, 11.1–50.7), Keratoya River at Bhajanpur, Dinajpur Dist., 6 Apr. 1978; UMMZ 205354 (37, 12.7–45.7), USNM 231694 (5), AMNH 43096 (5), and 50010 (5), ANSP 148728 (5), and FMNH 94284 (5), Tangam River at Thakurgaon, 6 Apr. 1973; CFRS uncat. (19, 34.2–71.9), Koilla Creek, 13 km W of Ramgarh, Chittagong Dist., 3 Feb. 1978; CFRS uncat. (8, 25–40), Feni River at Ramgarh, Chittagong Hill Tracts, 3 Feb. 1978; CFRS uncat. (3, 46.4–62.5), Tangam River at Kestapur, Dinajpur Dist., no date; AMNH 19648 (2) Sevoke River, Darjeeling.

ACKNOWLEDGMENTS

My sincere thanks and appreciation go to Karl F. Lagler, The University of Michigan, and John R. Snell, A. Q. Chowdhury, and Kermit E. Sneed, Irrigation Fishery Development Project, Bangladesh, for help in obtaining and shipping the specimens to The University of Michigan. I owe a great deal to my close friend and associate Ataur Rahman and many others in the Directorate of Fisheries, Government of Bangladesh, who greatly facilitated the field work. William N. Eschmeyer (CAS) and Donn E. Rosen (AMNH) loaned specimens. Reeve M. Bailey, Gerald R. Smith, Barry Chernoff, and Michael L. Smith of The University of Michigan offered helpful suggestions pertaining to many aspects of manuscript preparation. Tyson Roberts kindly donated several specimens of *P. balitora* from Nepal to the UMMZ. Mark Orsen and Karna Steelquist of The University of Michigan gave much-needed advice on illustrations. This work was supported in part by the UCLA Department of Biology Fisheries Program.

LITERATURE CITED

CHEN, Y. 1980. Acta Hydrobiologica Sinica (not seen).

DAVID, A. 1953. On some new records of fish from the Damodar and Mahanadi river systems. J. Zool. Soc. India 5(2): 243–254.

DAY, F. E. 1878. The fishes of India, etc. 2 vols. London.

GRAY, J. S. 1834. Illustrations of Indian zoology of new and hitherto unfigured Indian animals from the collection of General Hardwicke. 2 vols. London.

GUDGER, E. W. 1924. The sources of the material for Hamilton-Buchanan's fishes of the Ganges, the fate of his collections, drawings and notes, and the use made of his data. J. Proc. Asiatic Soc. Bengal 19(4):121–136.

HAMILTON (formerly BUCHANAN), F. 1822. An account of the fishes found in the river Ganges and its branches. Edinburgh. 405 p., 39 pls.

HORA, S. L. 1925. Notes on fishes in the Indian Museum. XII—The systematic position of the genus *Psilorhynchus* McClelland. Rec. Indian Mus. (Calcutta) 27:457–460.

———. 1929. An aid to the study of Hamilton Buchanan's "Gangetic Fishes." Mem. Indian Mus. (Calcutta) 9(4):169–192.

———, AND K. S. MISRA. 1941. Fishes collected by the Vernay-Hopwood upper Chindwin Expedition, 1935. J. Bombay Nat. Hist. Soc. 42(3):478–482.

———, AND D. D. MUKERJI. 1935. Fishes of the Naga Hills, Assam. Rec. Indian Mus. (Calcutta) 37:381–404.

MCCLELLAND, J. 1839. Indian Cyprinidae. Asiat. Res. 19: 217–471.

MENON, A. G. K. 1974. A check-list of fishes of the Himalayas and the Indo-Gangetic plains. Inland Fisheries Society of India, Spec. Publ. 1.

———, AND A. K. DATTA. 1961. Zoological results of the Indian Cho-Oyu Expedition (1958) in Nepal. 7—Pisces. *Psilorhynchus pseudecheneis* a new cyprinid fish from Nepal. Rec. Indian Mus. (Calcutta) 59:253–255.

SHAW, G. E., AND E. O. SHEBBEARE. 1937. The fishes of Northern Bengal. J. Asiat. Soc. Bengal, Science 3:1–137.

CALIFORNIA ACADEMY OF SCIENCES
Golden Gate Park
San Francisco, California 94118

PROCEEDINGS
OF THE
CALIFORNIA ACADEMY OF SCIENCES

Vol. 43, No. 7, pp. 77-85, 1 fig., 5 tables. July 6, 1983

SIZE AND DISTRIBUTION OF THE CALIFORNIA SEA LION POPULATION IN MEXICO

By

Burney J. Le Boeuf,[1] *David Aurioles,*[2] *Richard Condit,*[1]
Claudio Fox,[2] *Robert Gisiner,*[3] *Rigoberto Romero,*[2]
and Francisco Sinsel[2]

ABSTRACT: **California sea lions were censused during the 1979 and 1981 breeding seasons on rookeries and hauling grounds in the Gulf of California and the Pacific coast of Mexico. Correcting for underestimate bias and uncensused islands yielded estimates of approximately 20,000 sea lions in the Gulf with an annual production of 7,000 pups, and 63,000 sea lions on the Pacific coast with an annual production of 29,000 pups. Counts on seven major rookeries in the Gulf in 1979 were 35% higher than in 1966. Sixteen percent of the California sea lion population in the United States and Mexico (estimated at 145,000 animals) resides in the Gulf and 46% inhabits the Pacific coast of Mexico.**

INTRODUCTION

The California sea lion, *Zalophus californianus,* along with numerous species of birds and whales, is a top trophic-level predator in the productive waters of the Gulf of California. In the southern part of the Gulf, it feeds predominantly on a variety of fishes and occasionally on squid (Aurioles, Fox, and Sinsel 1981). The full impact of this pinniped on Gulf of California fisheries is unknown because few systematic censuses of these animals have been conducted.

Long before California sea lions in the Gulf of California were counted, they were exploited. Early inhabitants of Baja California, Sonora, and Sinaloa killed California sea lions for their meat. Between 1860 and 1870, whalers killed thousands of sea lions for their oil and skins. Later, the animals were hunted for their "trimmings"—vibrissae and genitalia which were sold in the Orient as aphrodisiacs. Local slaughter for oil and meat continued until the early 1960's on some islands in the Gulf, e.g., Puerto Refugio on Ángel de la Guarda (Lluch 1969), and poaching is still going on today.

The first systematic census of the sea lions in the Gulf was conducted by Lluch (1969). He estimated 6,027 total animals on eight islands from counts made in 1963, 1964, and 1966 at the peak of the breeding season. Orr, Schonewald, and Kenyon (1970) censused several islands between 1960 and 1968, but with the exception of Los Islotes, no rookery was censused during the breeding season. Mate (1977) estimated 9,428 sea lions in the Gulf of California from aerial censuses taken in June 1975, but his data are difficult to compare with other censuses because

---

[1] Department of Biology and Center for Coastal Marine Studies, University of California, Santa Cruz, California 95064.

[2] Centro de Investigaciones, Biologicas de Baja California, La Paz, Baja California, Mexico.

[3] 571 West B Street, Dixon, California 95620.

FIGURE 1. The route of R/V *Ellen B. Scripps* on expeditions in 1979 and 1981 from San Diego, California, to California sea lion rookeries along the Pacific coast of Baja California, Mexico, and in the Gulf of California. The itineraries were similar in both years except for deviations taken in 1979 which are noted by solid lines. The numbers refer to rookeries not censused (1–6) and islands supporting nonbreeding aggregations (7–12). The code is: 1 = Los Coronados; 2 = Isla San Gerónimo; 3 = Punta Rosarito; 4 = Isla Magdalena; 5 = Isla Lobos; 6 = Farallón at Mazatlán; 7 = Isla Salsipuedes; 8 = Cabo Haro; 9 = Roca Vela; 10 = Isla Patos; 11 = Cabo Lobos; 12 = Punta Lobos.

they are categorized by latitude rather than by island.

The main purpose of this report is to present recent data on the number and distribution of California sea lions in the Gulf of California during the breeding season and to compare these data to earlier counts and to counts obtained on islands on the west coast of Baja California, Mexico. In addition, we report weights and measurements of sea lion pups obtained from Gulf and Pacific rookeries.

METHODS

CENSUSES.—The data in this report were collected on two expeditions aboard the Scripps Institution of Oceanography research vessel *Ellen B. Scripps*. Inclusive dates were 21 June to 21 July 1979 and 1 to 30 June 1981. The track records are shown in Figure 1.

Both expeditions were timed to coincide with the breeding season of California sea lions and to facilitate counting sea lions in the Gulf. At Los Islotes, the peak number of breeding females occurs at the end of June, and the maximum number of pups are observed on about 10 July (Aurioles, Romero, and Fox 1978). We were aided in locating all suspected rookeries in the Gulf by previous investigations and by information obtained from local fisherman. The only rookeries not censused in the Gulf were Isla Lobos and the farallón at Mazatlán. We did not census the following rookeries on the outer Pacific coast of the peninsula: Isla Natividad, Los Coronados, Isla San Gerónimo,[4] and Punta Rosarito. Estimates of the sea lion population on these Gulf and Pacific rookeries are available from other sources (e.g., Mate 1977).

Censuses were conducted from a dinghy or launch, from the ship, and on foot. Most counts were made from a 4-m Avon or Zodiac inflatable dinghy powered by a 15- or 25-hp outboard motor. One person operated the boat and one or two people censused. Small islands were circumnavigated; on large islands, a dinghy was launched after sea lion aggregations were sighted from the ship. In ideal conditions, the boat was run slowly within 10 m of the shoreline. This did not alarm the sea lions and accurate counts were obtained. When waves or wind were strong, or extensive kelp beds surrounded an island, the boat was operated 30 to 70 m offshore. In bad weather, binoculars were used from the research vessel from 0.5 to 1 km offshore. This was necessary at Isla Santa Margarita and three small nonbreeding aggregations on Isla Magdalena, Salsipuedes, and Cabo Haro in 1981.

We censused sea lions in six categories: adult males, subadult males, females, juveniles, pups, and miscellaneous. Adult males are the largest animals with large dorsal head crests and thick necks. Subadult males are smaller, have thinner necks, and little crest development. For most analyses, these two age categories are combined. Females and juveniles are distinguished from males by their smaller size, thinner neck, and light brown color compared to dark brown in males. Juveniles are the smallest class in this group and include one- to two-year-olds, and possibly some three-year-olds. The miscella-

---

[4] Also spelled Isla San Jerónimo.

neous category encompasses any animal except pups that could not be readily categorized because of high animal density or poor censusing conditions. Pups are the unmistakable, but easily concealed, young of the year.

VALIDITY AND RELIABILITY ESTIMATES.—Validity tests were performed using ground counts and boat counts of the same rookery. After a census was conducted from a dinghy, one person went ashore, counted adults from a hiding place, and then frightened the adults into the water and quickly counted the pups. This was done at six places in 1981. In addition, at two sites we compared counts from the ship with counts from a dinghy. Estimates of reliability were obtained by having two censusers make simultaneous counts at all rookeries in 1979 and at five rookeries in 1981. For these areas, the mean of the two censuses conducted is presented.

WEIGHTS AND MEASUREMENTS.—A crew of three to six people weighed and measured 111 pups on six rookeries, one in the Pacific and five in the Gulf. Landing near a rookery caused adults to flee into the water leaving their pups behind. The procedure consisted of capturing a one- to three-week-old pup by the hindflippers and restraining it on a flat rock. Curvilinear length (tip of nose to tip of tail) was measured along the contour of the dorsal midline. The pup was then placed in a light leather dog harness and weighed with a hand-held spring scale (25-kg capacity ± 0.5 kg). After extracting a blood sample, the pup was tagged with an "All-Flex" cattle ear tag in the trailing edge of a foreflipper, its sex was determined, and it was carried back to where it was captured. Mothers retrieved their pups shortly after pups were released or soon after the launch and crew departed from the rookery.

RESULTS

WEATHER.—Weather conditions in 1979 were ideal for censusing in the Gulf; seas were calm; winds of 0–5 knots were variable in direction. Conditions were fair for censusing Pacific coast islands except at Isla Santa Margarita where high surf prevailed. Wind and choppy water made censusing in the Gulf difficult in 1981, especially on the windward sides of Islas San Esteban, San Pedro Mártir, Granito, and San Ignacio Farallón; on the Pacific side, heavy surf made landings or censusing by dinghy impossible at Islas Magdalena and Santa Margarita and on the west side of Isla Cedros.

GULF OF CALIFORNIA.—More than 15,000 sea lions were counted in the Gulf in 1979 and more than 14,000 in 1981 (Table 1). Major rookeries in the Gulf were found on islands in the center or midriff area: San Esteban and Ángel de la Guarda (Los Machos, Granito, and Los Cantiles). In 1979 and 1981, 76 and 71% of the sea lions counted were observed in the area from the north end of Ángel de la Guarda (29°35′N) south to San Pedro Nolasco (27°58′N). Most of the sea lions in the north end of the Gulf were located on Isla San Jorge. Relatively few sea lions breed in the southern end of the Gulf, and these were concentrated on Los Islotes and San Ignacio Farallón.

No pups were observed in the small groups of sea lions present on Isla Salsipuedes, Cabo Haro, Roca Vela, Isla Patos, Cabo Lobos, and Punta Lobos. No sea lions were observed during careful surveys of Isla Coronado, Tortuga, Raza, Mejía, Cabo Tepopa, Los Frailes, Cabo San Lucas, and the eastern half of Islas San Lorenzo, Las Ánimas, and Espíritu Santo. A few males or juveniles were observed on Islas Carmen, San Lorenzo, and Partida.

Eleven Gulf rookeries produced a minimum of 3,422 pups in 1979, 2,277 in 1981 (Table 1). The largest category of the animals counted on rookeries were female (48% in 1979 and 60% in 1981). The mean operational sex ratio (adult males:adult females) for rookeries was 1:8.30 (N = 9, SD = 5.61) in 1979 and 1:9.41 (N = 10, SD = 3.83) in 1981. The overall operational sex ratio for rookeries in these years were 1:5.84 and 1:8.94, respectively.

Sea lions in the Gulf occupied cobblestone coves or the boulder-strewn shoreline. Few breeding groups were seen on sand or gravel beaches, which tended to be occupied by nonbreeding males. Most territorial males were observed "patrolling" the water in front of the females. Females and pups occupied a narrow zone near the water's edge and rarely were observed 10 m or or more inland. In some locations, rafts of females floated in the shallows and the females occasionally vocalized to their pups onshore. Even on islands supporting numerous sea lions, the population was broken up into small groups, and a small number of animals took up a large part of the shoreline.

TABLE 1. CENSUSES OF CALIFORNIA SEA LIONS IN THE GULF OF CALIFORNIA, 29 JUNE TO 8 JULY 1979 (top figures) AND 8–21 JUNE 1981 (bottom figures, in italics). "–" denotes that no census was taken. Abbreviations for census methods: G = ground, L = launch, S = ship.

Islands	Census methods	Males	Females	Pups	Juv.	Misc.	Totals
Los Islotes	G, L	18	88	28	4		138
	G	*11*	*26*	*7*	*0*		*44*
San Ignacio Farallón	—	—	—	—	—	—	—
	G, L	*10*	*133*	*64*	*36*	*80*	*323*
Cabo Haro	L	1	32		16		49
	S	*25*					*25*
San Pedro Nolasco	L	76	382	232	133	23	846
	L	*82*	*696*	*125*	*201*	*22*	*1,126*
San Pedro Mártir	L	150	903	321	167	93	1,634
	G, L	*134*	*1,061*	*252*	*120*	*125*	*1,692*
San Esteban	G, L	504	2,044	820	325	268	3,961
	G, L, S	*295*	*2,252*	*705*	*239*	*102*	*3,593*
Salsipuedes	L	8	34		56		98
	S		*19*		*15*		*34*
Roca Blanca	L	8	121	40	38		207
	—	—	—	—	—	—	—
Patos	L	454			19		473
	—	—	—	—	—	—	—
Ángel de la Guarda							
Los Machos	L	35	709	168	404		1,316
	L, S	*84*	*762*	*226*	*247*	*70*	*1,389*
Granito	L	87	436	337	242		1,102
	G, L	*73*	*658*	*161*	*79*	*47*	*1,018*
Los Cantiles	L	163	969	446	219	13	1,810
	L	*91*	*688*	*270*	*102*	*229*	*1,380*
Roca Vela	L	3	50		30		83
	—	—	—	—	—	—	—
Cabo Lobos	L	50	48		72		170
	—	—	—	—	—	—	—
San Jorge	L	167	1,398	1,030	632	26	3,253
	L	*165*	*2,034*	*457*	*667*	*21*	*3,344*
Rocas Consag	—	—	—	—	—	—	—
	L	*18*	*295*	*10*	*98*		*421*
Totals 1979		1,724	7,214	3,422	2,357	423	15,140
Totals 1981		*988*	*8,639*	*2,277*	*1,789*	*696*	*14,389*

Approximately 10–20% of the females observed were still nursing yearlings, and some small groups were made up almost entirely of such pairs.

PACIFIC COAST.—Approximately 23,000 sea lions were counted on Pacific coast rookeries in 1979, a greater number than in 1981 (Table 2). However, some islands censused in 1979 were not censused in 1981, and vice versa. A better estimate of the total number of animals associated with the rookeries shown in Table 2 is 27,895—obtained by adding the 1981 census count for Islas Cedros (4,730) and Magdalena (47) to the 1979 total census.

At least 6,529 pups were produced on the islands censused in 1979. If the number of pups counted on Isla Cedros in 1981 (2,138) is added to that, annual pup production was at least 8,667 pups.

As in the Gulf, females were in the majority (53% of animals counted in 1979 and 55% in 1981). The mean operational sex ratio of rookeries in 1979 was 1:6.87 (N = 6, SD = 5.83), the overall sex ratio was 1:3.58. Less than 2% of the females were observed nursing yearlings.

Large aggregations of sea lions were observed on each rookery visited with the exception of Isla de Guadalupe. The females were hauled out in clumps well above the surf line, usually on sandy beaches. Territorial males stationed themselves

TABLE 2. CENSUSES OF CALIFORNIA SEA LIONS ON THE PACIFIC COAST OF BAJA CALIFORNIA, 13–20 JULY 1979 (top figures) AND 3–5 JUNE 1981 (bottom figures, in italics). Numbers in parentheses are calculated from total number of animals censused; "–" denotes that no census was taken. Abbreviations for census methods: G = ground, L = launch, S = ship.

Islands	Census method	Males	Females	Pups	Juv.	Misc.	Totals
San Martín	G	25	9		40		74
	–	–	–	–	–	–	–
Guadalupe	L, S	5	85	2	8		100
	–	–	–	–	–	–	–
San Benito							
Oeste	G, L	355	502	283	13		1,153
	G, L	*21*	*115*	*1*		*150*	*287*
Centro	G, L	817	3,718	2,560	88		7,183
	G	*79*	*1,985*	*1,185*	*38*		*3,287*
Este	L	183	1,070	900	59		2,212
	L	*(97)*	*(441)*	*(304)*	*(10)*		*852*
Cedros	–	–	–	–	–	–	–
	G, L	*270*	*1,880*	*2,138*	*282*	*160*	*4,730*
Asunción	G, L	1,793	4,183	1,582	506		8,064
	G	*(105)*	*(2,780)*	*(406)*	*(608)*		*3,899*
Magdalena	–	–	–	–	–	–	–
	S					*47*	*47*
Santa Margarita	L, G	265	2,676	1,202	114		4,257
	S	*(108)*	*(1,086)*	*(652)*	*(46)*		*1,892*
Punta Lobos	L	6	35		14		55
	–	–	–	–	–	–	–
Totals 1979		3,449	12,278	6,529	842		23,098
Totals 1981		*680*	*8,287*	*4,686*	*984*	*357*	*14,994*

on land with the females. Nonbreeding males were observed considerable distances inland on nearby rocks or on unoccupied beaches. In smaller groups that were sometimes seen in coves or on rocky ledges, territorial males were either on land or in the water near the females.

Eighteen sea lions were observed at sea in the Pacific and in the Gulf in 1981. They were solitary and most were within a few kilometers of a rookery. Three exceptions were one sea lion seen near Cabo Pulmo, one east of Cabo San Lucas, and one near Isla Coronados.

CENSUS METHOD BIAS.—Comparison counts using different census methods are shown in Table 3. Ground counts of pups exceeded those taken from a launch, with the underestimate from a launch being greatest when the animals were distributed in rocky areas. Launch and ground counts of adults were similar; the slightly higher counts from a launch were partly because launch counts always preceded ground counts. The latter were conducted in the morning when the temperature was rising and some adults were entering the water to cool off. Ship counts of adults were lower than those taken from the launch, and pups were most difficult to see from the large vessel.

Two measures of inter-observer agreement were obtained. In 1979, independent counts of two censuses on 13 rookeries were correlated. Correlation coefficients were high and positive for total animals (0.976), females (0.935), and pups (0.926). Correlation coefficients were lower for juveniles (0.777) and males (0.712), animals which are more difficult to categorize, i.e., subadult males or juveniles can be confused with adult females. In 1981, two independent censuses were conducted on parts of five rookeries in the Gulf. The results, shown in Table 4, are similar to those obtained in 1979 in that agreement is usually high for total animals and females and relatively low for juveniles. Independent counts of pups in 1981 were more discrepant than in 1979.

PUPS WEIGHTS AND MEASUREMENTS.—The mean weight and curvilinear length of newborn pups is shown in Table 5. On each rookery, the mean weight and mean length of males is greater than that of females. For all rookeries combined,

Table 3. A Comparison of Census Methods on Short Sections of Rookeries. Abbreviations for census methods: G = ground, L = launch, S = ship.

Island	Weather and terrain	Census method	Adults	Pups
Cedros	Calm sea; animals packed tightly on sandy beach with some in arroyo behind beach.	L	—	55
		G	—	80
San Pedro Mártir	Calm sea, overcast sky; animals on pebbly beach.	L	—	25
		G	—	42
Granito (A.G.)	Calm sea on protected side; animals distributed on small cobblestones & large boulders backed by vertical cliffs.	L	269	45
		G	231	117
San Ignacio Farallón	Calm sea; animals on rocky shoreline containing a large open cave, flat shelves & large boulders.	L	65	4
		G	58	52
San Esteban	Slight chop; animals on long sandy spit, in rock stubble at base of vertical cliffs & in shallow sea caves.	S	264	0
		L	388	2
Los Machos (A.G.)	Calm sea; animals on sandy beaches, rock tables & among boulders at base of cliffs.	S	347	0
		L	488	179

males were significantly heavier ($t = 5.42$, $df = 109$, $P = < 0.05$) and longer ($t = 4.88$, $df = 109$, $P = <0.05$) than females. The mean weights of pups of both sexes from Cedros Island, the only Pacific rookery represented, are lower than that of pups from any Gulf rookery, but these differences are not statistically significant.

Discussion

We counted 15,140 California sea lions in the Gulf of California in 1979. This number is 61% higher than an aerial census in July 1975 by Mate (1977) and 151% higher than a launch and ground census in 1963–1966 by Lluch (1969). Is our higher count due to increased censusing effort, the census methods employed, or to a genuine increase in the population? Each explanation has some validity.

Our census was more complete than Lluch's. Fifty-four percent of the animals we counted in 1979 were on rookeries and resting places Lluch did not visit; Los Islotes, San Esteban, Roca Blanca, Ángel de la Guarda (Los Machos and Los Cantiles), Cabo Haro, Islas Salsipuedes and Patos, and Cabo Lobos. If sea lions were found on these islands in the mid-1960's in the same relative proportions as in 1979, the total number of animals would have approximated 13,000, 16% fewer than we counted in 1979.

Terrain and climatic conditions in the Gulf are such that an aerial census like that conducted by Mate (1977) from a small airplane underestimates the number of animals present more than counts from a launch or on foot. Mate explains that his count of 9,428 was low because of the difficulty of counting and photographing animals from the air over the dark, rocky terrain, with many animals in the water by mid-morning. An indication of the different results of these two censusing methods is that Mate counted only 122 pups in the entire Gulf compared to our 3,422.

Because of discrepancies in method and location of censusing, entire censuses are not very useful for determining population change. However, comparisons of individual rookeries indicate that the population in Mexico has increased. For seven rookeries, our counts can be compared with Lluch's (1969). Both the dates and method of censusing were similar. He counted 5,977 animals and we counted 7,662 and 8,091 animals in our two censuses. These represent increases of 28 and 35% over a period of 13 to 16 years. Our counts were higher on San Jorge (77%), San Pedro Mártir (56%), and Rocas Consag (181%), and lower on Granito (40%), Roca Vela (81%), and San Ignacio Farallón (alias Topolobampo) (24%). Counts on San Pedro Nolasco were similar in 1966 and 1979 but increased by 32% in 1981. Finally, it is not clear if the population decreased from 1979 to 1981, because the two censuses were conducted at slightly different times during the breeding season. The 1981 census was made prior to peak season, accounting for the lower count.

There are numerous difficulties in simply counting large groups of sea lions, leading to underestimates of animals present. Counts vary with the census method used, weather condi-

TABLE 4. COMPARISON OF INDEPENDENT CENSUSES TAKEN AT SEA LION ROOKERIES IN THE GULF OF CALIFORNIA IN JUNE 1981. Abbreviations: G = ground, L = launch, RC = R. Condit, FS = F. Sinsel, CF = C. Fox.

Rookery	Census method	Weather, light, terrain	Censuser	Males	Females	Pups	Juv.	Totals
Los Islotes	G	Clear sky, fading light; rough terrain, boulder & cobblestones.	RC	11	26	7	0	44
			FS	16	14	6	6	42
San Pedro Mártir	L	Windy, overcast; choppy to heavy seas; 2 sandy beaches, cobble coves, rock tables, large boulders backed by steep cliffs.	RC	69	925	72	124	1,190
			FS	134	1,186	252	120	1,692
Los Machos (A.G.) (partial)	L	Sunny, flat sea; most females & pups on sandy beaches, juveniles & subadult males on rock tables & in boulder fields.	RC	84	832	226	247	1,389
			FS	67	1,069	293	109	1,535
Granito (A.G.)	L	S side calm; N side very choppy, poor censusing conditions; 1 sandy beach on each side bordered by irregular rocky coastline backed by steep cliffs.	RC	60	621	163	72	916
			FS/CF	87	789	159	87	1,122
San Esteban	L	Calm sea N & W sides; steep cliffs with caves & rocky shelves; long sandy or cobbly beaches.	RC	234	1,865	369	500	2,968
			FS	212	1,824	545	160	2,741
Totals			C	458	4,269	837	943	6,507
			FS/CF	516	4,882	1,255	482	7,132

tions, terrain, the experience and reliability of censusers, and the size, age, and sex composition of groups being counted. Moreover, the number of sea lions on land varies with time of year and the time of day. A special difficulty for estimating breeding females is that some will always be at sea feeding during the breeding season. As a result, counts provide only minimum estimates of the number of animals present. Empirically based correction factors must be employed to estimate actual population numbers.

We reason that the actual number of sea lions counted in the Gulf of California underestimates the number of animals and that a more valid estimate is 20,144 animals. This estimate is derived by applying three correction factors to the 1979 total count of 15,140 animals (the 1979 census is selected over the 1981 census because it is closer to the peak of the breeding season). This count is augmented by: (a) 744 animals, representing known rookeries not censused in 1979; San Ignacio Farallón (323) and Rocas Consag (421); (b) 3,496 pups, assuming that pups counted reflect only 50% of the pups present; (c) 764 females, assuming that 10% of the females are at sea feeding (see Bonnell et al. 1978). We believe that 20,144 total animals in the Gulf and an annual production of approximately 7,000 pups are reasonable, conservative estimates.

Using the same assumptions, we can estimate the number of sea lions on the Pacific coast of Mexico. Before doing this, it should be noted that previous censuses from launches or on foot are of limited use for estimating population size because they are only partial counts of the area or they were conducted outside the breeding season, e.g., Bartholomew and Hubbs (1952), Rice, Kenyon, and Lluch (1965), Orr, Schonewald, and Kenyon (1970), Brownell, DeLong, and Schreiber (1974). Aerial censuses of sea lions on the

Table 5. Weights and Measurements of California Sea Lion Pups Obtained 11–28 June 1981. For each island listed, the mean weight (in kilograms) or mean length (in centimeters) is shown plus or minus one standard deviation. N is in parentheses.

	Weight		Length	
Rookeries	Males	Females	Males	Females
San Pedro Mártir	8.75 ± 1.89 (6)	7.50 ± 1.96 (4)	76.42 ± 4.58 (6)	71.43 ± 8.94 (4)
San Esteban	10.17 ± 1.54 (6)	8.00 ± 1.06 (9)	74.93 ± 3.00 (6)	74.08 ± 5.03 (9)
Granito (A.G.)	9.19 ± 1.04 (16)	7.75 ± 0.97 (13)	75.17 ± 2.62 (16)	71.48 ± 3.14 (13)
San Jorge	8.86 ± 0.92 (9)	7.71 ± 1.14 (12)	75.01 ± 2.30 (9)	72.55 ± 3.16 (12)
San Ignacio Farallón	8.80 ± 1.10 (5)	8.20 ± 1.30 (5)	76.20 ± 0.92 (5)	70.34 ± 3.31 (5)
Cedros	8.54 ± 1.45 (12)	7.29 ± 1.93 (14)	76.79 ± 3.37 (12)	72.82 ± 3.91 (14)
Totals	9.01 ± 1.32 (54)	7.60 ± 1.45 (57)	75.71 ± 2.93 (54)	72.34 ± 4.18 (57)

Pacific coast of Mexico by Mate (1977) (see Bonnell et al. 1978) yielded a direct count of 45,872 animals. We estimate that the total number of sea lions on the Pacific coast of Mexico is approximately 63,020 animals, a number which includes the annual production of 29,000 pups. We start with the direct count of 23,098 animals obtained in 1979. We increase this number by: (a) 4,777 representing two rookeries we counted in 1981 but not in 1979 (Islas Cedros and Magdalena, see Table 2); (b) 12,682 representing the following rookeries we did not census but which were censused by Mate (1977) (see also Bonnell et al., 1978): Los Coronados (297), San Gerónimo (1,113), Punta Rosarito (2,722), Natividad (5,785), and Punta Tosca (2,765); (c) 8,667 pups, assuming that 50% of the pups counted from launches were missed; (d) 11,445 pups, to compensate for the failure to count pups from aerial censuses; and (e) 2,351 females, assuming that 10% of the females were at sea. Augmentations in categories b, d, and e are based on Mate's aerial census in 1975 (Mate 1977). Since he did not categorize animals by age or sex, we added pup and female counts to his numbers using ratios derived from our censuses.

From these estimates and censuses conducted in the United States, we can estimate the size of the population. Bonnell et al. (1978) estimated 50,000 animals in southern California waters from aerial censuses and 4,000 in the northern part of the nonbreeding range. Thus, the total number of California sea lions in the United States and Mexico is approximately 145,000 animals. Of this total, 16% are in the Gulf of California, 46% are on the Pacific coast of Mexico, 35% are in southern California, and 3% range as far north as Vancouver Island, British Columbia (Hancock 1970; Bigg 1973). Our estimate of the United States and Mexico population of this species exceeds the figure of 125,000 estimated by Bonnell et al. (1978). Both estimates do not include the geographically separated subspecific populations on the Galápagos Islands and in Japan.

The distribution of breeding animals in the Gulf differs from that most commonly observed on Pacific coast rookeries. In the Gulf, male territories are predominantly aquatic, fronting on small groups of females and pups distributed in a narrow zone along the water's edge on cobblestone beaches, among boulders, or on rocky ledges. On Pacific coast rookeries in Mexico and California, females are most often hauled out in large groups well above the surf line on sandy beaches or on flat rock outcroppings sloping into the sea (Peterson and Bartholomew 1967; Odell 1975; Bonnell et al. 1978); male territories are semi-aquatic or usually terrestrial. Higher temperatures in the Gulf may account in part for these differences in behavior and distribution.

Acknowledgments

We thank Drs. Felix Cordoba Alva and Carlos de Alba Perez for help in obtaining permits and making logistical arrangements in Mexico; George Shor, Robert Haines, and others at Scripps Institution of Oceanography for helping to make the R/V *Ellen B. Scripps* available to us; Captains Hansen and Whitman and their crews for safe and efficient conduct; and Dr. Leo Ortiz, Dr. James Estes, Dr. Martha Field, Dr. Robert Brownell, Jr., Steve Davenport, Edward Keith, Kathy Panken, John Peterson, Joanne Reiter, Marianne Riedman, and Keith Skaug for field assistance. These expeditions were supported in part by National Science Foundation grant DEB 77-17063 AO1 to B. Le Boeuf.

LITERATURE CITED

AURIOLES, D., C. FOX, AND F. SINSEL. 1981. Species of fishes identified with the otoliths found in scats of sea lions at "Los Islotes" Island, B.C.S., Gulf of California, Mexico. Abstract, 4th Biennial Conference on the Biology of Marine Mammals, Dec. 14–18, 1981, San Francisco, California.

———, R. ROMERO, AND C. FOX. 1978. Censos poblaciones de lobos marinos (*Zalophus californianus*) por edades y sexos en la bahía de la Paz y sus alrededores. Pages 139–154 *in* Informe General de Labores, 1978. Centro de Investigaciones Biologicas de Baja California, A.C.

BARTHOLOMEW, G. A., AND C. L. HUBBS. 1952. Winter populations of pinnipeds about Guadalupe, San Benito, and Cedros Islands, Baja California. J. Mammal. 33:160–171.

BIGG, M. A. 1973. Census of California sea lions on southern Vancouver Island, British Columbia. J. Mammal. 54:285–287.

BONNELL, M. L., B. J. LE BOEUF, M. O. PIERSON, D. H. DETTMAN, AND G. D. FARRENS. 1978. Pinnipeds of the southern California Bight. Vol. III, Part 1, 535 p. *in* K. S. Norris, B. J. Le Boeuf, and G. L. Hunt, Jr., eds., Marine Mammal and Seabird Surveys of the Southern California Bight Area, 1975–1978. Bureau of Land Management, Dept. of Interior Contract AA550-CT7-37, Government Printing Office, Wash., D.C.

BROWNELL, R. L., JR., R. L. DE LONG, AND R. W. SCHREIBER. 1974. Pinniped populations at Islas de Guadalupe, San Benito, Cedros and Natividad, Baja California, in 1968. J. Mammal. 55:469–472.

HANCOCK, D. 1970. California sea lion as a regular visitant off the British Columbia coast. J. Mammal. 51:614.

LLUCH, B. D. 1969. El lobo marino de California (*Zalophus californianus californianus* Lesson, 1828) (Allen, 1880), en dos mamiferos marinos de Baja California. Inst. Mex. Rec. Nat. Renovables., 3–69.

MATE, B. 1977. Aerial censusing of pinnipeds in the Eastern Pacific for assessment of population numbers, migratory distributions, rookery stability, breeding effort, and recruitment. Report to Marine Mammal Commission Contract MM5AC001, 28 Feb. 1977. 68 p.

ODELL, D. K. 1975. Breeding biology of the California sea lion, *Zalophus californianus*. Rapp. P.-V. Reun. Cons. Int. Explor. Mer 169:374–378.

ORR, R. T., J. SCHONEWALD, AND K. W. KENYON. 1970. The California sea lion: skull growth and a comparison of two populations. Proc. Calif. Acad. Sci., ser. 4, 37:381–394.

PETERSON, R. S., AND G. A. BARTHOLOMEW. 1967. The natural history and behavior of the California sea lion. Spec. Pub. No. 1, Amer. Soc. Mammal. 79 p.

RICE, D. W., K. W. KENYON, AND D. LLUCH. 1965. Pinniped populations at Islas Guadalupe, San Benito, and Cedros, Baja California, in 1965. Trans. San Diego Soc. Nat. Hist. 14:73–84.

CALIFORNIA ACADEMY OF SCIENCES
Golden Gate Park
San Francisco, California 94118

PROCEEDINGS
OF THE
CALIFORNIA ACADEMY OF SCIENCES

Vol. 43, No. 8, pp. 87-110, 15 figs. July 6, 1983

MEGAMOUTH—A NEW SPECIES, GENUS, AND FAMILY OF LAMNOID SHARK (*MEGACHASMA PELAGIOS,* FAMILY MEGACHASMIDAE) FROM THE HAWAIIAN ISLANDS

By
Leighton R. Taylor
Waikiki Aquarium, 2777 Kalakaua Ave., Honolulu, Hawaii 96815

L. J. V. Compagno
Tiburon Center for Environmental Studies, San Francisco State University,
P.O. Box 855, Tiburon, California 94920

and
Paul J. Struhsaker
1050 Koloa St., Honolulu, Hawaii 96816

Abstract: ***Megachasma pelagios*, a new genus and species of lamnoid shark assigned to the new family Megachasmidae, is described and defined from a single adult male, 4.46 m total length. The holotype and only known specimen was collected approximately 42 km NE of Oahu, Hawaii. Structure and habitus distinctly differ from other lamnoid sharks, particularly in head and tooth morphology and in mesopelagic filter feeding.**

Introduction

On 15 November 1976, the research vessel *AFB-14* of the Naval Undersea Center (now the Naval Ocean Systems Center), Kaneohe, Hawaii, was conducting oceanographic research in waters about 42 km northeast of Kahuku Point, Oahu, at about 21°51′N and 157°46′W. From 1015 to 1415 Hawaiian Standard Time the ship had deployed two large parachutes as sea anchors at a depth of about 165 m in water with a bottom depth of approximately 4600 m. When the parachutes were hauled to the surface, using a small winch with an 180 kg pull shut-off, one of them had entangled in it a large adult male shark 4.46 m (14.6 ft) long and 750 kg (1653 lbs) (Figs. 1–4). Crew members of the *AFB-14* realized that the shark was unusual and brought it aboard with much difficulty. The shark was shipped to the Kaneohe Bay facility of the Naval Undersea Center and tied alongside the dock overnight.

The senior author inspected it the next morning. Preliminary examination indicated that it represented a very distinct, undescribed species, and it was decided that it should be preserved intact. Accordingly, the shark was winched out of the water by the tail using a Navy crane, but the caudal fin broke off and the shark fell into the water and had to be retrieved by divers. The shark was quick-frozen at Hawaiian Tuna Packers, Honolulu, while a large preservation tank

Figure 1. Artist's conception of *Megachasma pelagios* in its natural habitat, slowly swimming with open mouth and feeding on planktonic animals. (From a painting by Richard Ellis.)

was constructed. On 29 November 1976, the shark was transported frozen to the Kewalo dock site of the National Marine Fisheries Service for thawing and injection with formalin. Subsequent examination of the shark by the authors and colleagues indicated that it is a lamniform shark (order Lamniformes of Compagno 1973a) that is not assignable to any known genus or family and is herein described as *Megachasma pelagios,* new genus and species, and placed in the new family Megachasmidae.

The discovery of the novel shark was widely reported in newspapers (e.g., Anonymous 1 and 2, 1976, and Dunford 1976). It was dubbed the "Megamouth shark" in reference to its unusually large oral cavity. This common name has since been adopted by several authors (Compagno 1977, 1979, and 1981; Taylor 1977; Tinker 1978; Faughnan 1980; Clark 1981), and we suggest that it be considered as the accepted common name for the species.

This strange shark is extraordinary in its distinctness from other sharks and its great size. Most sharks are small, less than 2 m long at maturity (Compagno 1981). The new shark joins the company of the few giant sharks commonly reaching total lengths over 4 m, including the broadnose sixgill shark (*Hexanchus griseus*), Pacific sleeper shark (*Somniosus pacificus*), Greenland shark (*S. microcephalus*), whale shark (*Rhiniodon typus*), great white shark (*Carcharodon carcharias*), tiger shark (*Galeocerdo cuvier*), and great hammerhead (*Sphyrna mokarran*). The common thresher (*Alopias vulpinus*) and bigeye thresher (*A. superciliosus*) also reach total lengths over 4 m, but these sharks have greatly elongated caudal fins and hence are relatively small-bodied in comparison to the giant species. Although new species of small sharks are discovered fairly frequently, giant sharks are not, and almost all of the great species were described in the 18th and 19th centuries.

Because the only known specimen of *Megachasma pelagios* is an adult male, and because it is very common for female sharks to reach a somewhat larger size than males, it is reasonable to expect larger specimens of this species.

METHODS

On 30 November 1976, the thawed shark was placed in a large, above-ground plastic pool filled with seawater. Comprehensive measurements of the shark were recorded, following the procedures of Bigelow and Schroeder (1948). Skin samples were taken from the mouth, tongue, pectoral fin, caudal fin, back below first dorsal fin, and gill-rakers for later examination using a Cambridge S410 Stereoscan electron microscope.

Skin samples from the mouth lining and tongue were sectioned and stained using standard histological techniques. A short incision, approximately 30 cm long, was made on the ventral surface to gain access to the stomach and valvular intestine, and stomach contents were removed. The valvular intestine was removed, slit medially to count the ring valves and to remove intestinal worms for parasitologists (Dailey and Vogelbein 1982), and separately preserved. Samples of muscle tissue and liver were taken for electrophoretic analysis. Extensive sets of still photos were made of the preservation process by the authors and Mr. Paul Meyers of the Naval Undersea Center, who also made 16 mm movies of these techniques.

The body cavity and musculature of the shark were injected with 25 l of 100% formalin (40% aqueous formaldehyde gas solution). The shark was then lifted by crane and cargo sling into a 4 × 3.5 × 1 m fiberglass box and covered with a 40% seawater-formalin solution. After six months in formalin, the specimen was deposited in the fish collection of the Bernice P. Bishop Museum, Honolulu, where it was rinsed for 30 days in water and then placed in 55% isopropyl alcohol. Tooth samples were removed for examination of their morphology, and one tooth was sectioned and stained for tooth histology. A "peel" dissection was made on the right side of the head to examine the neurocranium and jaw structure of the shark, and similar dissections were made on the right pectoral fin and right clasper. Vertebrae were excised from the base of the caudal fin and from beneath the first dorsal fin and sectioned to examine their calcification patterns.

Terminology for descriptive morphology of *Megachasma pelagios* follows Bigelow and Schroeder (1948) and Compagno (1970, 1973a, 1973b, and 1979).

Megachasmidae, new family

TYPE-GENUS.—*Megachasma* Taylor, Compagno, and Struhsaker, new genus.

FAMILY DESCRIPTION.—Giant neoselachian sharks of the order Lamniformes (as defined by

FIGURE 2. Holotype of *Megachasma pelagios,* within 12 hours of its capture. Note the extreme protrusibility of the jaws and the gill filaments visible in the first gill opening.

Compagno 1973a) reaching at least 4.46 m length when adult. Trunk cylindrical but not highly fusiform, tapering rearward from the head. Caudal peduncle short, stout, slightly compressed, and without lateral keels or ridges; a shallow, longitudinally oval upper precaudal pit present, but no lower pit. Head broad, very large and long, and not pointed, length greater than abdomen

FIGURE 3. Frontal view. Note Navy research vessel and winch which retrieved shark in background. (Official U.S. Navy photograph.)

between pectoral and pelvic bases. Snout very short, depressed, and broadly rounded, not conical or bladelike. Eyes lateral on head, length less than one-fourth length of longest gill openings. Nostrils small, widths about $\frac{1}{11}$ internarial width, with short, low anterior nasal flaps; nostrils lateral and opposite the first fourth of mouth. Gill openings moderately large, not expanded onto dorsal surface of head; internal gill openings with numerous gill-rakers of a unique type, formed as elongated, slender, cartilage-cored dermal papillae covered by imbricated denticles (Fig. 6). Mouth terminal and very large, broadly arched, extremely long, and extending far behind eyes when jaws are not protruded; jaws strongly protrusible, capable of extension well in front of snout. No true labial furrows or labial cartilages, but with inner labial grooves present along edges of mouth corners.

Teeth similar in upper and lower jaws, weakly differentiated, with moderately long, broad, flattened roots, very short labial root lobes, and very long, broad, expanded lingual protuberance; moderately strong basal ledges and grooves on the labial crown face; a broad, enameloid-free neck on the crown foot; a strong, narrow, lingually hooked cusp with cutting edges confined to its tip, no striations or ridges on the cusp. Teeth not compressed and bladelike, relatively small, and very numerous, over 100 rows in each jaw and in three or four functional series. Toothless spaces on symphyses of jaws extremely broad, especially on upper jaw. Teeth in each jaw half apparently continuously varying and without discrete row groups; no gap or reduced intermediate teeth between teeth in anterior and lateral positions in upper jaw.

Lateral trunk denticles with broad, teardrop, or wedge-shaped, flattened crowns, not erect, hooked, or directed anteriorly or dorsoventrally; pedicels of trunk denticles low and broad (Fig. 11). Wavy grooves of naked skin on the pectoral, pelvic, and caudal fin webs. Pectoral fins relatively narrow, long and blunt-tipped, length from origin to free rear tip about half as long as pectoral anterior margin. Origins of pectoral fins under fourth gill openings. Pectoral fins more than three times area of first dorsal fin, with anterior margins more than three times length of pelvic anterior margins. Pectoral fin skeleton plesodic, with pectoral radials extending into the distal fin web nearly to its edge; ceratotrichia reduced along distal fin margin and not extending proximally to radial musculature of fin. Pectoral fins very small, angular, smaller than first dorsal fin but larger than second dorsal, with an aplesodic fin skeleton. Claspers moderately slender and elongated, with attenuated tips and external spurs (Fig. 11). First dorsal fin moderately large, angular and relatively low, with a narrowly rounded apex and an aplesodic fin skeleton; origin of first dorsal much closer to pectoral fin bases than pelvic bases, and free near tip, well in front of pelvic origins. Second dorsal fin less than one-third area of first dorsal and slightly less than half as high, angular and broad-based, with its origin about over the pelvic fin insertions. Neither second dorsal nor anal bases pivoted. Anal fin about half area of second dorsal, angular and broad-based, with its origin about opposite free rear tip of second dorsal and its free rear tip well in front of ventral caudal origin; insertion of anal separated from ventral caudal origin by space greater than base or anal. Caudal fin with a long dorsal lobe nearly half length of rest of shark, a long ventral lobe about ⅖ as long as dorsal lobe, a deeply notched postventral caudal margin, a weak subterminal notch, and no undulations or ripples on the dorsal or preventral caudal margins; caudal fin not lunate or crescentic, dorsal caudal vertebral axis moderately elevated at an angle to body axis (heterocercal).

Neurocranium (Fig. 13) with tripodal rostrum formed of a small, moderately elongated, medial rostral cartilage originating from expanded internasal plate and pair of basally enlarged, triangular lateral rostral cartilages that taper anteromedially to fuse with medial rostral cartilage and form a narrow, flattened, unfenestrated rostral node. Base of medial rostral cartilage elevated by dorsally arched internasal septum above level of bases of lateral rostral cartilages and nasal capsules, so that medial rostral cartilage arches anteroventrally to meet rostral node. Rostrum short, less than half nasobasal length of cranium. Nasal capsules small, greatly compressed, far lateral to each other and separated by flattened internasal septum. Entire anterior surfaces of nasal capsules forming bases of lateral rostral cartilages. Broad subethmoid fossa not extending anterior to nasal capsules. Cranial roof very broad and flat, not arched above the orbits, with a huge transverse anterior fontanelle; basal plate broadly arched. Orbits with low preorbital processes, complete supraorbital crests, and broad, low postorbital processes. A deep pit on each side of ventral surface of cranium between base of suborbital shelf and basal plate in front of stapedial fenestrae, for orbital processes of palatoquadrates. Otic capsules broad and relatively long, without elongated pterotic horns.

Jaws very long and stout, much longer than cranium, extending from the cranial rostral node to well behind the occiput when retracted. Palatoquadrates with long, stout palatine processes lacking dental bullae; strong, low, knoblike, cartilaginous orbital processes, and low, strong quadrate processes. Orbital processes articulating on ventral surfaces of suborbital shelves and basal plate below orbits, quadrate processes far below postorbital processes of cranium and not contacting them. Anterior ends of Meckel's cartilages extending below level of anterior ends of palatoquadrates, no "overbite" of palatoquadrates on Meckel's cartilages. Vertebral column with well-developed cartilaginous centra separated by broad bands of notochordal sheath, but with primary and secondary calcification virtually absent. Intestinal valve with 24 turns.

Classification.—Compagno (1973a, 1977) divided the living elasmobranch fishes, or neoselachians, into four superorders, of which the Galeomorphii or galeomorph sharks clearly includes the new family Megachasmidae and genus *Megachasma*. Megachasmidae has the following galeomorph characters: head and body not greatly depressed and not expanded laterally; spiracles without valves; five pairs of laterally situated gill openings; denticles covering almost entire body, not absent ventrally, nor enlarged on midline of back, and not enlarged on pectoral fins in adult males; pectoral fins without anteriorly expanded triangular lobes covering gills or fused to sides of head above them; propterygium of pectoral fin skeleton not anteriorly expanded; pectoral fins not modified into propulsive organs; pectoral girdle not articulating with vertebral column; vent confluent with pelvic fins; two dorsal fins and an anal fin present; caudal fin heterocercal, with a subterminal notch on the dorsal caudal lobe and with ventral lobe shorter than dorsal lobe; neurocranium with strong suborbital shelves, no antorbital cartilages, ectethmoid processes, or enlarged ectethmoid chambers on the nasal capsules, rostrum not trough-shaped, no basal angle on basal plate, no lateral commissures on otic capsules, and with incomplete postorbital walls; no palatobasal articulation of palatoquadrates with neurocranium; hyoid arch complete, no pseudohyoids; vertebral column without synarcuals, and vertebral centra without concentric calcifications.

The Galeomorphii of Compagno (1973a, 1977) was subdivided into four orders, Heterodontiformes, Orectolobiformes, Carcharhiniformes, and Lamniformes; of these, the family Megachasmidae falls in the order Lamniformes or lamnoid sharks. Lamnoid characters of Megachasmidae include its simple nostrils of the ordinary shark type, entirely separate from the mouth, with small anterior nasal flaps, diagonal incurrent and excurrent apertures, and no perinasal folds and grooves, anterior barbels, or nasoral grooves; a long mouth extending behind the eyes when jaws are retracted; no supraorbital and subocular ridges; eyes circular and laterally without nictitating eyelids, subocular pouches, or postorbital eyelid muscles; osteodont teeth (Fig. 9) with weak basal ledges; posterior teeth not enlarged and formed into molariform crushers; claspers with external spurs on the T-3 cartilage and with elongated, tubular, expanded marginal cartilages; dorsal fins spineless, with segmented basal cartilages; cranium with a tripodal rostrum, nasal capsules not anteroposteriorly elongated and trumpet-shaped; no ethmopalatine grooves for the articulation of the palatoquadrate orbital processes, complete preorbital walls, separate foramina for superficial ophthalmic nerves in orbits and for hyomandibular nerves on otic capsules, and relatively long otic capsules; jaws long, extending posterior to the occiput; mouth gape not restricted anteriorly, labial cartilages, folds and grooves reduced or absent; pectoral fin skeleton with a small propterygium, moderately large mesopterygium, and large metapterygium; mesopterygium and metapterygium not elongated parallel to the axes of their radials, and not proximally shaftlike, distally expanded and without a fenestra between them; preorbitalis or levator labii superioris muscles relatively small and anteroposteriorly positioned on the jaws, with origins on posteroventral surfaces of the nasal capsules, fibers nearly horizontal when jaws are retracted, and insertions far posterior on the adductor mandibulae muscles at the jaw angles; adductor mandibulae muscles anteriorly notched; levator palatoquadrati muscles simple, not subdivided into anterior constrictor and spiracular muscles; no craniomandibular or mandibulocutaneous muscles; and an elongated, ring-valve intestine.

Relationships to Other Lamnoids.—Within the Lamniformes, the family Megachasmidae represents a very distinct and singular taxon, well separated from all other families. Other lamnoids of the families Odontaspididae, Mitsukurinidae, Pseudocarchariidae, Alopiidae, Cetorhinidae, and Lamnidae all differ from the Megachasmidae in having a more elongated, more narrowly rounded, conical or bladelike snout; no papillose gill-rakers (denticle gill-rakers present in Cetorhinidae); mouth subterminal on head and less enlarged; tongue smaller; upper anterior and lateral teeth separated by a gap that may or may not have reduced intermediate teeth; tooth rows either less than 60 in each jaw, or more than 200 (Cetorhinidae); toothless space on upper symphysis relatively narrow; no wavy grooves of naked skin on the pectoral, pelvic, and caudal fins; lateral rostral cartilages narrow-based and only covering part of the dorsal surfaces of the nasal capsules or the preorbital processes; base of medial rostral cartilage well below bases of lateral rostral cartilages and with shaft of cartilage below rostral node; nasal capsules nearly spherical, not compressed, and with ventral nasal apertures; cranial roof narrow to only moderately expanded anteriorly, with anterior fontanelle varying from moderate to greatly reduced; orbital processes more or less reduced on palatoquadrates, articulating with the suborbital shelves where present; jaws shorter, beginning well behind the snout tip when retracted; and with primary calcification of the double cones and secondary radii well developed in their vertebral centra.

Members of the family Odontaspididae (including the genera *Eugomphodus* and *Odontaspis*) further differ from *Megachasma* and the Megachasmidae in having prominent, transverse precaudal pits; labial folds, furrows and cartilages present (with the possible exception of *E. tricuspidatus*); nostrils in front of the mouth; teeth with strong labial root lobes, moderate lingual protuberances, narrow necks on the crown, and labiolingually diagonal attachment surfaces; symphyseal, anterior, lateral, intermediate, and posterior tooth-row groups well differentiated along dental bands, with anteriors and laterals enlarged; pectoral fins smaller, shorter, broader, less elongated, and not falcate, and with aplesodic fin skeletons; pectoral fin origins behind fifth gill openings; claspers stouter and blunt-tipped, with blunt clasper spurs; origin of first dorsal fin well posterior to pectoral insertions; second dorsal fin more than half as high as first dorsal; caudal fin shorter, less than half as long as rest of shark; subterminal notch of caudal fin deep; ventral caudal lobe shorter, dorsal caudal margin with rippled edges; rostral node compressed, with vertical fenestra and strut; cranial roof narrow and arched above orbits; and otic capsules with strong pterotic horns.

The family Pseudocarchariidae, which like Megachasmidae has a single, oceanic, highly distinct species (*Pseudocarcharias kamoharai*), differs from *Megachasma* in many characters, including its more slender body and shorter head; slender, cylindrical caudal peduncle with low lateral keels and upper and lower transverse, crescentic precaudal pits; much larger eyes; nostrils anterior to mouth; more elongated gill openings, extending onto dorsal surface of head; teeth with strong labial root lobes, moderate lingual protuberances, a narrow neck on the crown, and labiolingually diagonal attachment surfaces; anteriors, intermediates, and lateroposteriors well differentiated in dental bands; anteriors and anterior-laterals enlarged, pectoral fins smaller, broader, less elongated, and not falcate, with aplesodic fin skeletons; origins of pectoral fins behind fifth gill openings; anal fin with a narrow base and pivotable; caudal fin with a shorter dorsal and ventral caudal lobe; rostrum longer, with appendices, a compressed rostral node, and vertical fenestrae and struts; basal plate and cranial roof extremely narrow, with narrow, slotlike, vertical anterior fontanelle; orbits of cranium very large; pterotic horns present and well developed on otic capsules; palatine processes of palatoquadrates enlarged and forming large dental bullae, articulating with the orbital notches of the cranium; and quadrate processes of palatoquadrates elevated and contacting postorbital processes.

The benthopelagic family Mitsukurinidae also has a single living, strongly distinct species (*Mitsukurina owstoni*). The Mitsukurinidae differs from the Megachasmidae in lacking precaudal pits; having a greatly elongated, flattened, bladelike snout; smaller eyes; a very narrow, elongated mouth; lower labial furrows; teeth with strong labial root lobes, moderate lingual protuberances, a narrow neck and striations on the crown, and labiolingually diagonal attachment surfaces; symphyseals, anteriors, laterals, and posteriors well differentiated in dental bands, with anteriors and laterals enlarged; lateral trunk denticles with narrow, hooked, semierect crowns; pectoral fins smaller than pelvic fins, shorter, broader, not elongated and falcate, and with aplesodic fin skeletons; pectoral origins behind fifth gill openings; first and second dorsal fins equal-sized, smaller than pelvic and anal fins; anal fin large, broadly rounded, and separated from lower caudal origin by a narrow notch; anal fin origin about opposite or close behind second dorsal origin; no ventral caudal lobe; rostrum of cranium greatly elongated, longer than nasobasal length of cranium, with a compressed, extremely long rostral node; subethmoid fossa extending anterior to the nasal capsules; supraorbital crest reduced to separate preorbital and postorbital processes; and with palatine processes of palatoquadrates deflected ventrally, with prominent bullae.

The three highly specialized lamnoid families Alopiidae, Lamnidae, and Cetorhinidae have numerous additional differences from the Megachasmidae. The Alopiidae further differs from the Megachasmidae in having a shorter head; crescentic upper precaudal pits; larger eyes; nostrils anterior to mouth; shorter gill openings; a much smaller mouth and less highly protrusible jaws; teeth with weaker lingual protuberances, stronger labial root lobes, and differentiated anteriors, lateroposteriors, and (variably) intermediates and symphyseals; claspers very slender, without spurs; pelvic fins plesodic; first dorsal fin higher and plesodic, with its origin well posterior to the pectoral insertions; second dorsal much smaller relative to first dorsal, with a narrow, pivotable base; anal fin smaller, with narrow, pivotable base; caudal fin about as long as rest of shark, with a rippled dorsal margin; rostral node of rostrum compressed, with a vertical fenestra and strut; internasal septum narrow and high; subethmoid fossa very narrow; cranial roof narrow, flat or strongly arched; orbits large to gigantic; and palatine processes of palatoquadrates with small dental bullae.

The Lamnidae differs from the Megachasmidae in the following additional characters: trunk more fusiform; caudal peduncle greatly depressed, with strong lateral keels, and with transverse, crescentic, upper and lower precaudal pits; nostrils anterior to the mouth; gill openings longer, extending partway onto dorsal surface of head; jaws less protrusible; teeth with low lingual protuberances, enlarged anteriors, laterals, and intermediates; pectoral fin origins behind fifth gill openings; second dorsal much smaller relative to first dorsal, with a narrow, pivotable base; anal fin slightly larger than second dorsal, with a narrow, pivotable base; caudal fin shorter, less than half length of rest of shark, nearly symmetrical and lunate in Lamnidae, with a relatively shorter dorsal lobe, ripples in dorsal margin, and a longer ventral lobe; cranial roof narrow and arched; otic capsules with elongated pterotic horns; palatine processes of palatoquadrates with prominent dental bullae articulating with underside of ethmoid region of cranium; and quadrate processes of palatoquadrates very high.

Finally, the family Cetorhinidae with the only other filter-feeding lamnoids of the genus *Cetorhinus*, differs from the family Megachasmidae in the following particulars: trunk more fusiform; caudal peduncle somewhat depressed, with strong lateral keels and transverse, crescentic upper and lower precaudal pits; nostrils anterior to mouth; gill openings much larger, expanded onto dorsal and ventral surfaces of head; jaws little protrusible; pectoral fins with their origins behind fifth gill openings; lateral trunk denticles with erect, hooked, narrow crowns, directed anteriorly and dorsoventrally as well as posteriorly; claspers stout, with broad tips and heavy spurs; first dorsal fin with its origin far posterior to pectoral insertions, and midbase closer to pelvic bases than to pectoral bases; caudal fin shorter, less than half length of rest of shark, nearly symmetrical and lunate, with a shorter dorsal lobe and longer ventral one; medial rostral cartilage very broad, platelike, and ventrally excavated by the broad anterior expansion of the subethmoid fossa; lateral rostral cartilages joining each other posterior to their junction with the rostral node, and extending anterior to that junction as a medial rod; cranial roof moderately broad, highly arched above orbits; supraorbital crests fenestrate basally; and jaws very slender and weak.

The phenetic comparisons between Megachasmidae and other lamnoids presented above are not intended to be exhaustive, but serve to demonstrate the separation of Megachasmidae from related families. They do not broach the question of the relationship of the megamouth shark to other lamnoids. A detailed account of lamnoid interrelationships is beyond the scope of this paper, but suffice it to note here that many of the characters of *Megachasma pelagios*, such as its snout and jaw structure, gill-rakers, dermal grooves on fins, reduced vertebrae, and ethmoid morphology are evidently unique derived characters of this shark that do not offer a clue to its relationships. Its teeth are superficially similar to those of the basking shark (*Cetorhinus maximus*), but this may be parallel evolution of vestigial structures in two very different lamnoid filter-feeders (as suggested by the superficial similarity of the teeth of the orectoloboid whale shark, *Rhiniodon typus*). *Megachasma* most resembles members of the Odontaspididae (especially the genus *Odontaspis*) and Pseudocarchariidae in its body shape, fin shape, relative fin sizes (except for the pectoral fins), fin positions, and relationships of interspaces between fins to fin size. By comparison with the derived families Alopiidae, Cetorhinidae, and Lamnidae, these similarities between Megachasmidae, Odontaspididae, and Pseudocarchariidae may prove to be common primitive characters not of importance in demonstrating phyletic relationships among these families. *Megachasma* shares the derived character state of plesodic pectoral fins with the Alopiidae, Cetorhinidae, and Lamnidae, but presently appears to have little else in common with these derived families.

On the other hand, two characters of *Megachasma*, if correctly interpreted as primitive, suggest that Megachasmidae is the sister-group of all other living lamnoids. The absence of differentiated anteriors, laterals, and intermediates (or a toothless gap between anteriors and laterals) in *Megachasma* may indicate that it is primitive in lacking them, and that all other lamnoids (including *Cetorhinus*) can be united by the presence of these tooth-row groups as a shared derived character. However, the unusually broad, toothless space at the upper symphysis of *Megachasma* suggests another possibility, that it is derived in having lost these row groups, at least in the upper jaw; and that the simple gradient monognathic heterodonty in the dentral bands is secondary and correlated with the evolution of gill-rakers as the primary feeding structures in *Megachasma*.

The second character is the well-developed orbital processes on the palatoquadrates of *Megachasma*, which suggest a primitive condition by comparison with other, non-lamnoid sharks. The reduced (Alopiidae, Odontaspididae, Mitsukurinidae, and Cetorhinidae) or apparently nonexistent (Lamnidae, Pseudocarchariidae) orbital processes of other lamnoids would by this interpretation represent a shared derived character of lamnoids other than *Megachasma*. A detailed assessment of these characters and others, grouping the various lamnoid genera and families will be considered in detail elsewhere (Compagno, in preparation).

A possible fossil relative of *M. pelagios* is represented by isolated small teeth (2–15 mm high) known since the 1960's from early Miocene deposits in the southeastern San Joaquin Valley of California (Shelton P. Applegate, pers. comm.), and subsequently found in other localities in the late Oligocene or early Miocene of northern California (Phillips et al. 1976) and central Oregon (Bruce J. Welton, pers. comm.). The shark represented by these teeth has never been named, but is known from abundant tooth material from southern California. Its affinities have been much debated among palaeoichthyologists, but it appears most likely to be a lamnoid because of its osteodont tooth histology and external tooth morphology. Dr. Bruce J. Welton is preparing a paper describing this shark, and will compare it with *M. pelagios*, of which it is possibly a fossil congener but is distinctly more primitive.

Megachasma, new genus

Type-species.—*Megachasma pelagios* Taylor, Compagno, and Struhsaker, new species.

Derivation of Name.—*mega*, from Greek, large, great; *chasma*, yawning hole, open mouth.

Generic Diagnosis.—Characters of the new genus are those of the new family Megachasmidae (see above).

Megachasma pelagios, sp.nov.

Megamouth Shark

Holotype.—An adult male, 4460 mm total length, Bernice P. Bishop Museum, Honolulu, Oahu, Hawaii, BPBM 22730.

Type-locality.—Hawaiian Islands, about 42 km ne Kahuku Point, Oahu, 21°51′N, 157°46′W, at about 165 m depth in water about 4600 m deep.

Derivation of Species Name.—*pelagios*, from Greek, of the open sea.

Measurements and Proportions.—These are given below as measurements in millimeters, followed by their proportions as percentages of total length and precaudal length, given in that order in parentheses.

Total length: 4460 mm (100% total length, 144.3% precaudal length).

FIGURE 4. Lateral-view drawing of the holotype of *Megachasma pelagios*, with jaws in retracted position. Drawn by L. J. V. Compagno.

Precaudal length (snout to upper caudal origin): 3090 (69.3, 100).

Tip of snout to: upper symphysis, 66 (1.5, 2.1); nostrils, 100 (2.2, 3.2); orbits, 240 (5.4, 7.8); spiracles, 450 (10.1, 14.6); 1st gill openings, 850 (19.1, 27.5); 2nd gill openings, 920 (20.6, 29.8); 3rd gill openings, 1020 (22.0, 33.0); 4th gill openings, 1150 (25.8, 37.2); 5th gill openings (head length), 1180 (26.5, 38.2); pectoral origins, 1110 (24.9, 35.9); pelvic origins, 2270 (50.9, 73.5); 1st dorsal origin, 1540 (34.5, 49.8); 2nd dorsal origin, 2530 (56.7; 81.9); anal origin, 2830 (63.5, 91.6); vent, 2295 (51.5, 74.3).

Distance between: vent and caudal tip, 2165 (48.5, 70.1); 1st and 2nd dorsal origins, 625 (14.0, 20.3); 1st and 2nd dorsal bases, 590 (13.2, 19.1); 2nd dorsal and upper caudal origins, 428 (9.6, 13.9); 2nd dorsal base and upper caudal origin, 395 (8.9, 12.8); pectoral and pelvic origins, 510 (11.4, 16.5); pelvic and anal bases, 330 (7.4, 10.7); anal and lower caudal origins, 315 (7.1, 10.2); anal base and lower caudal origin, 230 (5.2, 7.4).

Eyes (palpebral apertures or fleshy orbits): length, 56 (1.3, 108); height, 54 (1.2, 1.7); width across anterior corners (interorbital), 370 (8.3, 12.0); eyeball diameter, 84 (1.9, 2.7).

Nostrils: width, 30 (.07, 1.0); internarial space, 340 (7.6, 8.8).

Spiracles: diameter, 6 (0.1, 0.2); space between spiracles and eyes, 176 (3.9, 5.7).

Mouth (jaws in retracted position): length, 273 (6.1, 8.8); width, 827 (18.5, 26.8); width across outer edges of jaws, 1025 (23.0, 33.2); length of lower jaw, 820 (18.4, 26.5).

Gill opening widths (heights): 1st, 265 (5.9, 8.6); 2nd, 258 (5.8, 8.4); 3rd, 264 (5.9, 8.5); 4th, 256 (5.7, 8.3); 5th 234 (5.2, 7.6).

Head height: at spiracles, 500 (11.2, 16.2); at 1st gill openings, 625 (14.0, 20.2); at 5th gill openings, 630 (14.1, 20.4).

Trunk height: at 1st dorsal origin, 640 (14.3, 20.7); at pelvic origins, 515 (11.5, 16.7); at pelvic insertions, 440 (9.9, 14.2).

Girth: at 1st dorsal origin, 1800 (40.4, 58.2); at 2nd dorsal origin, 1140 (25.6, 36.9).

Caudal peduncle height: at 2nd dorsal insertion, 341 (7.6, 11.0); at upper caudal origin, 237 (5.3, 7.7).

Caudal peduncle width: at 2nd insertion, 146 (3.3, 4.7); at upper caudal origin, 109 (2.4, 3.5).

Pectoral fins, length of: anterior margin, 837 (18.8, 27.1); posterior margin, 615 (13.8, 19.9); base, 262 (5.9, 8.5); origin to free rear tip, 453 (10.1, 14.7); inner margin, 190 (4.3, 6.1).

Pelvic fins, length of: anterior margin, 264 (5.9, 8.5); posterior margin, 181 (4.1, 5.9); base, 207 (4.6, 6.7); origin to free rear tip, 245 (5.5, 7.9); inner margin, 38 (0.8, 1.2); height, 255 (5.7, 8.3); origin to rear tip of clasper, 575 (12.9, 18.6).

Claspers: inner length from vent to tip, 550 (12.3, 17.8); outer length from clasper base to tip, 355 (8.0, 11.5); width at outer pelvic base, 47 (1.1, 1.5).

1st dorsal fin, length of: anterior margin, 415 (9.3, 13.4); posterior margin, 265 (5.9, 8.6); base, 404 (9.1, 13.1); inner margin, 82 (1.8, 2.7); height, 226 (5.1, 7.3).

2nd dorsal fin, length of: anterior margin, 198 (4.4, 6.4); posterior margin, 158 (3.5, 5.1); base, 191 (4.3, 6.2); inner margin, 80 (1.8, 2.6); height, 104 (2.3, 3.4).

Anal fin, length of: anterior margin, 196 (4.4, 6.3); posterior margin, 80 (1.8, 2.6); base, 159

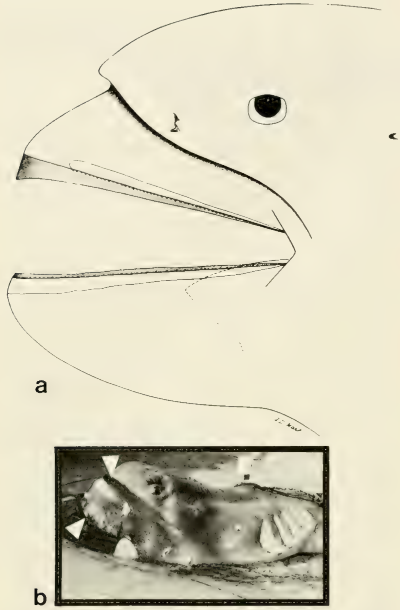


FIGURE 5. (*a*) Schematic head drawing of *Megachasma pelagios* with jaws protruded. (*b*) Photograph of fresh shark with jaws protruded. (Upper arrow points to anteriormost edge of neurocranium; lower arrow to upper jaw and teeth.)

(3.6, 5.1); inner margin, 67 (1.5, 2.2); height, 78 (1.7, 2.5).

Caudal fin, length of: dorsal margin, 1443 (32.3, 46.7); preventral margin, 625 (14.0, 20.2); lower postventral margin, 377 (8.5, 12.2); upper postventral margin, 1220 (27.4, 39.5); subterminal margin, 57 (1.3, 1.8); terminal margin, 96 (2.2, 3.1); terminal lobe or sector, 139 (3.1, 4.5); width of dorsal lobe at postventral notch, 471 (10.6, 15.2); width of ventral lobe at postventral notch, 273 (6.1, 8.8).

Intestinal valve: length, 690 (15.5, 22.3); diameter, 145 (3.3, 4.7); thickness of broadest anterior ring, 25 (0.6, 0.8).

DESCRIPTION (based on the holotype and only known specimen).—Head length from snout tip to 5th gill openings, 26% of total length and 1.6 times distance between pectoral and pelvic fin bases. Head broad, cylindrical, and approximately circular in transverse section at eyes, but somewhat laterally expanded and oval in section over jaws when jaws are retracted; not depressed. Outline of head in lateral view nearly straight dorsally, except for bluntly convex snout, strongly convex ventrally along edges of lower jaws and nearly straight beneath gills; in dorsoventral view, anteriorly rounded and convex and tapering posteriorly to gills. Snout length from tip to edge of mouth about 12.5 times in mouth width. Snout broadly rounded in dorsal view, with lateral margin slightly indented anterior to nostrils; in lateral view, convex dorsally and concave ventrally to fit the front of the retracted upper jaw (Fig. 5). External eye opening (palpebral aperture) or fleshy orbit without anterior or posterior notches, length about 21 times in head length. Irises of eyes black, nearly filling orbits. Eyeballs large, diameter 14 times in head length. Spiracles small, their lengths about $^{1}/_{10}$ orbit length, located about 3 orbit lengths behind eyes and about opposite ventral margins of eyes. Gill openings of nearly equal length, the longest (1st and 3rd) about 4.5 in head length and 4.7 times eye length, the smallest (5th) about $^{9}/_{10}$ length of longest. Edges of gill openings nearly straight, not incised, and with filaments not exposed when jaws are retracted. Gill openings with upper ends falling below level of eyes, and midheight of head at gill openings. Internal gill openings with numerous gill-raker papillae arranged in about 4 rows on their anterior and posterior edges, including both anterior and posterior edges of 1st gill cavity between hyoid and 1st branchial arches and posterior edge of 5th gill cavity on anterior edge of 5th gill arch. Gill-raker papillae small, about 10–15 mm long, densely packed, slender, tapering to blunt point, arranged with tips pointing anteromedially into pharynx, with thick epidermis and dermis covering hyaline cartilage core layered with flattened, imbricated denticles (Fig. 6). Nostrils with large lateral incurrent aperture, anterior nasal flap with an undulated, truncated posterior edge, and low keel on dorsal surface, but no distinct mesonarial flap, small medial excurrent aperture with low posterior nasal flap on its rim. Nostrils lateral to mouth edge and 2.4 times closer to snout tip than to eyes. Nostril width 1.8 in orbit length, 8.8 times in longest gill opening. Inner labial grooves at mouth corners on both upper and lower jaws just lateral to dental bands and medial to vertical fold of skin sheathing adductor mandibulae muscles. Mouth width when jaws are retracted about 1.4 in head length; mouth length

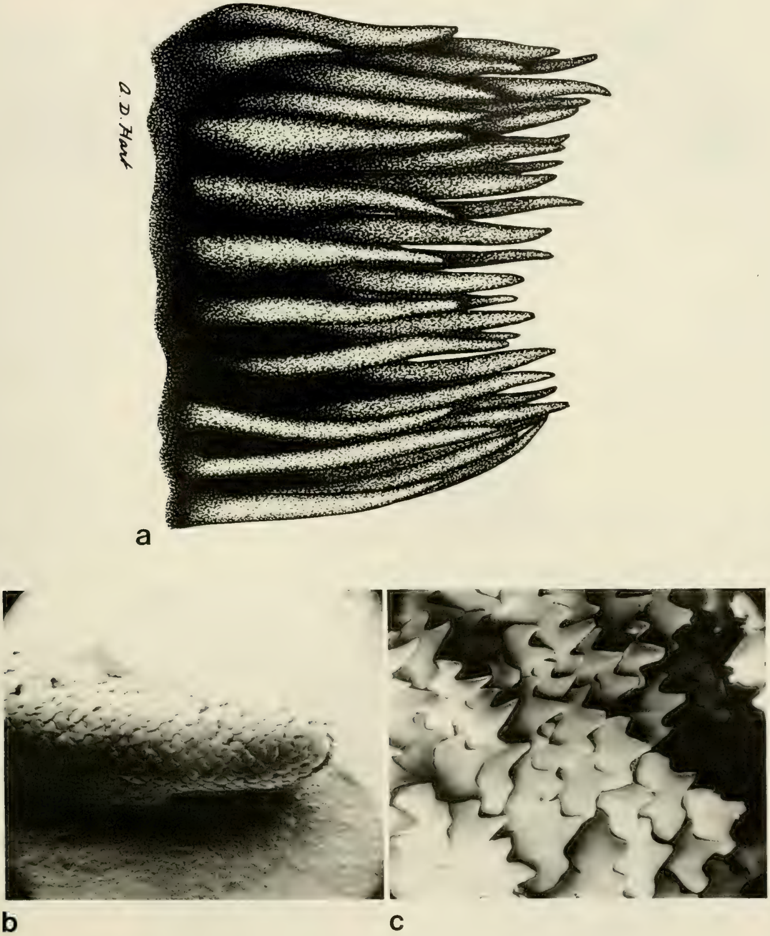


FIGURE 6. Gill-raker papillae of *Megachasma pelagios.* (*a*) Drawing of a group of gill-raker papillae. (*b*) Scanning electron micrograph of the tip of a single papilla, showing the closely imbricated denticles (20× magnification). (*c*) Scanning electron micrograph of denticles from *b*, at higher magnification (51×).

about 3 times in width. A broad fold of skin forming a deep pocket on dorsal surface of upper jaws below snout, and a vertical fold of skin enclosing anterior edges of adductor mandibulae muscles at each mouth corner. Tips of upper jaws can extend at least 6 orbit lengths in front of snout tip, with mouth corners passing anterior to eyes. Tongue extremely large, broadly rounded and thick, enclosing greatly enlarged basihyoid cartilage; tongue almost entirely filling mouth cavity when jaws are closed. Deep pocket under front of tongue, freeing it anteroventrally; pocket about 4 orbit lengths deep from anterior tongue edge to its basal attachment to mouth. Maxillary

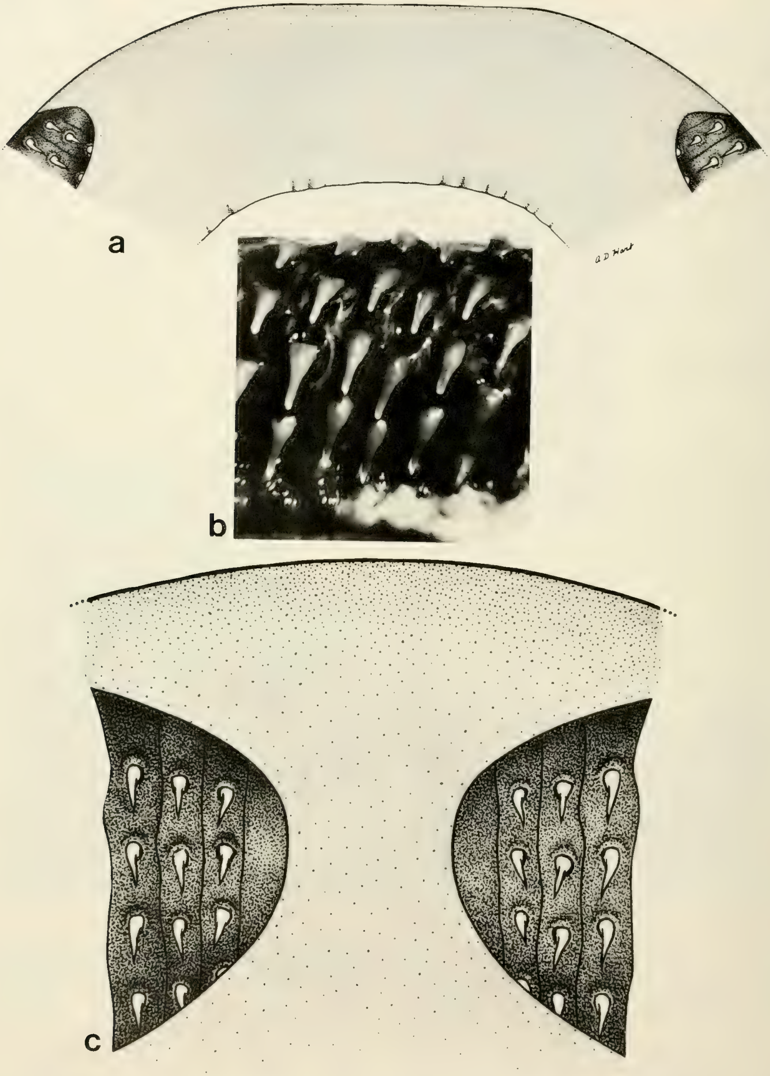


FIGURE 7. Illustrations of (*a*) upper symphysis and (*c*) lower symphysis of *Megachasma pelagios*, showing bare, toothless patches and mesial ends of dental bands. (*b*) Close-up of rows of teeth from upper jaw.

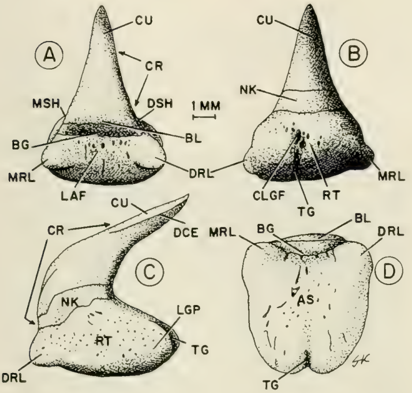


FIGURE 8. Illustration of a lower tooth of *Megachasma pelagios* from about midlength on the lower left dental band in (*A*) labial; (*B*) lingual; (*C*) distal; and (*D*) basal views. Abbreviations: AS, attachment surface of root; BG, basal groove; BL, basal ledge; CLGF, centrolingual foramen; CR, crown; CU, cusp; DCE, distal cutting edge; DRL, distal root lobe; DSH, distal shoulder; LAF, labial foramina; LGP, lingual protuberance; MRL, mesial root lobe; MSH, mesial shoulder; NK, neck; RT, root; TG, transverse groove. Drawn by L. J. V. Compagno.

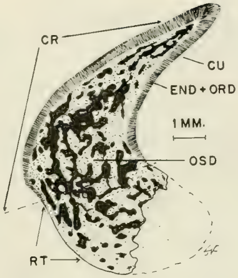


FIGURE 9. Diagrammatic sagittal section of a lower tooth of *Megachasma pelagios* from about midlength on the lower left dental band, lingual protuberance broken off. Abbreviations: CR, crown; CU, cusp; END + ORD, enameloid + orthodentine; OSD, osteodentine; RT, root. The teeth of *M. pelagios* are of the "osteodont" type, with a crown having a core of osteodentine and no pulp cavity or canal. Drawn by L. J. V. Compagno.

valve of upper jaw arcuate and relatively narrow, width less than an eye diameter. No enlarged buccal papillae in mouth cavity, but with scattered circular organs of undetermined function on tongue and mouth.

Teeth very small and relatively numerous, in 56 rows in left upper, 59 rows in left lower, 52 rows in right upper, and 69 rows in right lower jaw halves, or 56–52/59–69; total tooth-row counts 108/128. Teeth not arranged in diagonal files. Symphyseal toothless space about 4 orbit diameters wide in upper jaw and less than one eye-length wide in lower jaw (Fig. 7). Dental bands of upper and lower jaws show strong gradient monognathic heterodonty; starting from small teeth at symphysis, teeth increase in size to about 10 mm high in about 10 tooth rows distal to symphysis, then begin to gradually decrease in size and increase in width relative to height to distal ends of dental bands. Teeth (Fig. 8) have no cusplets, narrow crown shoulders, partial transverse groove on linguobasal attachment surface of root, large centrolingual foramen, and scattered labial foramina below basal ledge. A sectioned tooth (Fig. 9) shows thick osteodentine core in crown, surrounded by relatively thin layers of pallial orthodentine and enameloid, and no pulp canal or cavity; crown osteodentine continuous with that of root, which forms its sole component.

Body stout, trunk circular or vertically oval in section at first dorsal base. Length of head and trunk from snout tip to vent 50% of total length. Trunk relatively short, length from 5th gill opening to vent 1.1 times head length. No predorsal, interdorsal, or postdorsal ridges on midline of back and precaudal lobe; no lateral ridges on body. Precaudal lobe from vent to upper caudal origin short, 19.2% of total length. Height of caudal peduncle at insertion of second dorsal 2.3 times its width there and 1.2 times in distance from insertion of second dorsal to upper caudal origin; height of caudal peduncle at upper caudal origin 2.2 times its width there and 1.7 times in distance from insertion of second dorsal to upper caudal origin. Upper precaudal pit not transverse and crescentic.

Dermal denticles on body very small and flattened, giving skin a smooth texture. Denticles on sides of trunk below first dorsal fin (lateral trunk denticles) loosely spaced, not closely imbricated (Fig. 10), with a strong medial ridge and a pair of strong lateral ridges running entire length of crown, strong medial cusp, but with lateral cusps absent or hardly developed. Denticles on dorsal surfaces of pelvic fins (Fig. 11) similar to lateral

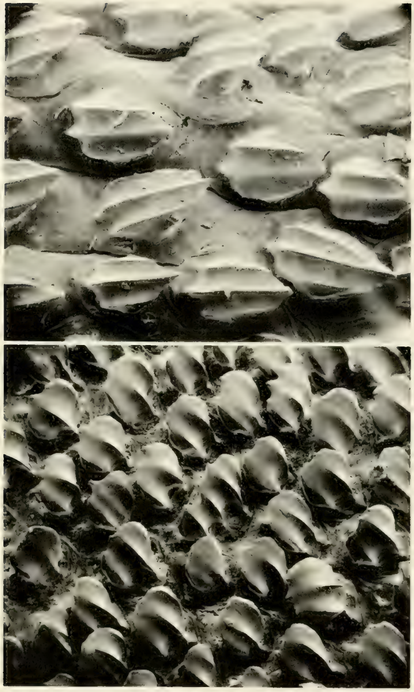


FIGURE 10. Scanning electron micrographs of dermal denticles of *Megachasma pelagios*. (*top*) Lateral trunk denticles from just below the base of the first dorsal fin (60× magnification). (*bottom*) Denticles from the surface of the tongue (67×).

trunk denticles, except for having lower ridges and being closely imbricated. Denticles from tongue are wide-spaced but broader and more transversely oval than lateral trunk denticles. Distal webs of upper surfaces of pectoral and pelvic fins, and dorsal caudal lobe, have conspicuous dark wavy lines, often parallel, which are channels of bare skin between areas of denticulate skin (Fig. 11).

Pectoral fins moderately broad basally but distally elongated, tapering, falcate, and broad-tipped. Anterior margins of pectoral fins moderately convex, apices broadly angular, posterior margins slightly convex, and free rear tips and inner margins smoothly rounded and broadly convex. Length of pectoral fin from origin to free rear tip 1.9 times in its anterior margin length. Apex of pectoral posterior to its free rear tip when fin is appressed to body.

Pectoral fin skeleton with all radials except last 5 on metapterygium greatly elongated, with broad, flattened tips. Radials with numerous segments, the longest with 10; distalmost segments elongated but only about ⅓ length of each radial. Pectoral fin propterygium supporting one radial, mesopterygium with 5 radials, metapterygium with 8 radials on basal segment and 8 on axis. Propterygium small and slightly elongated distally. Mesopterygium moderately elongated distally, fairly broad and wedge-shaped with radials inserted on distal end at an angle to axis of elongation. Metapterygium diagonally elongated across fin base with radials inserted at an angle to long axis. Metapterygial axis of 5 segments, about ⅔ as long as basal metapterygium. Basal and radial cartilages of pectoral fins not highly calcified; fins rather flexible, despite having plesodic skeletons.

Pelvic fins with anterior margin slightly concave anteriorly but convex posteriorly, apex very narrowly rounded, and inner margins slightly concave. Inner margins, posterior margins, and free rear tips of pelvics forming broad triangle.

Claspers relatively slender, width at base 7.6 times outer length from pelvic bases to tips, inner length from vent to tip 12.3 percent of total length. Rear tips of claspers reaching almost to midbase of anal fin when claspers are horizontal. Clasper tip elongated, forming a very narrow, slender process (Fig. 11), glans anterior to elongated tip slightly spatulate and flattened, shaft cylindrical. Clasper groove open, with edges not fused dorsally; no pseudopera or lateral clasper groove and fold. Small, sharp-tipped, hardened clasper spur on ventral lobe, lateral to groove. Large, large-mouthed, prominent pseudosiphon on the dorsal clasper lobe.

First dorsal fin with anterior margin slightly concave anteriorly and convex posteriorly, posterior margin nearly straight, free rear tip acute and slightly attenuated, and inner margin slightly concave. Origin about opposite or slightly posterior to pectoral fin insertions, midpoint of dorsal base about 2.6 times closer to pectoral insertions than pelvic origins, dorsal fin insertion anterior to pelvic origins by about 0.8 times first dorsal base, and free rear tip about 2.9 times dorsal inner margin anterior to pelvic origins. Posterior margin slanting posteroventrally from dorsal apex, insertion well posterior to level of

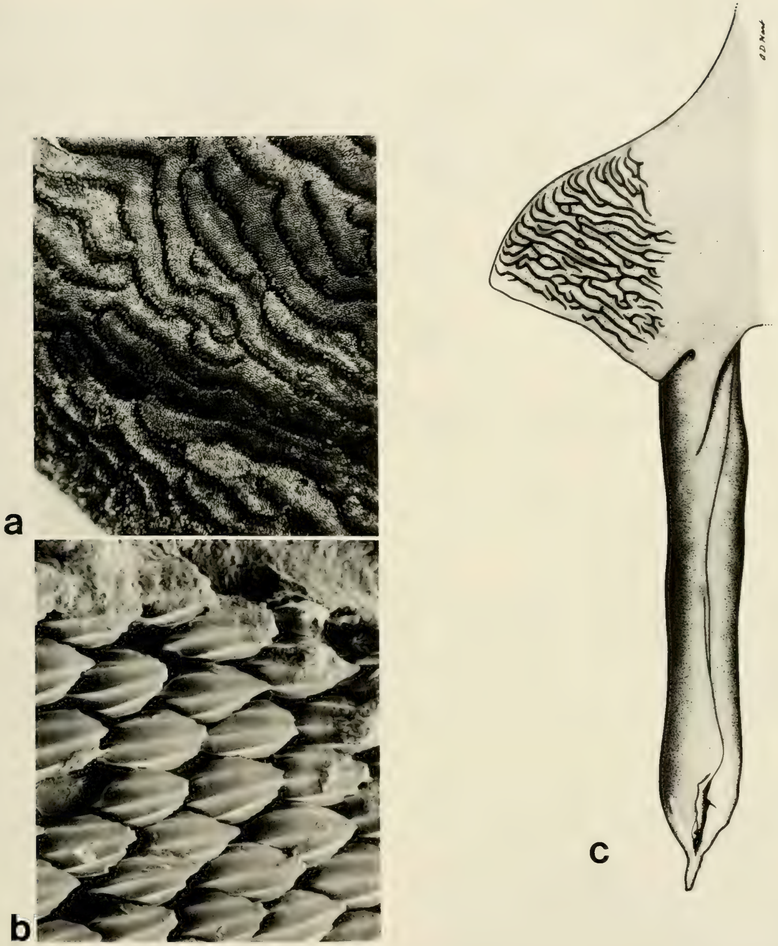
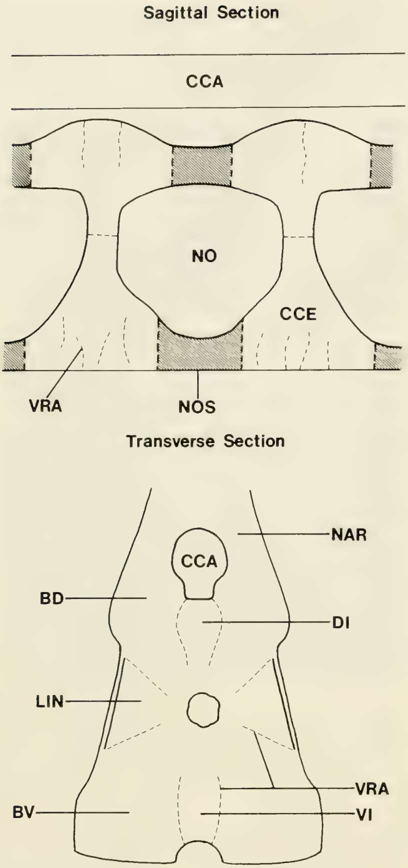


FIGURE 11. Right pelvic fin and clasper of *Megachasma pelagios*, showing channels of naked skin on dorsal surface of pelvic fin. (*a*) Close-up photograph of the channels. (*b*) Scanning electron micrograph of denticles from the anterior edge of the pelvic fin (54× magnification). (*c*) Drawing of the pelvic fin and clasper.

dorsal apex. Base 1.5 times in interdorsal space and 3.6 times in dorsal caudal margin, height 1.8 times in base, and inner margin 2.8 times in height.

Second dorsal fin low, height 0.46 times first dorsal height, base 0.47 times first dorsal base. Anterior margin nearly straight, apex narrowly rounded, posterior margin slightly concave, free rear tip angular and attenuated, and inner margin slightly concave. Free rear tip about over anal fin origin. Posterior margin of second dorsal slanted posteroventrally from apex, insertion


Sagittal Section

Transverse Section

FIGURE 12. Monospondylous precaudal vertebrae of *Megachasma pelagios*, in (*top*) sagittal section, and (*bottom*) transverse section. Abbreviations: *Sagittal section:* CCA, central canal; CCE, cartilaginous centrum; NO, notochord; NOS, notochordal sheaths; VRA, vestigial radii. *Transverse section:* CCA and VRA, as above; BD, basidorsal; BV, basiventral; DI, dorsal intermedial; LIN, lateral intermedial; NAR, neural arch; VI, ventral intermedial. (From drawings by L. J. V. Compagno.)

posterior to apex. Base 2.1 times in distance from insertion to upper caudal origin, height 1.8 times base, and inner margin 1.2 times height.

Anal fin low, height 0.8 times second dorsal height, base length 0.8 second dorsal base. Anterior margin concave anteriorly but convex posteriorly, apex broadly rounded, posterior margin moderately concave or notched, free rear to acute and attentuated, and inner margin slightly concave. Posterior margin of anal fin slanted posterodorsally from apex, with anal apex just below insertion. Base 1.4 times in distance from insertion to lower caudal origin, height 2.0 times in base, and inner margin 1.2 times in fin height.

Caudal fin relatively asymmetrical, with basally broad dorsal lobe, and short terminal lobe. Length of dorsal margin 2.1 times in precaudal length, of preventral caudal margin 2.3 times in dorsal caudal margin, and of terminal lobe from caudal tip to subterminal notch about 10.3 times in dorsal caudal margin. Dorsal caudal margin slightly but continuously convex in lateral view, preventral margin almost straight dorsally but becoming more convex ventrally. Tip of ventral caudal lobe broadly angular, lower and upper postventral margins slightly convex, notch between postventral margins broadly angular, subterminal notch shallowly concave, subterminal margin slightly concave, and terminal margin slightly convex. Subterminal margin length 0.6 times terminal margin length. Ventral lobe of caudal fin aplesodic, not supported by hypural radials but by ceratotrichia and connective tissue only.

Vertebrae (Fig. 12) examined from beneath first dorsal fin (monospondylous precaudal vertebrae) and at base of caudal fin (diplospondylous caudal vertebrae). These found to have extremely reduced calcification, both of the primary double cone of vertebral centra (which is almost entirely formed of uncalcified cartilage and connective tissue in *M. pelagios*), and of intermedial areas between basidorsals and basiventrals. Vertebral centra consist of biconic or bioconcave discs of cartilage, separated by broad bands of unchondrified notochordal sheath and spherical cavities containing notochordal tissue. Calcification in monospondylous precaudal centra restricted to some irregular calcification on lateral centrum body, a layer on ventral part of neural canal, a layer on midventral groove on underside of centrum, and paired thin zones partly bounding intermedial areas between basals, including 2 dorsals, 2 ventrals, and 2 pairs of laterals. These intermedial calcifications resemble radii of other lamnoids, but differ in being only partially developed across intermedial areas and in not forming discrete longitudinal plates. These

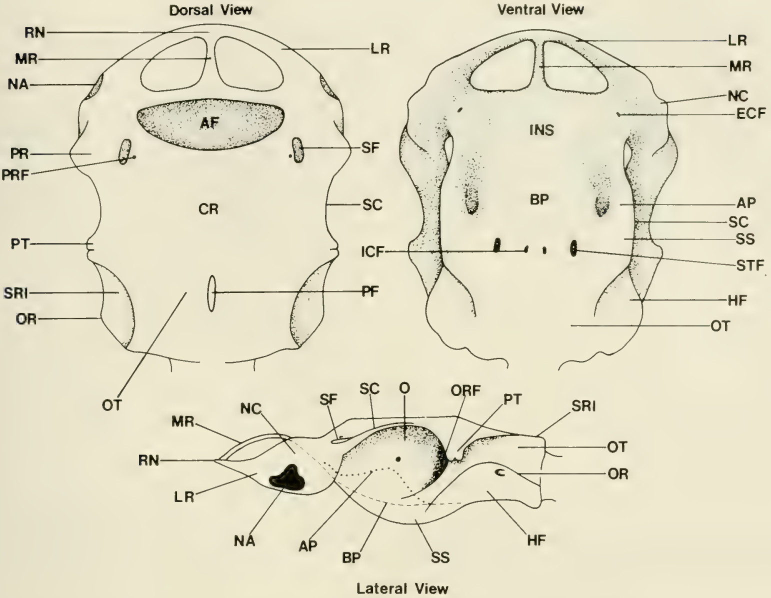


FIGURE 13. Neurocranium of *Megachasma pelagios,* in dorsal, ventral, and lateral views. Abbreviations: *Dorsal view:* AF, anterior fontanelle; CR, cranial roof; LR, lateral rostral cartilage; MR, medial rostral cartilage; NA, nasal aperture; OR, opisthotic ridge; OT, otic capsule; PF, parietal fossa; PR, preorbital process; PRF, profundus foramen; PT, postorbital process; RN, rostral node; SC, supraorbital crest; SF, supraorbital fenestra; SRI, sphenopterotic ridge. *Ventral view:* LR, MR, and OT as above; AP, articular pit; BP, basal plate; ECF, ectethmoid foramen; HF, hyomandibular facet; ICF, internal carotid foramen; INS, internasal septum; NC, nasal capsule; SC, suborbital crest; SS, suborbital shelf; STF, stapedial fenestra. *Lateral view:* O, orbit; ORF, orbital fissure; SC, suborbital crest; SCA, sphenopterotic capsule; all others as above. (From drawings by L. J. V. Compagno.)

intermedial calcified zones interpreted as representing vestigial radii, greatly reduced in *Megachasma* but probably well developed in its precursors. Basal caudal centra similar to monospondylous precaudal centra, except for having intermedial calcifications even more reduced to a set of dorsal and ventral pairs only. The poorly calcified vertebral centra of *Megachasma* recall the septate vertebral columns of large species of *Somniosus* (subgenus *Somniosus,* for *S. pacificus* and *S. microcephalus*) and some other squaloids (see Compagno 1977), with reduction of form and calcification of centra and hypertrophy of notochordal tissue in between centra. The lamnoids *Mitsukurina* and *Pseudocarcharias* have extremely simple centra with double cones and radii reduced to 8 slightly branched plates (2 bounding each intermedial area), but *Megachasma* goes far beyond these genera in reduction of its centra, in calcification, and in intrusion of notochordal tissue. *Mitsukurina* and *Pseudocarcharias* retain normal, close-set double cones, despite their simple radii.

Neurocranium (Fig. 13) dissected on one side only, and reconstructed bilaterally. Cranium relatively large, extremely broad and moderately flat; nasobasal length (from base of medial rostral cartilage to occipital condyles) about 8.9 percent total length and 12.8 percent precaudal length; greatest width of cranium across preorbital processes about equal to nasobasal length, and greatest height from cranial roof to ventral edges of suborbital shelves 0.4 times in nasobasal length and greatest cranial width. Rostrum relatively short but very broad, length of medial rostral cartilage from its base to anterior edge of rostral node about 26 percent nasobasal length; width across outer bases of lateral rostral cartilages 2.2

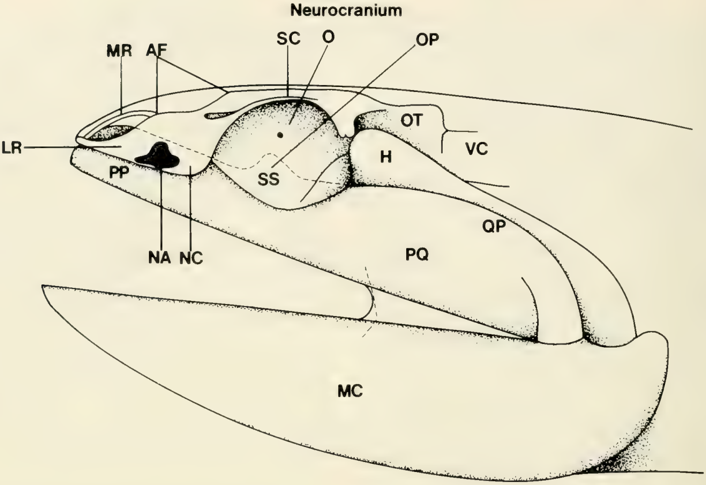


FIGURE 14. Jaw suspension of *Megachasma pelagios*, in lateral view, jaws retracted. Abbreviations: H, hyomandibular; MC, Meckel's cartilage; OP, orbital process; PP, palatine process; PQ, palatoquadrate; QP, quadrate process; VC, vertebral column; all others as in Figure 12. (From drawings by L. J. V. Compagno.)

times length of medial rostral cartilage. Entire ethmoid region of cranium, including rostrum, nasal capsules, and internasal septum, and the anterior basal plate molded dorsally around enlarged palatine processes of palatoquadrates (Fig. 14). Lateral rostral cartilages with broad bases that cover entire anterior surfaces of nasal capsules; diagonally compressed from dorsomedial to ventrolateral, and extending anteromedially as tapering triangular bars to meet rostral node separately on either side. Medial rostral cartilage and its base on internasal septum deflected upward over symphysis of palatoquadrates (jaws in retracted position), so that base originates at a level slightly above lateral rostral cartilages and the moderately depressed, narrow, barlike shaft arches anterodorsally and anteroventrally to rostral node. Rostral node a simple, depressed, narrow plate, not vertically or horizontally fenestrated, anteriorly expanded, vertically compressed, nor with rostral appendices.

Nasal capsules extraordinarily modified, highly compressed, platelike, wedge-shaped structures with nasal fenestra mainly on their lateral faces. Plane of compression of nasal capsules congruent with large-based lateral rostral cartilages, together forming a lateral wall to expansion cavity enclosing palatine processes. Ectethmoid foramen present on dorsomedial surface of each nasal capsule. Large subethmoid fossa on ventral surface of depressed, laterally expanded internasal septum, extending anteriorly beneath rostrum and medially to nasal capsules, and posterolaterally to merge on either side with large orbital process cavity in basal plate. Foramina for nasal canals laterally situated in cranial cavity (not anterolateral), with canals running anterolaterally to nasal capsules.

Basal plate very broad, width across orbital notches about 68 percent nasobasal length, broadly arched over rear ends of palatoquadrate palatine processes (when retracted) but relatively flat posterior to internal carotid foramina. Entire ventral surface of suborbital shelves, basal plate, and internasal septum padded with thick, soft, spongy connective tissue, probably to cushion it from palatoquadrates. Basal plate with pair of internal carotid foramina located about 59 percent nasobasal length behind medial rostral cartilage, separated by a convex space with width 80 percent nasobasal length and 1.1 times in distance between internal carotid foramina and stapedial fenestrae. Stapedial fenestrae small, width about 3 percent nasobasal length, apertures about 1.6 times closer to internal carotid formina than to lateral edges of suborbital shelves. Stapedial fenestrae apparently without greatly convoluted arteries or a rete mirabile elaborated from efferent spiracular arteries. Basal plate nearly horizontal posteriorly, without medial keels.

Orbits nearly circular in lateral view, with large optic nerve foramen slightly dorsal to its center. Orbits moderately large, with horizontal diameters about 43 percent of nasobasal length. Supraorbital crests broad, not fenestrate basally, only moderately concave in dorsal view. Preorbital processes not strongly exserted from supraorbital crests, and extending ventrally to posterior edges of nasal capsules. Small preorbital canal fenestra for superficial ophthalmic nerves present between broad preorbital process and cranial roof on each side; profundus nerve foramen just mesial to fenestra. Postorbital processes ventrally produced almost to level of optic nerve foramen, bifurcate distally. Foramina of orbital wall not examined in detail but including foramina for superficial ophthalmic nerve anterior cerebral veins, optic nerve, and large, deep, trigeminofacialis chamber or orbital fissure. Suborbital shelves nearly vertical, large, thick basally but distally thin, arcuate, and with sides nearly parallel in ventral view.

Otic capsules large and subquadrate, with lengths about 36 percent nasobasal length and width about 82 percent nasobasal length. Hyomandibular facets huge, ventromedially incised, and broadly arcuate, extending along entire length of otic capsules from otic processes anteriorly to partway onto bases of suborbital shelves, but not exserted posteriorly from occiput. Hyomandibular nerve foramina just below opisthotic ridges and about midway along their lengths on otic capsules. Sphenopterotic ridges arching posteromedially in dorsal view, ending posteriorly in a bluntly rounded corner. Opisthotic ridges on dorsal surface of hyomandibular facets low and curved posteroventrally. Occiput flat and not exserted rearwards, with glossopharyngeal and vagus nerve foramina.

Jaws (Figs. 5, 14) poorly calcified; length of palatoquadrates about 16 percent total length, Meckel's cartilages 18.4 percent total length. Palatine processes of palatoquadrates articulating at symphysis and extending for about ⅖ of palatoquadrate length to orbital processes. Meckel's cartilages huge, ventrally arcuate, dorsally nearly straight, thick, and compressed, with long posterior extensions from their mandibular articulations with palatoquadrates. Meckel's cartilages articulating closely at mandibular symphysis.

Manipulation of the jaws of the fresh-caught *Megachasma pelagios* suggested that the jaws are highly protrusible, but not necessarily as a mechanism to quickly eject them outward to capture prey, as in some other lamnoids (most notably *Mitsukurina*), nor to bring the upper teeth to bear on prey items, as in *Carcharodon carcharias*. The jaws may be protruded forward and outward to expand the mouth aperture and form a hoop-net for capturing plankters, though we do not know the exact shape of the jaws deployed in this configuration without photographic documentation of a live *M. pelagios* feeding. The basking shark is able to deploy its much slimmer jaws almost in a circle while feeding and has been photographed many times with jaws expanded (but not protruded); however, the exact shape of the mouth opening in a living, feeding basking shark would be somewhat difficult to work out from a dead, preserved specimen. The jaw structure of *M. pelagios* suggests that the jaws move downward, anteriorly, and outward at the mouth corners, and the distal ends of the hyomandibulae swing anterolateroventrally as protrusion occurs. The mechanism of jaw protrusion is poorly understood with the limited dissection possible during preparation of this description (the desire to limit damage to the specimen prior to making a cast of it prohibited a thorough investigation of the jaw mechanism and the hyobranchial skeleton and musculature), but the large, straplike, diagonal preorbitalis muscles may help to pull the jaws forward.

The jaw musculature was not investigated in detail, but sufficient information was collected to determine that the jaw muscles are similar to those in other lamnoids. Levator palatoquadrati muscle simple, originating on sphenopterotic ridges of otic capsules and running posteroventrally to insert on quadrate processes of palatoquadrates. Adductor mandibulae muscles moderately large but small and weak compared to the huge jaws, and limited anteriorly by mouth corners. Levator hyomandibuli muscles broad and relatively large.

The viscera were not examined in detail, ex-

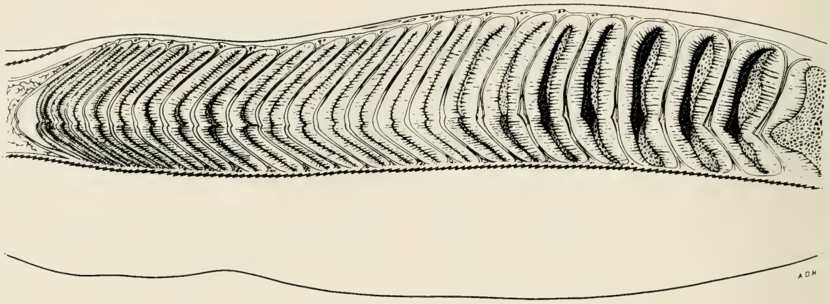


FIGURE 15. Drawing of the valvular intestine of *Megachasma pelagios* with the dorsolateral quadrant removed to show the ring valves with highly fimbricated edges (anterior to the right).

cept to note that the liver is relatively small (though very oily) and that the valvular intestine is an elongated ring-valve type rather similar to that of other lamnoids (Fig. 15). Each ring has a densely fimbriated surface, apparently to increase the absorptive surface, with a maximum thickness of 23–25 mm at the pyloric end of the intestine but becoming increasingly thin towards the rectum.

Color. When preserved, dorsal surface of head, trunk and tail, dorsal surfaces of pectoral and pelvic fins, dorsal fins, center of anal fin, and caudal fin dark gray to blue-black; sides of body lighter, underside of body and fins light gray, except for underside of head and lower jaw which are dark gray and mottled with black, undersurface of pectoral fins which have an abruptly black anterior margin about an eye diameter wide, and underside of pelvic fins with a dusky anterior margin. Tips and posterior margins of dorsal surfaces of pectoral and pelvic fins abruptly white, as are posterior margins of dorsal and anal fins and postventral caudal margins. Tissue of oral cavity and tongue blackish in preservative, but with oral lining silvery when fresh.

Feeding Habits and Biology

The stomach contents were a thick reddish soup abundantly stocked with the euphausiid shrimp *Thysanopoda pectinata,* a species attaining a median length of 31 mm (Hu 1978). According to Hu (1978), *T. pectinata* off the west coast of Oahu (21°15′–20′N, 158°15′–30′W) shows a moderate day and night migration pattern. During the day most are caught between 350 and 750 m depth, with some ranging up to 300 m and down to 1100 m, but at night the bulk are between 150 and 500 m depth, with some up to 75 m and down to 525 m. Apparently, when captured, *Megachasma pelagios* would have been in the upper depths (165 m) where these euphausiids are commonest at night, and quite possibly might have been feeding on them when it became entangled in the parachute.

The megamouth shark unites an eclectic combination of habitus characters that (along with its apparent epipelagic habitat and filter-feeding habits) suggests an unusual mode of life. Deepwater epibenthic and epipelagic sharks often show a decrease in specific gravity and increase in hydrostatic support by the enlargement of their abdominal cavity and liver volume to produce a large, oily, hepatic "float." *M. pelagios,* in contrast, has reduced specific gravity in the form of extremely poor calcification; a soft, almost entirely hyaline cartilage skeleton; very soft, loose skin; and flabby, loose connective tissue and muscles. These features, and its soft, rubbery precaudal fins; lack of a keel on the caudal peduncle, weak precaudal pit; lack of dorsal caudal ripples; and highly flexible, asymmetric caudal fin suggest that *M. pelagios* is a slow, weak swimmer.

It is interesting to compare *M. pelagios* with the other two species of large, filter-feeding sharks: the basking shark and the whale shark. The basking shark is the only lamnoid filter-feeder besides megamouth, but in contrast has many adaptations for a higher activity level and sustained powerful swimming, including a strongly calcified skeleton, firm muscles, stiff fins, dense skin, and tough connective tissue; a huge, oily liver and elongated body cavity; a more fusiform body, lunate caudal fin, strong caudal keels and precaudal pits, and huge gill openings. The filter apparatus of *Cetorhinus*, with its vast gill cavities and slender, smooth, streamlined gill-raker denticles, is clearly adapted for a higher rate of water flow than is possible with the smaller gill cavities, more restricted internal gill apertures, and less streamlined gill-raker papillae of *Megachasma*. The basking shark is a slow but strong swimmer, which has often been observed and photographed while feeding at or near the surface with its mouth distended to form a circular scoop. Although its mouth is relatively smaller than that of megamouth, the basking shark is probably a much more efficient dynamic filterer because of its stronger swimming abilities and high-flow filter apparatus. The prey of the basking shark is far smaller than what is known for megamouth, consisting entirely of microscopic crustaceans (especially copepods). The basking shark prefers cool to cold coastal waters rich in nutrients and plankton.

The whale shark resembles the basking shark in its strong swimming adaptations, except that it has a less fusiform body, flattened anteriorly; a shorter body cavity and much smaller liver; and much smaller external gill openings (but larger than those of megamouth). The filter apparatus of *Rhiniodon* differs from that of *Megachasma* and *Cetorhinus* in not being confined to the margins of the internal gill openings; instead, the gill filter elements of *Rhiniodon* cross and bar these openings. They are compressed, triangular, cartilage-cored, connective-tissue-covered, parallel plates that transversely bridge the internal gill openings and connect adjacent holobranchs. The plates have highly lobulated pharyngeal margins that form an interconnected network, or dense filter grid, and are divided into paired dorsal and ventral groups of plates or screens over each internal gill opening. The dense screens of *Rhiniodon* are obviously efficient filters, but are incapable of sustaining a high flow of water through them. However, this filter apparatus, combined with a broad but very short, transverse mouth; very long, broad, low pharynx, and relatively small gill openings apparently adapts the whale shark to a combination of suction feeding (as in *Ginglymostoma* and other orectoloboids) and filter-feeding not found in *Megachasma* and *Cetorhinus*. The bellowslike pharynx and filter screens of the whale shark may provide it with a more versatile feeding apparatus than in *Cetorhinus* (and presumably *Megachasma*) by allowing it to suck in and filter out a wide variety of prey animals, independent of the shark's forward movement. Although the whale shark can ingest small crustaceans, it also eats squid and commonly takes small schooling fishes such as anchovies and sardines, and even small albacore and tuna (Bigelow and Schroeder 1948). It is not known whether *Rhiniodon* can filter out crustacean prey as small as the copepods favored by *Cetorhinus*, but almost certainly the euphausiids eaten by *Megachasma* are in the prey-size range of the whale shark, which is a warm-temperature to tropical, coastal to oceanic, slow but strong-swimming shark, often seen basking or cruising at the surface and feeding on schools of fishes. It often positions itself vertically beneath a school of prey, unlike the horizontal attitude *Cetorhinus* maintains while feeding at the surface.

The soft, flabby body and fins, low-flow branchial filter apparatus, and small gill openings suggest that *Megachasma* is less active and possibly a less efficient filter-feeder than *Cetorhinus* or *Rhiniodon*. Nevertheless, this species has a specialized, presumably efficient mechanism for capturing small oceanic animals in its oversized jaws which are enlarged to increase the diameter of its "net" and thickened to provide adequate support from its rubbery hyaline cartilage. The greatly distensible mouth and pharynx, closely packed gill-raker papillae, and large tongue probably help to expel water from the pharynx when it closes its mouth. *Megachasma* can be imagined as slowly swimming through schools of euphausiid shrimp and possibly other prey with jaws widely opened, occasionally closing its mouth and contracting its pharynx to expel water and concentrate its prey before swallowing it.

Inspection of the mouth of megamouth 24 hr after capture revealed a bright silvery lining punctuated by small circular porelike structures. At the time it was speculated that these might be bioluminescent organs, but we have no evidence of this. Histological sections of mouthlining were made but were problematical because of the deteriorated state of the tissue.

That *Megachasma* may not be a more active filter-feeder such as *Cetorhinus* or *Rhiniodon* may be related to its tropical deepwater oceanic habitat, which has a relative paucity of nutrients and prey in comparison to the cool coastal surface waters favored by *Cetorhinus* and the tropical coastal waters preferred by *Rhiniodon*. Various mesopelagic teleosts have reduced skeletal and other tissues as adaptations to a nutrient-poor environment, and *Megachasma* may be similarly limited to a reduced level of tissue development and hence a low activity level for a filter-feeding shark, far less than is possible in the habitats frequented by *Cetorhinus* and *Rhiniodon.*

Two distinctive scars, one on the throat, another behind the right pectoral fin, suggest that megamouth may be the only known selachian victim of *Isistius brasiliensis,* the "cookie-cutter" shark, that is believed responsible for similar marks found on tuna, porpoise, and billfish caught in Hawaiian waters (Jones 1971). The soft skin and midwater habitat of megamouth may make it vulnerable to *Isistius* attacks.

Megachasma pelagios, itself the representative of a new family of sharks, is the host of a new family of tapeworms Mixodigmatidae (order Trypanorhynchida), described by Dailey and Vogelbein (1982) for the new genus and species *Mixodigma leptaleum.* These parasitic tapeworms from the valvular intestine presented taxonomic problems over placement in existing trypanorhynch families comparable to the difficulties encountered in attempting to place *Megachasma pelagios* in an existing lamnoid shark family.

ACKNOWLEDGMENTS

Many people contributed to the study of this interesting animal. We acknowledge Lt. Linda Hubble, John Hobbs, and Rick Kahakini for their recovery of the animal and their recognition of the find; Hawaiian Tuna Packers, National Marine Fisheries Services Honolulu dockside staff, Phillip Motta, Bruce Carlson, Captain Gary Naftel and the crew of the R.V. *Easy Rider,* Mathew James, Les Matsuura, Marge Awai, and Arnold Suzumoto for curatorial assistance; Dr. Arthur Popper, Dr. James Margolis, and Karen Margolis for preparation of scanning electron micrographs; Dr. James Kendall for histological preparations of epithelial tissues; Drs. Thomas Clarke and K. Gopalakrishnan for identification of stomach contents; Drs. Carl L. Hubbs, Richard Rosenblatt, John McCosker, Bruce Welton, Murray Dailey, Scott Johnson, Tyson Roberts, and John Randall, and Mr. Richard Ellis, for discussions relating to nomenclature and the scientific importance of the animal; Allan Hart, Rebecca Brown, and Mary Morioka for scientific illustrations; Ruth Naftel for organizational support; and Pam Miike for typing the manuscript. Particular thanks go to Richard Ellis and John McCosker for preparation of a preliminary manuscript which was of great help in the production of this final paper.

LITERATURE CITED

ANONYMOUS 1. 1976. A novel variation of jaws. Science News 110(25 and 26):385–416.

ANONYMOUS 2. 1976. The big one that got away. Smithsonian 7(12):12.

BIGELOW, HENRY B., AND W. C. SCHROEDER. 1948. Sharks. Fishes of the western North Atlantic. Memoir 1, Sears Foundation for Marine Research, Pt. 1, vol. 1:59–576.

CLARK, EUGENIE. 1981. Sharks: magnificent and misunderstood. National Geographic 160(February):138–187.

COMPAGNO, L. J. V. 1970. Systematics of the genus *Hemitriakis* (Selachii: Carcharinidae), and related genera. Proceedings of the California Academy of Sciences, ser. 4, 38(4): 63–98, 8 figs.

———. 1973a. Interrelationships of living elasmobranchs. Pages 15–61 *in* Interrelationships of fishes. P. H. Greenwood, R. S. Miles, and C. Patterson, editors. Zoological Journal of the Linnean Society of London 53(suppl. 11).

———. 1973b. *Gogolia filewoodi,* a new genus and species of shark from New Guinea (Carcharhiniformes: Triakidae), with a redefinition of the family Triakidae and a key to triakid genera. Proceedings of the California Academy of Sciences, ser. 4, 39(19):383–410, figs. 1–7, table 1.

———. 1977. Phyletic relationships of living sharks and rays. American Zoologist 17(2):303–322, 15 figs.

———. 1979. Carcharhinoid sharks: morphology, systematics, and phylogeny. Ph.D. Thesis, Stanford University, 932 p.

———. 1981. Legend versus reality: the Jaws image and shark diversity. Oceanus 24(4)(Winter 1981/82):3–16.

DAILEY, MURRAY D., AND WOLFGANG VOGELBEIN. 1982. Mixodigmatidae, a new family of cestode (Trypanorhyncha) from a deep sea, planktivorous shark. Journal of Parasitology 68(1):145–149, 8 figs.

DUNFORD, B. 1976. Huge shark may be new species. Honolulu Star-Bulletin 65(322), p. 1, 2 pictures.

FAUGHNAN, VICTOR. 1980. National shark-o-pedia. Undersea Resources, Ltd., Honolulu, Hawaii.

HU, VERNON J. H. 1978. Relationships between vertical migration and diet in four species of euphausids. Limnology and Oceanography 23(2):296–306, 5 figs.

JONES, E. C. 1971. *Isistius brasiliensis,* a squaloid shark, the probable cause of crater wounds on fishes and cetaceans. National Marine Fisheries Service Fishery Bulletin 69(4): 791–798.

PHILLIPS, F. J., B. WELTON, AND J. WELTON. 1976. Paleontologic studies of the Middle Tertiary Skooner Gulch and Gallaway Formations at Point Arena, California. Pages 137–154 *in* Neogene symposium; Society of Economic Paleontologists and Mineralologists Pacific Section, Annual Meeting, April 1976.

TAYLOR, LEIGHTON R. 1977. Megamouth, a new family of shark. Oceans Magazine 10:46–47, 5 pls.

TINKER, SPENCER W. 1978. Fishes of Hawaii. Hawaiian Service, Inc., Honolulu. 532 p.

PROCEEDINGS
OF THE
CALIFORNIA ACADEMY OF SCIENCES

Vol. 43, No. 9, pp. 111-121, 5 figs., 8 tables. January 17, 1984

THE CRANIAL MORPHOMETRY OF GALAPAGOS TORTOISES

By

Charles R. Crumly[1]

Department of Zoology and Physiology, Rutgers—The State University,
Newark, New Jersey 07102

Abstract: Saddlebacked tortoises have smaller and slightly broader skulls than non-saddlebacked tortoises. Unlike the two types of shells, the skulls of saddlebacked and non-saddlebacked tortoises are difficult to distinguish, even as large adults. Factor analysis, although suggestive of different growth trends, does not delineate *Geochelone ephippium, G. guntheri,* and/or *G. nigrita.* Discriminant function analysis easily distinguishes these species. *Geochelone ephippium* is discriminated from the other two species on the basis of overall size and *G. nigrita* has a smaller exposed basisphenoid than *G. guntheri.* Species represented by small samples were compared to *Geochelone guntheri, G. ephippium,* and *G. nigrita* by means of a discriminant function analysis classification procedure. The results suggest that skull variation does not parallel shell variation.

Introduction

The classification of Galapagos tortoises (genus *Geochelone*) has changed over the years, depending on the prevalent philosophy pertaining to closely related forms. These insular tortoises have been considered different species (Van Denburgh 1914) or different subspecies (Wermuth and Mertens 1961, 1977; Crumly 1980, 1982; MacFarland et al. 1974a, b). Perhaps the best a priori taxonomic strategy was employed by Fritts (*in press*), who considered each geographically isolated population a separate entity until more detailed analysis could be completed. These different philosophies, compounded by the frequent lack of accurate locality data, are reflected in the confusing nomenclatural history of Galapagos tortoises (Table 1).

Although the nomenclatural status of these various populations remains changeable, it is clear that all Galapagos tortoises are more closely related to each other than to other tortoises. This interpretation is supported by morphologic analyses (Crumly 1980, 1982; Fritts *in press*) and electrophoretic studies (Marlow and Patton 1981).

Despite their close relationships, Galapagos tortoises exhibit great structural diversity. The shells best reflect this diversity and are of two basic types: domed, like those of most other tortoise species; and saddlebacked, resembling an ancient Moroccan saddle. The saddlebacked shell type seems derived from the domed type, but Fritts (*in press*) has noticed subtle differences between saddlebacked forms that suggest this morphology evolved more than once. Marlow and Patton (1981) corroborate Fritts's suggestion. Furthermore, the saddlebacked shell, long considered unique to certain Galapagos tortoises, appears independently in *Geochelone vosmaeri*

---

[1] Present address: Division of Reptiles and Amphibians, Department of Vertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560.

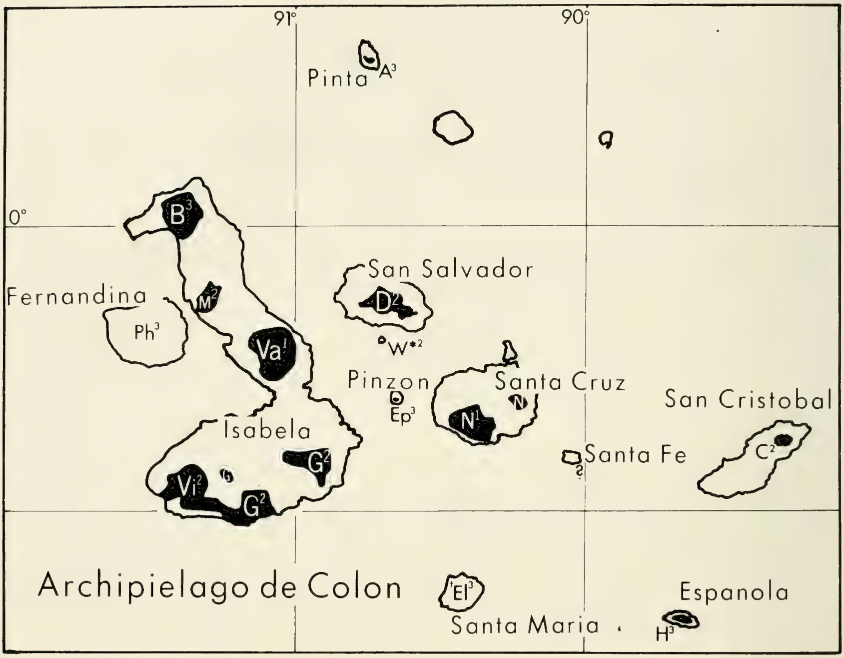


FIGURE 1. Present distribution of *Geochelone* species in the Galapagos Islands. A = *abingdonii*, B = *becki*, C = *chathamensis*, D = *darwini*, El = *elephantopus*, Ep = *ephippium*, G = *guntheri*, H = *hoodensis*, M = *microphyes*, N = *nigrita*, Ph = *phantasticus*, Va = *vandenburghi*, Vi = *vicina*, W = *wallacei*, ? = unnamed form, 1 = domed, 2 = intermediate, 3 = saddlebacked, * = species probably invalid (from MacFarland et al. 1974a).

of Rodrigues Island in the Indian Ocean (Arnold 1979).

Fritts (*in press*) showed that island (or volcano) topography is a reliable predictor of shell shape in Galapagos tortoises. Based on captive breeding data, he also suggested that shell differences are genetically determined. The topographic, climatic, and morphologic information combined in Fritts's model suggests that these tortoises possess great adaptive plasticity. This plasticity, reflected in differences in shell shape, has not been documented for other anatomical regions.

The purpose of this study is to determine whether variation in cranial morphometry parallels variation in the two shell types, first proposed by Van Denburgh (1914) and corroborated by Fritts (*in press*).

MATERIALS AND METHODS

Sixteen measurements (Fig. 2, Table 2) were recorded from over 100 skulls, listed below. (The museum acronyms used are those recommended by Duellman et al. 1978.)

G. abingdonii: CAS 8112; USNM 29269.
G. becki: CAS 8120.
G. chathamensis: CAS 8127, 8128, 8130, 8131, 8133; USNM 29255.
G. darwini: CAS 8106, 8108, 39601.
G. ephippium: AMNH 93383; CAS 8299, 8313, 8358, 8377–8380; MCZ 11068; USNM 29309, 29251.
G. guntheri: CAS 8225, 8267, 8413, 8406, 8401, 8399, 8400, 8396, 8415, 8256, 8408, 8405, 8199, 8194, 8210.

TABLE 1. SPECIFIC NAMES APPLIED TO GALAPAGOS TORTOISES.*

Island name		Carapace type	Günther 1875, 1877	Rothschild 1901, 1902, 1903, 1915	Van Denburgh 1907, 1914	Garman 1917	Wermuth and Mertens 1961, 1977	MacFarland et al. 1974	Pritchard 1979
Spanish	English								
Espanola	Hood	Saddlebacked	*microphyes*	*hoodensis*	*hoodensis*	*microphyes*	*hoodensis*	*hoodensis*	*hoodensis*
Fernandina	Narborough	Saddlebacked			*phantastica*		*phantastica*	*phantastica*	*phantastica*
Isabela	Albemarle	Saddlebacked		*becki*	*becki*	*macrophyes*	*elephantopus*	*becki*	*becki*
	N. Albemarle (Cape Berkeley)								
	Tagus Cove	Intermediate		*microphyes*	*microphyes*	*macrophyes* & *microphyes*	*elephantopus*	*microphyes*	*microphyes*
	S.E. Albemarle (Villamil Mt.)	Intermediate		*guntheri*	*guntheri*	*microphyes*	*elephantopus*	*guntheri*	*guntheri*
	S. Albemarle (Iguana Cove)	Intermediate	*vicina*	*vicina*	*vicina*	*microphyes*	*elephantopus*	*vicina*	*vicina*
	Cowley Mt.	Domed			distinctive but not named		*elephantopus*	*vandenburghi*	*vandenburghi*
Pinta	Abingdon	Saddlebacked	*abingdonii*	*abingdonii*	*abingdonii*	*elephantopus*	*abingdonii*	*abingdonii*	*abingdonii*
Pinzón	Duncan	Saddlebacked		*ephippium*	*ephippium*	*elephantopus*	*ephippium*	*ephippium*	*ephippium*
Rábida	Jervis	Intermediate		*wallacei*	*wallacei*	*nigra*	*wallacei*	*wallacei***	*wallacei*
San Cristóbal	Chatham	Intermediate	distinctive but not named	*chathamensis*	*chathamensis*	*microphyes*	*chathamensis*	*chathamensis*	*chathamensis*
San Salvador (Santiago)	James	Intermediate	*elephantopus* or *nigrita*	*darwini*	*darwini*	*nigrita*	*darwini*	*darwini*	*darwini*
Santa Cruz	Indefatigable	Domed	distinctive but not named	*porteri*	*porteri*	*nigra*	*nigrita*	*porteri*	*porteri*
Santa María (Floreana)	Charles	Saddlebacked	*ephippium*	*galapagoensis*	*elephantopus*	*nigrita*	*galapagoensis*	*galapagoensis*	*galapagoensis*

* Fritts (*in press*) is in the process of revising the classification and taxonomy of Galapagos tortoises.

** These authors have convincingly shown that *wallacei* is invalid because tortoises probably never occurred naturally on Rabida.

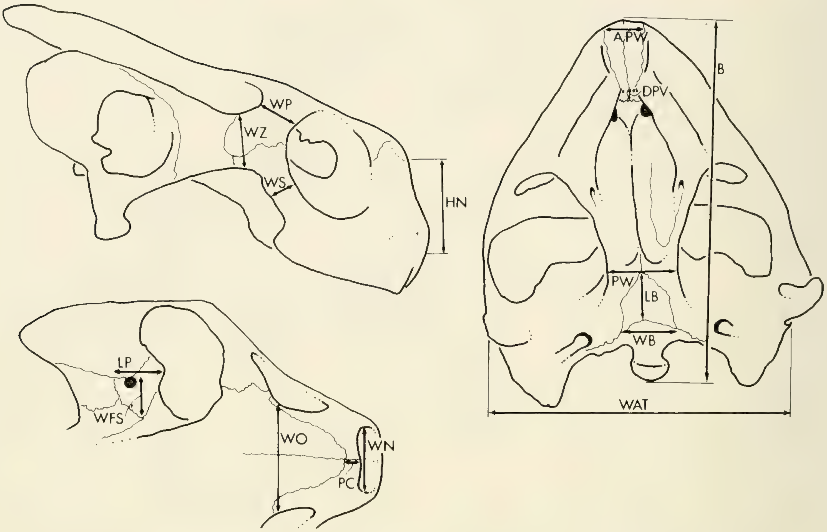


FIGURE 2. Measurements taken from Galapagos tortoise skulls (see Table 2 for explanations of abbreviations).

G. hoodensis: CAS 8121, 8122.

G. microphyes: CAS 8158.

G. nigrita: CAS 8381, 8289, 8286, 8385; MVZ 67613–67615, 59528, 67624–67629, 67631–67633; USNM 104330–104331.

G. phantastica: CAS 8101.

G. vandenburghi: CAS 8141.

G. vicina: CAS 8179, 8193, 8177; USNM 129247.

G. wallacei (probably an invalid form, *fide* MacFarland et al. 1974a): CAS 8134.

Geochelone sp. (but definitely Galapagos tortoise species): AMNH 7288, 42961, 63415, 36420, 36568–36570, 63416; CAS 8298, 8404, 8411, 8409, 8402, 8377, 8407, 8410, 8403, 8414, 8397, 8412, 8272; Calif. State Univ., Fullerton Coll. 3 uncat.; FMNH 13523, 1 uncat.; LACM (Vert. Paleo.) pr 63, pr 58, pr 64; MCZ 46606, 11070, 11069, 32098, 1905, 4668; MVZ 80075; SDSNH 56605, 55458; USNM 65896, 102904, 129393, 15192, 29338, 29305, 29254, 29252, 15190, 15193, 29256.

Means and standard deviations were calculated for each of the 16 measurements and correlation coefficients were also calculated.

At the recommendation of Fritts (pers. comm.), I followed the last thorough taxonomic review (Van Denburgh 1914) in which the different forms were given species-level designations. The species names used by Van Denburgh (1914) are followed with one exception; *G. porteri* is considered a junior synonym of *G. nigrita* (*fide* Fritts *in press*). Statistical comparisons between island

TABLE 2. SKULL MEASUREMENTS RECORDED FOR GALAPAGOS TORTOISES. (All measurements taken with dial calipers and recorded to nearest 0.01 mm.)

Variable—Description

B—Basicranial length
WAT—Width of skull at anterior tympanic opening
WO—Width between orbits
HN—Height of external narial opening
WN—Width of external narial opening
LB—Length of basisphenoid
WB—Width of basisphenoid
WZ—Width of quadratojugal
WP—Width of postorbital
WS—Width of jugal
DPV—Distance (greatest) from prepalatine foramina (or foramen, if only one present) to vomer
LP—Length of prootic
WFS—Width of prootic at stapedial foramen
PW—Width of pterygoid waist
APW—Width of anterior premaxillae
PC—Length of sagittal contact of prefrontals

TABLE 3. MEANS AND STANDARD DEVIATIONS FOR 16 VARIABLES IN FIVE GALAPAGOS TORTOISE SPECIES. Measurements are illustrated in Figure 2 and abbreviations are listed in Table 2. Most sample sizes are small; all measurements are in millimeters.

	G. ephippium (N = 9)		*G. guntheri* (N = 15)		*G. nigrita* (N = 18)		*G. vicina* (N = 4)		*G. chathamensis* (N = 6)	
Variable	X	SD	X	SD	X	SD	X	SD	X	SD
B	96.7	11.4	128.0	21.4	121.5	39.2	109.0	49.2	98.1	27.3
WAT	73.9	9.2	106.6	19.9	98.4	31.8	86.0	38.9	80.4	25.0
WO	25.1	3.1	35.4	7.3	37.0	13.3	28.4	12.6	28.4	7.7
HN	12.5	2.0	18.6	3.4	18.6	6.0	16.1	7.3	13.9	4.1
WN	17.0	2.2	25.1	4.4	23.1	7.7	21.3	9.2	18.5	4.7
LB	13.3	3.2	18.7	4.2	14.7	4.3	18.1	8.9	14.7	5.6
WB	14.6	2.2	19.1	4.3	17.1	4.6	15.8	7.2	13.8	3.4
WZ	9.3	3.6	14.3	4.4	13.3	4.7	12.6	6.8	10.1	3.5
WP	7.0	2.2	9.5	2.5	9.0	3.5	8.8	4.5	7.3	3.0
WS	7.3	2.3	12.0	3.0	9.5	4.0	9.6	5.1	7.9	3.1
DPV	3.2	0.8	4.2	0.8	4.2	1.5	3.7	2.4	3.1	1.0
LP	14.1	2.1	21.0	5.6	18.1	6.5	14.8	6.6	15.2	3.7
WFS	10.0	2.0	16.0	6.1	12.8	6.1	8.9	6.3	12.5	6.2
PW	19.2	1.8	25.9	5.1	26.1	8.4	21.9	8.6	19.0	4.0
APW	10.5	1.8	15.2	2.4	14.1	4.9	11.8	8.0	10.5	3.0
PC	8.6	1.5	10.6	4.0	13.3	5.4	8.5	3.9	8.2	3.9

populations were hampered by incomplete locality data; 50 of 116 specimens (43%) examined possessed doubtful or unknown locality data. The specimens without locality data were readily identified as Galapagos tortoises, but could not be identified to species without locality data. These specimens were used in the computation of correlation coefficients and in factor analysis, but could not be used in other statistical procedures.

To facilitate my analyses, populations were combined based on the shell types advocated by Van Denburgh (1914) and Fritts (*in press*). Thus, the saddlebacked forms (*G. abingdonii* [N = 2], *G. phantastica* [N = 1], *G. becki* [N = 1], *G. hoodensis* [N = 2], and *G. ephippium* [N = 9]) were combined, yielding a sample of 15 individuals. The non-saddlebacked forms (intermediate and domed shells of Van Denburgh 1914) were also combined, forming a larger sample of 48 individuals (*G. chathamensis* [N = 6], *G. darwini* [N = 2], *G. guntheri* [N = 15], *G. microphyes* [N = 1], *G. nigrita* [N = 18], *G. vicina* [N = 4], and *G. vandenburghi* [N = 1]). These larger samples were then compared to determine whether cranial variation mirrored the already well known shell variation. Comparisons were also made among *G. ephippium*, *G. guntheri*, and *G. nigrita* to determine whether noncombined and combined samples contained the same magnitude of variation.

The Statistical Package for the Social Sciences (SPSS) was used on the WYLBUR facility at the Campus Computer Information Service (CCIS) at Rutgers—The State University for initial data examination. Final statistical analyses were accomplished using SPSS programs available

TABLE 4. MEANS AND STANDARD DEVIATIONS FOR SADDLEBACKED TORTOISES REPRESENTED BY SPECIMENS OF FIVE SPECIES AND NON-SADDLEBACKED TORTOISES REPRESENTED BY SPECIMENS OF SEVEN SPECIES. Measurements are illustrated in Figure 2 and abbreviations are listed in Table 2; all measurements are in millimeters.

	Saddlebacked (N = 15)		Nonsaddlebacked (N = 48)	
Variables	X	SD	X	SD
B	98.9	15.9	116.5	37.1
WAT	75.8	13.0	96.0	30.4
WO	26.4	4.6	32.9	11.2
HN	13.2	2.9	17.1	5.6
WN	17.5	2.4	22.6	7.2
LB	13.8	3.2	16.0	5.7
WB	14.5	2.0	17.1	5.5
WZ	9.5	3.4	13.1	5.3
WP	7.1	2.2	8.8	3.5
WS	7.3	2.3	9.9	3.9
DPV	2.9	1.2	3.9	1.4
LP	14.4	2.7	18.4	6.2
WFS	10.1	1.8	13.7	6.4
PW	20.1	2.9	24.6	7.8
APW	10.5	1.7	13.2	4.5
PC	7.9	1.4	10.2	5.2

TABLE 5. CORRELATION COEFFICIENTS BETWEEN ALL THE SKULL MEASUREMENTS ILLUSTRATED IN FIGURE 2 AND ABBREVIATED IN TABLE 2. All specimens measured are combined into a single sample. Nevertheless, all coefficients are significant to at least the $P = 0.05$ level.

Variable	B	WAT	WO	HN	WN	LB	WB	WZ	WP	WS	DPV	LP	WFS	PW	APW
WAT	.98														
WO	.94	.94													
HN	.96	.94	.93												
WN	.97	.96	.93	.95											
LB	.88	.86	.79	.84	.88										
WB	.92	.92	.87	.88	.92	.87									
WZ	.84	.86	.86	.81	.87	.78	.84								
WP	.87	.86	.88	.83	.87	.79	.80	.88							
WS	.91	.92	.87	.88	.91	.86	.89	.84	.84						
DPV	.69	.69	.69	.64	.72	.60	.68	.64	.66	.66					
LP	.95	.94	.91	.91	.94	.85	.91	.86	.84	.91	.63				
WFS	.90	.89	.87	.86	.89	.84	.85	.78	.77	.87	.55	.91			
PW	.92	.91	.90	.90	.91	.78	.88	.85	.83	.83	.69	.90	.82		
APW	.93	.93	.89	.91	.94	.84	.89	.82	.83	.89	.68	.86	.82	.85	
PC	.60	.56	.55	.63	.60	.38	.49	.43	.48	.48	.49	.55	.50	.54	.59

through the Office of Computer Services (OCS) at the Smithsonian Institution. Simple descriptive statistics, linear regression, factor analysis, and stepwise discriminant analyses were used to summarize observed cranial variation.

RESULTS

Geochelone ephippium appears to have the smallest skull and *G. guntheri* the largest skull of Galapagos tortoises (Table 3), but when maximum basicranial lengths (mean plus two standard deviations) are compared, *G. nigrita* appears to possess the largest skull ($B_{max.} = 171$ mm for *G. guntheri*, 200 mm for *G. nigrita*). The efficacy of this procedure is in some doubt since the $B_{max.}$ for *G. vicina* exceeds that of *G. nigrita*, even though no skull of the former is anywhere near as large as the latter. This may be the product of a small sample size for *G. vicina*, represented by only four specimens. The largest skulls in these samples are *G. ephippium*, 114.0 mm; *G. guntheri*, 157.7 mm; *G. nigrita*, 157.6 mm; and *G. vicina*, 142.7 mm. The *G. nigrita* sample includes the two smallest tortoises measured, which depresses the mean basicranial length and elevates the standard deviation.

Combined samples clearly show a size differential between saddlebacked and domed tortoises; saddlebacked tortoises have smaller skulls. This is supported by all 16 variables (see Table 4).

All correlation coefficients were significant to at least the $P = 0.05$ level (Table 5). Some variables, however, did not correlate as highly with other variables. Examples include PC, DPV, and LB. Because intervariable correlation was so high, linear regression showed slight, if any, tendency toward curvilinearity. The intercepts for saddlebacked forms were lower than the intercepts for non-saddlebacked forms, reflecting the difference in size between the two groups. Slopes, however, were practically identical. As an example, linear equations relating WO to LB for saddlebacked and non-saddlebacked tortoises have slopes of 1.38 and 1.37, respectively, whereas intercepts are 7.92 and 11.74, respectively ($r = 0.75$ for saddlebacks and 0.69 for nonsaddlebacks, $P \le 0.005$ for both).

Factor analysis yielded three factors, the first accounted for almost 95% of the data variance (see Table 6). Before rotation all 16 variables correlated most highly with this first factor. Rotation simplifies vectors derived by the analysis procedure and is necessary because factor analysis problems have more than one solution. There are two general rotation techniques: orthogonal and oblique. Orthogonal rotation solutions derive vectors along axes of data variation that are perpendicular to one another and thus uncorrelated. Oblique techniques, on the other hand, do not require that vectors be orthogonal, so vectors can be correlated. Even after varimax rotation, an orthogonal technique that simplifies the columns of a factor matrix by maximizing factor-variable loadings, 12 of the 16 variables correlate most highly with factor one. Varimax rotation

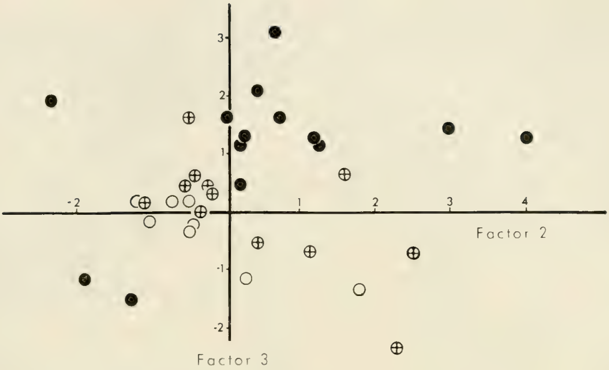


FIGURE 3. A plot of factor scores for factors two and three. *Geochelone nigrita* (solid circles), *G. guntheri* (cross-hatched circles) and *G. ephippium* (open circles). When factor scores for all tortoises are plotted there is a prominent trend from the lower-left to upper-right quadrant. Although this general trend for all tortoises is suggestive of a positive trend toward increased snout elongation with increased robustness (as illustrated by *G. nigrita*), the points for *G. ephippium* and *G. guntheri* show a negative relationship between robustness and snout elongation.

was chosen because it maximizes the variation accounted for by the factor vectors without all the variables loading highly on the same factor, as occurs in quartimax rotation.

Identifying vectors of data variation is speculative; but it seems likely that factor one summarizes variation in size. Thus, 95% of the variation in Galapagos tortoise skulls may be the result of variation in size. The other two factors are more difficult to interpret, partly because so little variation (only 5%) is summarized by these factors. Factor two summarizes variation in cranial width and the width of skull arches, emphasizing WO, WP, WZ, PW, and DPV. Therefore, factor two could be identified as some measure of robustness. Factor three, emphasizing PC and HN, suggests there is variation in the anterior part of the skull. A high factor three score results from an increase in PC and HN. This results from elongating the anteromedial portion of the triturating surface, which concomitantly yields a longer skull.

TABLE 6. STATISTICS PRODUCED BY FACTOR ANALYSIS USING VARIMAX ROTATION. All specimens were included in this analysis. Abbreviations used in the summarized factor matrix are listed in Table 2. Eigenvalues are measures of the relative importance of the factors.

Factor	1	2	3
Eigenvalue	13.19	0.47	0.28
% Variation	94.6	3.4	2.0
Summarization of Factor Matrix	WFS 0.82	WP 0.63	PC 0.75
	LB 0.80	DPV 0.60	HN 0.51
	LP 0.78	PW 0.53	
	WAT 0.76	WO 0.53	
	WS 0.76	WZ 0.72	
	B 0.76		
	WB 0.75		
	WN 0.73		
	HN 0.72		

A bivariate plot of the second and third factor scores for *G. nigrita, G. guntheri,* and *G. ephippium* (Fig. 3) indicates that as skulls become more robust, the anterior nasal part of the skull elongates; as robustness increases the skull becomes relatively longer. However, examining the individual points for *G. guntheri* and *G. ephippium* suggests just the opposite; as robustness increases elongation decreases. This negative relationship seems more pronounced in *G. guntheri.*

Three separate discriminant function analyses were done: one for *G. nigrita, G. ephippium,* and *G. guntheri*; one for the combined samples; and one comparing small samples to larger samples. In the first analysis, the three forms were distinguished by two factors (Table 7). Factor one summarized variation in 14 of the 16 variables but accounted for only 54.9% of the data variance. A high canonical correlation coefficient and a low Wilks's lambda indicate that this factor is good

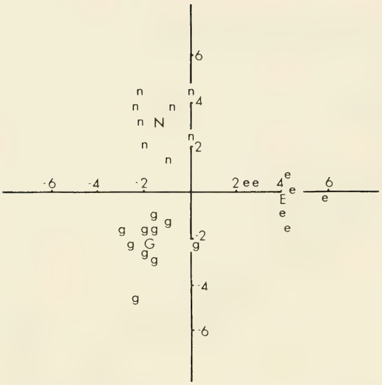


FIGURE 4. A plot of the discriminant scores derived from an analysis that included *Geochelone guntheri, G. nigrita,* and *G. ephippium.* Discriminant factor one is the horizontal axis and discriminant factor two is the vertical axis. Statistical separation of these three populations is marked. High positive scores along the horizontal axis indicate small size, whereas high positive scores along the vertical axis indicate a poorly exposed basisphenoid. Upper case letters indicate group centeroids.

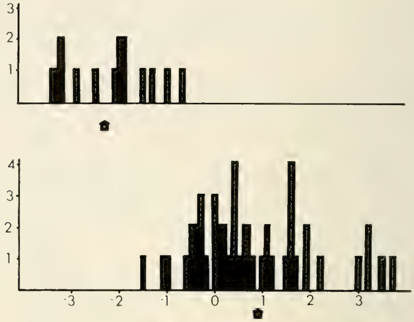


FIGURE 5. A histogram illustrating the results of a discriminant analysis of the saddlebacked and non-saddlebacked forms. The saddlebacked species are in the upper histogram, the non-saddlebacked species are in the lower histogram. The arrows indicate the median in each class. The discriminant scores (high positive scores indicate large size) are on the lower axis and the number of individuals are represented by left-hand axis. Although the saddlebacked and non-saddlebacked forms are clearly different sizes, there is significant overlap.

at distinguishing groups. *Geochelone ephippium* is separated from the other two forms by this factor. The discriminating variables are negatively correlated to factor one, and the species with a small skull is differentiated from the two species with large skulls, suggesting that factor one is an inverse measure of size. Factor two, which also has a high canonical correlation coefficient and a low Wilks's lambda, distinguishes *G. nigrita* from *G. guntheri* and accounts for the remaining variation in the data. Two variables are highly correlated with this second factor, LB and WB. *Geochelone nigrita* has high positive values for discriminating factor two, indicating that the basisphenoid is poorly exposed. Figure 4 graphically illustrates the completeness of separation.

TABLE 7. STATISTICS PRODUCED BY A DISCRIMINANT ANALYSIS OF *G. ephippium, G. guntheri* AND *G. nigrita.* Abbreviations are listed in Table 2. Eigenvalues are measures of the relative importance of the factors; high canonical correlation coefficients (near 1) and low Wilks's lambdas (near 0) indicate that factors are good discriminators.

Discriminant function	1	2
Eigenvalue	7.06	5.82
% Variation	54.8	45.2
Canonical correlation	0.94	0.92
Wilks's lambda	0.02 ($P = 0.003$)	0.15 ($P = 0.02$)
Pooled within groups correlations bet. canonical discr. fncts. & discr. variables	HN −0.22 LP −0.20 WN −0.19 WAT −0.19 APW −0.18 WO −0.18	LB −0.21 WB −0.17
Groups delineated from others	*G. ephippium* from *G. guntheri*	*G. nigrita*

Standardized canonical discriminant function coefficients are available upon request. These coefficients can be used to calculate discriminant scores for individual specimens whose identity is unknown; but choices are restricted to the populations originally compared (in this case *G. ephippium, G. guntheri,* or *G. nigrita*).

The second discriminant analysis applied to the combined samples. Because only two groups were analyzed, a single discriminating factor was computed. The Wilks's lambda was not low, suggesting that the two groups cannot be easily distinguished. The size differential between saddlebacked and non-saddlebacked tortoises is readily apparent (Fig. 5). Standardized canonical discriminant function coefficients are available upon request.

The third discriminant analysis compared

TABLE 8. CLASSIFICATION RESULTS OF A DISCRIMINANT ANALYSIS CLASSIFICATION PROCEDURE. Individual specimens were classified to one of three species: *G. ephippium* (a saddlebacked species), *G. guntheri* (an intermediate form) or *G. nigrita* (a domed form). Asterisk indicates invalid taxon (*fide* MacFarland et al. 1974a).

Shell type	Trivial name	Sex	Mus. no.	Classified as
domed	*vandenburghi*	?	CAS 8141	*ephippium*
intermediate	*chathamensis*	?	CAS 8133	*ephippium*
intermediate	*chathamensis*	?	CAS 8131	*ephippium*
intermediate	*chathamensis*	?	USNM 29255	*ephippium*
intermediate	*chathamensis*	male	CAS 8127	*ephippium*
intermediate	*chathamensis*	?	CAS 8130	*ephippium*
intermediate	*chathamensis*	?	CAS 8128	*ephippium*
intermediate	*darwini*	female	CAS 8106	*ephippium*
intermediate	*darwini*	male	CAS 8108	*guntheri*
intermediate	*microphyes*	male	CAS 8158	*guntheri*
intermediate	*vicina*	male	CAS 8179	*ephippium*
intermediate	*vicina*	female	CAS 8193	*ephippium*
intermediate	*vicina*	?	USNM 129247	*ephippium*
intermediate	*vicina*	male	CAS 8177	*guntheri*
intermediate	*wallacei**	male	CAS 8134	*guntheri*
saddlebacked	*abingdonii*	?	USNM 29269	*guntheri*
saddlebacked	*abingdonii*	male	CAS 8112	*guntheri*
saddlebacked	*becki*	female	CAS 8120	*ephippium*
saddlebacked	*hoodensis*	male	CAS 8121	*ephippium*
saddlebacked	*hoodensis*	female	CAS 8122	*ephippium*
saddlebacked	*phantastica*	male	CAS 8101	*guntheri*

small samples of tortoise species to large samples. Small samples were classified by the discriminant function classification procedure to one of three species (*G. guntheri, G. ephippium, G. nigrita*). The results of this procedure are summarized in Table 8. Some species with intermediate shell types (*fide* VanDenburgh 1914) were classified as saddlebacked species (e.g., *G. chathamensis* was classified as *G. ephippium*), whereas other species with intermediate shell types were classified as *G. guntheri,* an intermediate form. No species was classified as a domed form. Skull variation did not parallel shell variation in any meaningful way.

DISCUSSION

Small sample sizes and the paucity of accurate locality data limit the utility of this study. Therefore, samples were combined. (Thorpe, 1976, discusses the ramifications of such procedures.) Because most of the specimens in the United States were examined, this limitation cannot be overcome without costly and time-consuming removal of skulls from skins and stuffed specimens of known provenance.

The choice of a putative ancestral morphotype makes an enormous difference in how one interprets evolutionary processes, patterns, and mechanisms. The size of the ancestral Galapagos tortoise is not known. Auffenberg (1971) believed that the fossil *Geochelone hesterna* was a likely ancestral candidate for Galapagos tortoises as well as *Geochelone chilensis* from Argentina. The skull of *G. hesterna* is very much like a Galapagos tortoise skull. Although it is not as large as that of the largest of Galapagos domed tortoises, it is larger than that of the small saddlebacked tortoises. Thus, I favor an intermediate-sized ancestor for Galapagos tortoises, perhaps something smaller than *G. guntheri.* If so, then *G. nigrita* is the result of continued gigantism and *G. ephippium* is the result of dwarfism.

Why is there such flimsy coincidence between shell variation and cranial variation in Galapagos tortoises? Zangerl and Johnson (1957) and Zangerl (1969) have intimated that much of the shell variation observed in most species has little effect on an individual's survival or fitness. Fritts (*in press*) has shown the contrary for Galapagos tortoises. But this selection on shell morphology does not seem to apply to skull morphology. What other selective factors could be molding skull morphology?

I tend to agree with Bramble (1971), who felt that biomechanical constraints on chewing are the primary sources of selection upon turtle skulls.

How strong are these selective forces? Selective factors imposed by diet are known to be especially strong in other animals from Galapagos. For example, Boag and Grant (1981) discovered that finches in Galapagos experienced intense selection upon beak size and shape as the result of a one-year drought. Because of the long life of tortoises and their ability to survive long periods without food or water, however, short-term environmental changes such as those described by Boag and Grant are unlikely to affect tortoises as severely.

Another source of selective pressure is possible. During intraspecific agonistic encounters (Fritts, pers. comm.), the victor is the individual capable of raising its head the highest. Could apparent head width also affect the outcome of these battles? Interestingly, the relative head width of *Geochelone guntheri* and *G. ephippium* increases with size. These tortoises inhabit low dry islands (or parts of islands) where carrying capacities of the habitat may be lower and intraspecific competition therefore higher. In contrast, relative head width in *G. nigrita* decreases with size. This tortoise lives on a higher moist island where carrying capacities may be higher and intraspecific competition may not be as intense. Also, this apparent decrease in relative width actually accompanies an increase in the length of the masticatory surface area, perhaps allowing more efficient mastication.

Acknowledgments

I thank L. Barnes (LACM), R. Crombie (USNM), R. Drewes (CAS), G. Foley (AMNH), T. Fritts (SDSNH), A. Leviton (CAS), H. Marx (FMNH), W. Presch, A. Resetar (FMNH), J. Rosado (MCZ), H. Voris (FMNH), D. Wake (MVZ), E. Williams (MCZ), G. Zug (USNM), and R. Zweifel (AMNH) for making specimens available. I also thank R. Crombie, C. Ernst, T. Fritts, S. McDowell, E. Meyer, K. Miyata, D. Steadman, and G. Zug for reading parts or all of the manuscript and providing helpful suggestions. Funding, for which I am most thankful, came from a Sigma Xi Grant-In-Aid of Research, the Alvarado Community Hospital Research Foundation, the Vertebrate Zoology Reserve Fund of San Diego State University, and the Theodore Roosevelt Memorial Fund of the American Museum of Natural History. Data analysis, begun at Rutgers—The State University with Department of Zoology and Physiology support, was completed with the assistance of the Office of Computer Services during my tenure as a Smithsonian Predoctoral Fellow at the National Museum of Natural History.

Literature Cited

Arnold, E. N. 1979. Indian Ocean giant tortoises: their systematics and island adaptations. Phil. Trans. R. Soc. Lond. (B) 286:127–45.

Auffenberg, W. 1971. A new fossil tortoise, with remarks on the origin of South American testudinines. Copeia 1971: 106–17.

Boag, P. T., and P. R. Grant. 1981. Intense natural selection in a population of Darwin's finches (Geospizinae) in the Galapagos. Science 214:82–85.

Bramble, D. M. 1971. Functional morphology, evolution, and paleoecology of gopher tortoises. Ph.D. thesis, Univ. Calif., Berkeley. 341 p.

Crumly, C. R. 1980. The cranial osteology and evolution of the tortoise genus *Geochelone* (Testudines, Testudinidae). M.S. thesis, San Diego State Univ. 338 p.

———. 1982. A cladistic analysis of *Geochelone* using cranial osteology. J. Herpetol. 16(3):215–34.

Duellman, W. E., T. Fritts, and A. Leviton. 1978. Museum acronyms. Herp. Rev. 9(1):5–9.

Fritts, T. H. [*in press*]. Morphometrics of Galapagos tortoises: evolutionary implications.

Garman, S. 1917. The Galapagos tortoises. Mem. Mus. Comp. Zool. 30:262–96.

Günther, A. 1875. Description of the living and extinct races of gigantic tortoises. Parts I and II: The tortoises of the Galapagos Islands. Phil. Trans. R. Soc. Lond. (B) 165: 251–84.

———. 1877. The gigantic land tortoises (living and extinct) in the collection of the British Museum. British Museum, London. 96 p.

MacFarland, C. G., J. Villa, and B. Toro. 1974a. The Galapagos giant tortoises (*Geochelone elephantopus*). Part I: The status of the surviving populations. Biol. Conserv. 6: 118–33.

———. 1974b. The Galapagos giant tortoises (*Geochelone elephantopus*). Part II: Conservation methods. Biol. Conserv. 6:198–212.

Marlow, R., and J. L. Patton. 1981. Biochemical relationships of the Galapagos tortoises (*Geochelone elephantopus*). J. Zool., London 195:413–22.

Pritchard, P. C. H. 1979. Encyclopedia of turtles. T. F. H. Publishers. 895 p.

Rothschild, L. 1901. A new land tortoise from the Galapagos Islands. Nov. Zool. 8:372.

———. 1902. Description of a new species of gigantic land turtle from the Galapagos Islands. Nov. Zool. 9:619.

———. 1903. Description of a new species of gigantic tortoise from Indefatigable Island. Nov. Zool. 10:119.

———. 1915. The gigantic land tortoises of the Galapagos Islands in the Tring Museum. Nov. Zool. 22:403–17.

Thorpe, R. S. 1976. Biometrical analysis of geographic variation and racial affinities. Biol. Rev. 51:407–52.

Van Denburgh, J. 1907. Expedition of the California Academy of Sciences to the Galapagos Islands, 1905–1906. Part

I: Preliminary descriptions of four new races of gigantic land tortoises from the Galapagos Islands. Proc. Calif. Acad. Sci. 1:1–16.

———. 1914. Expedition of the California Academy of Sciences to the Galapagos Islands, 1905–1906. Part X: The gigantic land tortoises of the Galapagos Archipelago. Proc. Calif. Acad. Sci., ser. 4, 2:203–374.

Wermuth, H., and R. Mertens. 1961. Schildkroten, krokodile, und bruckenechsen. Gustav Fischer Verlag, Jena. 422 p.

———. 1977. Liste der rezenten Amphibien un Reptilien. Testudines, Crocodylia, Rhyncocephalia. Das Tierrich 100: 1–174.

Zangerl, R. 1969. The turtle shell. Pages 311–339 *in* Gans, C., A. d'A. Bellaris, and T. S. Parsons. Biology of the Reptilia, vol. 1, Academic Press, New York.

———, and R. G. Johnson. 1957. The nature of shield abnormalities in the turtle shell. Fieldiana: Geol. 10:341–62.

CALIFORNIA ACADEMY OF SCIENCES
Golden Gate Park
San Francisco, California 94118

PROCEEDINGS
OF THE
CALIFORNIA ACADEMY OF SCIENCES

Vol. 43, No. 10, pp. 123-140, 8 figs., 1 table | January 17, 1984

THE STATUS OF *TRYPOXYLON FIGULUS* (LINNAEUS, 1758), *MEDIUM* DE BEAUMONT, 1945, AND *MINUS* DE BEAUMONT, 1945 (HYMENOPTERA: SPHECIDAE)

By
Wojciech J. Pulawski
California Academy of Sciences, Golden Gate Park, San Francisco, California 94118

Abstract: *Trypoxylon figulus* (Linnaeus, 1758), *medium* de Beaumont, 1945, and *minus* de Beaumont, 1945, currently confused under the name *figulus*, are separated on the basis of newly discovered characters. *T. majus* Kohl, 1883, *figulus barbarum* de Beaumont, 1957, and *figulus yezo* Tsuneki, 1956, are newly synonymized with *figulus*, and *figulus koma* Tsuneki, 1956 is newly synonymized with *minus*. Neotypes are designated for *Sphex fuliginosus* Scopoli, 1763, and *Trypoxylon majus* Kohl, 1883, both synonyms of *figulus*, and a lectotype is designated for *Trypoxylon rubi* Wolf, 1959, a synonym of *medium*.

Introduction

De Beaumont (1945) was first to observe that *Trypoxylon figulus* of European authors actually consisted of three phena. Their status has been controversial over the years. De Beaumont (1945, 1964a) and Richards (1980) called them varieties, Blüthgen (1951) gave them species rank, and Wolf (1959) and Bohart and Menke (1976) treated them as subspecies. The last interpretation is untenable, since the three phena are largely sympatric. Tsuneki (1981) regarded *medium* as a good species, characterized by both external and genitalic characters, and considered *minus* as a simple form of *figulus*.

According to Valkeila (1961), specimens reared from one nest mostly are one phenon, but he reported that two phena (e.g., *majus* and *minus*) are found in some nests. He concluded that all three are individual variants of one species. Unfortunately, Valkeila's data cannot be verified. I have examined all of his specimens, which are presently kept at Helsinki University. Some specimens have identification labels by de Beaumont, but not a single label refers to nests or cells from which specimens were reared. Possibly Valkeila misidentified some specimens, but this cannot be determined because his identification labels give the name *figulus* only, without reference to form or varietal names. Another possible explanation is that offspring of two nests were accidentally confused.

A thorough examination of the three phena, based on more than 3800 specimens from many countries, convinced me that actually they are good species. My opinion is based on the following evidence:

1. Morphology. Although some males of *figulus* and *minus* cannot be distinguished with certainty, females are separated by structural gaps and do not intergrade; also the male of *medium* is easily recognized by its peculiar gonoforceps. Some previously unnoticed characters (antero-

ventral mesothoracic process, length of thoracic vestiture, female hindcoxal pit) are especially helpful in recognizing the three species.

2. Rearing. Of 91 specimens reared from trap nests in Liège, Belgium, by A. Jacob-Remacle, and examined by me, all are *minus* (7 ♀, 5 ♂ reared in 1976, 44 ♀, 35 ♂ reared in 1981). This result contradicts Valkeila's conclusions: If the three phena really are variants of one species, then one would expect some variation of phena in the Liège trap nest material.

3. Geographic distribution. All three species are largely sympatric, but only *figulus* and *medium* have been found in Great Britain, only *figulus* and *minus* in the Iberian Peninsula, and only *figulus* in North Africa and North America. If the three phena were just individual forms of one species, some variation should have occurred in North American populations, and all three phena should have been observed in Great Britain (all three do occur in the Netherlands, where climatic and ecological conditions are practically identical to those in England).

4. Habitat preference. Of 429 specimens collected by J. Leclercq in waterbowl traps in Liège, Belgium, in 1980 and 1981 (and examined by me), 4 are *medium* and the remainder are *minus* (202 ♀, 223 ♂). Not a single *figulus* was trapped, in spite of the fact that this species is common in Belgium.

I fully agree with Tsuneki (1981) that some of the previously used characters are not reliable. For example, the mesopleural punctures of *figulus* are dense and well defined according to de Beaumont (1945, 1964a), but in the smallest males they actually are as sparse and minute as in most *minus*. Such characters have not been used here.

Proper mounting is critical for studying the species considered. For example, the anteroventral mesothoracic region must not be damaged by the pin. When pinning the specimens, one should insert the pin so that it passes through the membrane between the mesothorax and forecoxae (which then extend laterad). In this position, the anteroventral mesothoracic region is easily visible. Unfortunately, many European collectors mount their specimens on cardboard rectangles with glue or minutiae (venter down rather than on a side), and such specimens must be relaxed and remounted before examination.

In the text below the locality records are arranged according to current administrative divisions for each country except Sweden and Finland, for which biogeographic provinces have been used. Localities given on specimen labels but not found on available maps or in gazeteers have not been considered.

An exclamation mark preceding the word *Holotype* or *Neotype* in the bibliographic citations indicates that the type has been examined.

SOURCES OF MATERIAL

The specimens examined came from institutional and private collections listed below. The acronyms preceding the names are the abbreviations by which these collections are referred to in the text.

AKM: Aimo K. Merisuo, Turku, Finland
AWE: Father Andreas W. Ebmer, Linz, Austria
BB: Padre Bruno Bonelli, Cavalese, Italy
BMNH: British Museum (Natural History), London, England (Mr. C. R. Vardy)
CAS: California Academy of Sciences, San Francisco, California (W. J. Pulawski)
CNC: Canada National Collection of Insects, Arachnids and Nematods, Biosystematics Research Institute, Ottawa, Ontario
CU: Cornell University, Department of Entomology and Limnology, Ithaca, New York (Dr. L. L. Pechuman)
DBB: Major Donald B. Baker, Ewell, Surrey, England
DEI: Institut für Pflanzenschutzforschung der Akademie der Landwirtschaftswissenschaften der DDR, Zweigstelle Eberswalde, Abteilung Taxonomie der Insekten (formerly Deutsches Entomologisches Institut), Eberswalde-Finow (Dr. J. Oehlke)
FIS: Forschungsinstitut Senckenberg, Frankfurt am Main, Federal Republic of Germany (Dr. J.-P. Kopelke)
FJS: Señor Francisco J. Suárez, Almería, Spain
FSAG: Faculté de Sciences Agronomiques, Gembloux, Belgium (Dr. J. Leclercq)
GP: Signor Guido Pagliano, Turin, Italy
GVR: Mr. Gerard van Rossem, Wageningen, The Netherlands
HD: Dr. Holger Dathe, Forschungsstelle für Wirbeltierforschung, Berlin, German Democratic Republic
HW: Herr Heinrich Wolf, Plettenberg, Federal Republic of Germany
HY: Helsingin Yliopisto (=University of Helsinki), Department of Agricultural and Forest Zoology, Finland, including E. Valkeila collection (Dr. Martti Koponen)
IEE: Instituto Español de Entomologia, Madrid, Spain (Dr. E. Mingo Perez)
JG: Dr. Joseph Gusenleitner, Linz, Austria
KMG: Mr. Kenneth M. Guichard, % British Museum (Natural History), London, England
KS: Professor Dr. Konrad Schmidt, Zoologisches Institut der Universität, Karlsruhe, Federal Republic of Germany
KT: Professor Katsui Tsuneki, Mishima, Japan
LEM: Lyman Entomological Museum & Research Laboratory, Ste. Anne de Bellevue, Quebec, Canada (Dr. A. Finnamore)
MGA: Muzeul de Istorie Naturala Grigore Antipa, Bucharest, Rumania (Mrs. X. Scobiola Palade)

TABLE 1. ANCESTRAL AND DERIVED CHARACTER STATES OF THREE SPECIES IN THE GENUS *TRYPOXYLON.*

Character	Ancestral	Derived
1. Thoracic pilosity	shorter (as in *medium*)	longer (as in *figulus*)
2. Anteroventral mesothoracic process	absent	present
3. Free margin of female clypeus	straight or sinuate	concave
4. Female hindcoxal pit	circular	oblong
5. Sete of hindcoxal pit	evenly distributed	channel-like structure
6. Male apical flagellomere	shorter (as in *medium*)	longer (as in *figulus*)
7. Gonoforceps process	absent	present

MHNG: Muséum d'Histoire Naturelle de Genève, Switzerland (Dr. Cl. Besuchet)
MSNM: Museo Civico di Storia Naturale, Milano, Italy (Dr. C. Leonardi)
MCZ: Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts
NHMB: Naturhistorisches Museum Bern, Bern, Switzerland (Dr. H. D. Volkart)
NHMV: Naturhistorisches Museum, Vienna, Austria (Dr. M. Fischer)
NRS: Naturhistoriska Riksmuseet, Stockholm V, Sweden (Mr. S. Erlandsson)
RMNH: Rijksmuseum van Natuurlijke Historie, Leiden, The Netherlands, including collections of J. P. van Lith and P. M. F. Verhoeff (Dr. K. van Achterberg)
SFG: Dr. Severiano Fernandez Gayubo, Departamento de Zoologia, Universidad de Salamanca, Spain
SMT: Staatliches Museum für Tierkunde, Dresden, German Democratic Republic (Dr. Regine Eck)
TMB: Természettudomanyi Múzeum, Budapest, Hungary (Dr. J. Papp)
TN: Mr. Toshiaku Nambu, Yorii-machi, Saitama Prefecture, Japan
USNM: United States National Museum (Smithsonian Institution), Washington, D.C.
VH: Dr. Volk Haeseler, Universität Oldenburg, Oldenburg, Federal Republic of Germany
VLK: Dr. Vladimir L. Kazenas, Zoological Institute, Kazakh Academy of Sciences, Alma Ata, USSR
WJP: Wojciech J. Pulawski, San Francisco, California
WSU: Washington State University, Department of Entomology, Pullman, Washington
ZMB: Museum für Naturkunde an der Humboldt Universität zu Berlin, German Democratic Republic (Dr. F. Koch)
ZMH: Zoologisches Institut und Zoologisches Museum der Universität Hamburg, Federal Republic of Germany (Dr. R. Abraham)
ZMK: Zoological Museum, Copenhagen, Denmark (Dr. O. Lomholdt)
ZMMU: Zoological Museum, Moscow State University, Moscow, USSR (Dr. L. V. Zimina, via Dr. A. P. Rasnitsyn)
ZMUB: Zoological Museum, University of Bergen, Norway (Dr. Lita Greve Jensen)
ZSM: Zoologische Staatssammlung München, Federal Republic of Germany (Dr. E. Diller)

ACKNOWLEDGMENTS

Study of the Linnean type of *Sphex figulus* at the Burlington House, London, was possible owing to the kind assistance of Michael C. Day of the British Museum (Natural History). North American specimens of *figulus* belonging to various U.S. and Canadian institutions listed above (except for LEM) were kindly forwarded by Rolin C. Coville, University of California, Berkeley, who had them on loan. Arnold S. Menke and Eric E. Grissell critically reviewed the manuscript and made many valuable suggestions. David H. Kavanaugh commented on the phylogenetic trees. Mary Ann Tenorio drew the phylogenetic schemes and distributional maps, and Donald J. Becker took the photographs with a Hitachi S-520 scanning electron microscope.

PHYLOGENETIC RELATIONSHIPS

Reconstructing phyletic relationships between three isolated species of a large genus like *Trypoxylon* is precarious, because polarities of morphological transformations can easily be misinterpreted. With this restriction in mind, I nevertheless think it worthwhile to analyze the relationships between *figulus, medium,* and *minus.* Their ancestral and derived character states, based on outgroup comparisons, are shown in Table 1.

Based on the above table, the three possible phylogenetic trees (only dichotomic trees are considered) are as shown in Fig. 1. Tree B is the most probable, since no single derived character state is shared by any two of the three species in the schemes A and C. Furthermore, trees A and C imply a parallel development of the elongate male flagellomere XI in *figulus* and *minus,* an unlikely event.

KEY TO THE SPECIES

1. Female: clypeal free margin evenly concave between orbit and median projection (Fig. 7A); mesopleural setae around scrobe shorter than midocellar diameter; hindcox-

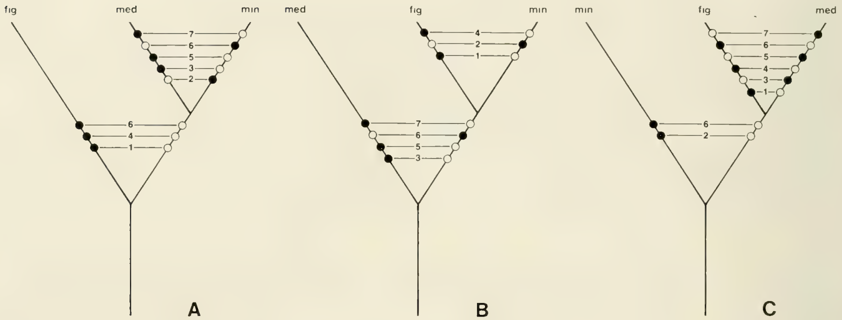


FIGURE 1. Hypothetical phylogenetic trees of *Trypoxylon figulus* (fig), *medium* (med), et *minus* (min). Open circles: generalized character states. Solid circles: derived character states. Numbers refer to characters listed on p. 125.

al pit nearly circular, its setae forming peculiar, channel-like structure (Fig. 7B–D). Male: maximum length of flagellomere X 0.75–0.9 times its width; maximum length of flagellomere XI generally 2.0–2.2 times its basal diameter (occasionally 2.4 times); gonoforceps with externoventral expansion at about midlength (Fig. 7E, F) .... *medium* de Beaumont

– Female: clypeal free margin (Fig. 2A, 5A) sinuate to nearly straight, except concave in occasional western European *figulus* in which mesopleural setae around scrobe are generally longer than midocellar diameter, and hindcoxal pit is generally oblong; setae of hindcoxal pit not forming channel-like structure. Male: maximum length of flagellomere X 0.5–0.8 its width; maximum length of flagellomere XI 2.2–3.6 times its basal diameter; gonoforceps not expanded exteroventrally (Fig. 2E, F) 2

2. Mesothorax without anteroventral process[1]; mesopleural setae around scrobe in most specimens longer than midocellar diameter (shorter in some individuals). Female: clypeal free margin sinuate between lobe and orbit (Fig. 2A), hindcoxal pit oblong (Fig. 2B–D) or (some specimens) circular, evanescent in Japanese specimens .... *figulus* (Linnaeus)

– Mesothorax with anteroventral process (Fig. 5B, C) in more than 95% of specimens; mesopleural setae around scrobe shorter than midocellar diameter. Female: clypeal free margin almost straight between lobe and orbit (Fig. 5A), hindcoxal pit circular (Fig. 5D–F) .... *minus* (de Beaumont)

Trypoxylon figulus (Linnaeus)

Sphex figulus LINNAEUS, 1758:570. ! Holotype: ♀, Sweden, Uppsala (Linnean Society, London). — DAY, 1979:62. — In *Trypoxylon*: LATREILLE, 1802:79; TSUNEKI, 1981:15 (redescription, geographic variation). — In *Apius*: JURINE, 1807: 142.

Sphex fuliginosus SCOPOLI, 1763:292 (as *fuliginosa*, incorrect original spelling). Holotype or syntypes: Carniolia (formerly in Austria, since 1919 part of Italy and Yugoslavia), lost, see ROGENHOFER UND DALLA TORRE, 1882:599. ! Neotype: ♀, Austria: "Carinthia, Ostkarawanken, Ebriach, 580–750 m, 21–29. VII.1964, G. van Rossem," present designation (CAS). — As probable synonym of *figulus*: VANDER LINDEN, 1829:42. — As synonym of *figulus*: subsequent authors.

Trypoxylon figulus var. *majus* KOHL, 1883:657, ♀, ♂ (as *major*, incorrect original spelling). Holotype or syntypes: ♀, Switzerland: no specific locality (originally NHMV, Vienna, now lost). ! Neotype: ♀, Switzerland, "P. 3 VIII 84" and "Cn. Tournier" (=Peney near Geneva, collection Tournier), present designation (MHNG). **New synonym.** — DE BEAUMONT, 1945:477 (var. *major*); BLÜTHGEN, 1951:234 (var. *major*); DE BEAUMONT, 1958:206 (forma *major*), 1959:30 (same); WOLF, 1959:15, 16 (*figulus major*); VALKEILA, 1961:244 (var. *major*); DE BEAUMONT, 1964a:290, 1964b:84 (forma *major*), 1965:56 (same), 1967:338 (same); BOHART AND MENKE, 1976: 346 (ssp. *major*); LOMHOLDT, 1976:267 (*figulus major*); RICHARDS, 1980:45 (var. *major*).

Trypoxylon apicale W. FOX, 1891:142, ♀ (as *apicalis*, incorrect

---

[1] In occasional males the anteroventral mesothoracic process is absent and the mesopleural setae are shorter than the midocellar diameter. Such specimens can be either *figulus* with unusually short mesopleural setae, or *minus* without mesothoracic process. I cannot find characters for distinguishing them.

original spelling). Lectotype: ♀, Canada (ANSP, Philadelphia), designated by Cresson, 1928:52. — Sandhouse, 1940: 156 (*apicale*). Synonymized by Pate, 1943:16.

Trypoxylon figulus barbarum de Beaumont, 1957: ♀, ♂. Holotype: ♂, Morocco: Marrakech (Mus. Zool. Lausanne). **New synonym.** — Bohart and Menke, 1976:346.

Trypoxylon figulus yezo Tsuneki, 1956:29, ♀, ♂. Holotype: ♀, Japan: Hokkaido [=Yezo]: Jozankei (K. Tsuneki collection, Mishima). **New synonym.** — Bohart and Menke, 1976: 346; Tsuneki, 1981:21 (summary of faunistic data).

Trypoxylon fieuzeti Giner Marí, 1959:389, ♂. ! Holotype: ♂, Morocco: Fez (IEE, Madrid). Synonymized with *figulus barbarum* by Suárez, *in* Giner Marí, 1959:400.

Comments on New Synonyms.—*T. figulus barbarum* was based mainly on the elongate male flagellomere XI. Because flagellomere XI varies in length (see Geographic Variation below) this subspecies is not recognized here. I also feel that a formal name for the Japanese populations (*figulus yezo*) is unwarranted on morphological or other grounds.

Comments on Neotypes.—The identity of *Sphex fuliginosus* has never been satisfactorily established, because the original description is inadequate and the original material is lost (Rogenhofer und Dalla Torre, 1882). Consequently, the name can only be defined by designation of a neotype. In selecting a specimen of *Trypoxylon figulus* as a neotype of *Sphex fuliginosus* I have followed the traditional interpretation of the last name.

The original material of *Trypoxylon majus* cannot be found in the Vienna Museum (Dr. M. Fischer's letter of 21 October 1982) and must be lost. However, this name indicates a large body size, and *figulus* averages larger than either *medium* or *minus*. A neotype of *majus* has also been designated.

Diagnosis.—Most specimens of *figulus* differ from *medium* and *minus* in having the mesopleural setae around the scrobe slightly longer than the midocellar diameter. However, the setae length is slightly less than this diameter in some specimens from southern France and the Iberian Peninsula (as they are in the other two species). The anteroventral mesothoracic carina is sinuate, curved posterad mesally, but unlike most *minus* it has no process. The free margin of the female clypeus (Fig. 2A) is usually sinuate between orbit and the median projection (free margin concave in *medium*, almost straight in *minus*). However, the free margin is almost evenly concave in certain specimens from Spain (almost like *medium*, which is unknown from Spain), in a specimen from Zirbelwald, Austria, and one from Balderschwang, Federal Germany. The female hindcoxal pit is mostly oblong (Fig. 2B–D) in western palearctic specimens, but occasionally it is nearly circular, as in *medium* and *minus*; it is evanescent in Japanese females. In the male, the maximum length of flagellomere X equals 0.65–0.8 of its width (the lowest ratios are observed is specimens in which flagellomere XI is short, and vice versa); the maximum length of flagellomere XI usually is 2.4–3.6 times the basal diameter instead of 2.0–2.2 in most *medium*, but only 2.2 times in occasional specimens (which differ from *medium* in having a longer mesopleural vestiture and a shorter flagellomere X). Body length 9–12 mm in female, 7.5–10 mm in male.

Geographic Variation.—In most males (including the two males seen from Portugal), the maximum length of flagellomere XI equals 2.4–2.7 times its basal diameter, but in occasional specimens it is only 2.2 times (e.g., in a male from Wachseldornmoos, Switzerland); it is 2.7–3.2 times its basal diameter in Spanish individuals, and 3.3–3.6 times in Moroccan individuals.

Life History.—Many specimens of *figulus* (voucher specimens examined by me) were reared from nests established in wood (Wolf, 1959). Six females and 17 males examined were reared by O. Lomholdt from nests in reed stems which had been used for thatching roofs at Tisvilde Hegn, Denmark.

Geographic Distribution (Figs. 3, 4).—Most of the Palearctic Region between Great Britain and Japan, and also eastern North America (eastern Canada and northeastern USA).

Records (Old World).—Algeria (1 ♂): El Harrach (as Maison Carrée, apical flagellomeres missing, BMNH).

Austria: (102 ♀, 50 ♂, NHMV if not indicated otherwise): **Kärnten:** Afritzer See (WJP), Ebene Reichenau (RMNH), Ebriach in Ostkarawanken (WJP), Eisenkappel, Mallnitz (ZMB), Mauthen (ZMB), Nötsch, Waidisch bei Ferlach (FSAG, JG). **Niederösterreich:** Bisamberg near Vienna (NHMV, CU), Bucklige Welt S Vienna, Brühl, Dornbach (CAS, NHMV), Eichkogel near Vienna (RMNH), Guntramsdorf (DEI), Hainbach (FSAG), Hainburg an der Donau (ZMB), Herzogenburg, Herzograd (JG), Kalksburg near Vienna, Krumbach, Lobau near Vienna (NHMV, ZMH), Marchfeld (ZMB), Mistelbach (ZMH), Mödling (ZMH), Oberweiden (DBB), Piesting, Purk (W Krems), Rappendorf bei Molk (AWE), Roggendorf bei Melk (JG), Rohr im Gebirge, Schneeberg, Stillfried (ZMH), Traismauer, Weidlingsbach (ZMH), Wien (NHMV, FSAG, ZMH) including Donauauen, Kahlenberg and Türkenschanze. **Oberösterreich:** Frauenstein (JG), Gemeinde Reichenthal (AWE), Gutau (FSAG, JG), Hofkirchen (FSAG), Innerbreitenau (FSAG, JG), Kalten-

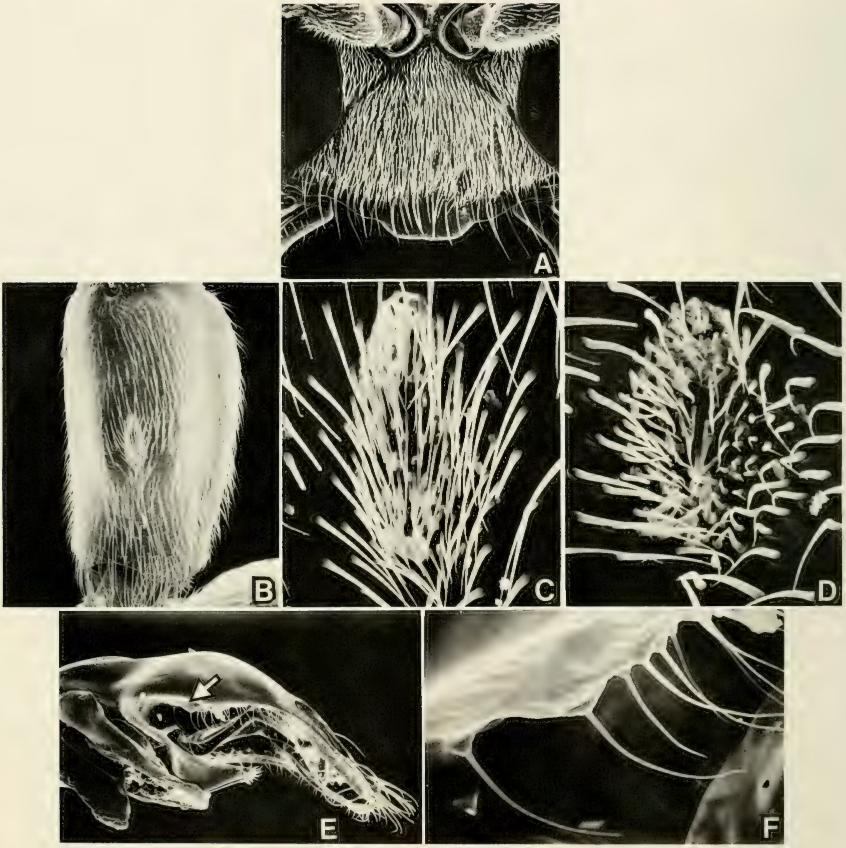


FIGURE 2. *Trypoxylon figulus:* A—female clypeus, B—female hindcoxa ventrally, C—female hindcoxal pit, vertical view, D—same, oblique view, E—male genitalia (arrow: area shown in F), F—same, portion of gonoforceps.

berg (AWE), Linz (HY, NHMV), Molln, Mühlviertel (JG), Neumarkt (JG), Oberwallsee bei Müllachen (JG), Riedegg bei Gallneukirchen (JG), Sankt Willibald (AWE), Ternberg (JG), Welserheide, Zeissberg bei Freistadt (FSAG, JG). **Salzburg:** Koppl bei Aschach (JG), Salzburg (BMNH). **Steiermark:** Leutschach (JG), Sankt Ulrich (JG), Tragöss-Oberort (DBB), Weinburg (FSAG). **Tirol:** Huben in eastern Tirol (ZMB), Innsbruck (NHMV, ZMB), Iselsberg (DBB), Lienz (RMNH), Obladis, Hopfgarten, Salvenberg (CAS), Zirbelwald near Obergurgl, 1 km SW Zwiselstein in Ötztal. **Voralberg:** Ittensberg.

Belgium (95 ♀, 63 ♂, FSAG if not indicated otherwise): **Brabant:** Evere, Genval, Gistoux, Grez-Doiceau, Mont-Saint-Guibert, Nethen, Rhode-Sainte Agathe, Thorembais-Saint-Trond, Uccle, Waterloo. **Hainaut:** Aiseau, Athis, Barry, Binche, Boussu, Bouvignies, Fleurus, Orcq, Seneffe, Taintignies, Velaines, Wanfercée. **Liège:** Acosse, Aubel, Barchon, Ben-Ahin, Beyne: ca 15 km SE Liège (BMNH), Beyne-Heusay, Cerexhe, Charneux, Chevron, Clermont-sur-Berwinne, Fléron, Forêt de Grunhault, Francorchamps, Henri-Chapelle, Hombourg, Jupille, La Calamine, La Reid, Lontzen, Montzen, Pepinster, Queue-du-Bois, Romsee, Spa, Xhendelesse, Welkenraedt. **Limburg:** Berg près de Tongres, Bocholt, Godsheide, Tongres. **Luxembourg:** Amonines, Hotton, Les Epioux, Lomprez, Ozo, Saint-Médard, Sampont, Smuid, Waharday, Wibrin. **Namur:** Aische, Alle (RMNH), Andenne, Baillonville, Belgrade, Bièvre, Branchon, Champion, Eghezée, Ernage, Feschaux, Gembloux, Gesves, Grand Leez, Ham-sur-Sambre, Lonzée, Mount-Gauthier, Saint-Aubin, Saint-Gérard, Saint-Marc, Sorinnes, Sauvenière, Sombreffe, Winenne.

Bulgaria (1 ♂): Rila Mts. (DEI).

FIGURE 3. *Trypoxylon figulus:* geographic distribution in the Old World.

FIGURE 4. *Trypoxylon figulus:* geographic distribution in the New World.

Czechoslovakia (1 ♀, 3 ♂): **Jihomoravsky Kraj:** Vranov W Znojmo (as Frain, NHMV). **Vapadoslovensky Kraj:** Šturovo (SMT).

Denmark (41 ♀, 33 ♂, ZMK if not indicated otherwise): **Ålborg:** Vegger. **Bornholm:** Bastemose. **Frederiksborg:** Asserbo, Hilleröd, Hundested, Jaegerspris Nordskov (tip of Hornsherred peninsula), Sorte Mose near Farum, Store Karlsminde near Lynæs, Tisvilde Hegn (FSAG, ZMK). **Holbæk:** Kongsøre. **Maribo:** Maribo. **København:** Holte. **Odense:** Æbelø. **Randers:** Glatved Strand on Djursland Peninsula, Mols Bjerge. **Ringkøbing:** Gindeskov, Kjelstrup (E Skjern). **Sønderborg:** Sønderborg. **Sorø:** Agersö. **Svenborg:** Langeland Island: Hellenor. **Tønder:** Rømø (VH), Stensbæk Plantage. **Vejle:** Klattrup.

Finland: (47 ♀, 48 ♂, HY unless indicated otherwise): **Abo:** Lohja, Perniö (AKM), Rymättylä (AKM), Turku (AKM). **Alandia:** Eckerö (AKM, HY), Finström (AKM), Hammarland, Jomala (AKM), Saltvik (AKM). **Karelia Borealis:** Pyhäselkä (Hammaslahti). **Nylandia:** Helsinki (CU, HY), Parvoo = Borgå, Pernaja. **Ostrobotnia Australis:** Koivulahti. **Satakunta:** Loimaa (AKM), Yläne (AKM). **Tavastia Australis:** Hattula, Hämeenlinna, Janakkala, Nastola (AKM), Pälkäne (AKM, HY), Somero (AKM), Urjala, Vanaja, Ylöjärvi.

France (35 ♀, 16 ♂): **Alpes-Maritimes:** Guillaumes (FSAG). **Ariège:** Ax-les-Thermes (ZMB). **Basses-Alpes:** Allos (FSAG), Annot (FSAG), Fugeret (FSAG), Les Dourbes (KMG), Montagane de Lure (ZMK), Peyresq (FSAG), Saint-André-les-Alpes (FSAG). **Bouche-du-Rhône:** Marseille (FIS). **Calvados:** Lisieux (FSAG). **Corse:** Corte (KMG). **Côtes-du-Nord:** Saint-Rieul. **Haute-Savoie:** Dent d'Oche (MHNG), Mont Jorat (RMNH), Val de Charmy (RMNH). **Haute-Vienne:** Rochechouart (FSAG). **Jura:** Arbois. **Loirê-et-Cher:** Blois (FSAG). **Loire-Atlantique:** Forêt de la Roche Bernard (RMNH), Herbignac (RMNH). **Saône-et-Loire:** Uchizy (FSAG). **Seine-et-Oise:** Poissy (IEE). **Var:** Fréjus (KMG), Gonfaron (FSAG), Montouroux (RMNH). **Vaucluse:** Carpentras (RMNH). **Yonne:** Foissy-sur-Vanne (FSAG).

Germany, Democratic (81 ♀, 29 ♂, DEI if not indicated otherwise): **Berlin:** Berlin (DEI, HD, ZMB, ZSM). **Cottbus:** Alt Döbern (ZMB), Muskau, Neu Zauche (ZMB), Schlieben (ZMB). **Dresden:** Daubitz (SMT), Gersdorf near Kamenz (SMT). **Erfurt:** Erfurt (CU), Gotha (ZSM). **Frankfurt:** Biesental, Eberswalde area. **Gera:** Blankenburg (ZMB), Jena (NHMV, ZMB). **Halle:** Gernrode (ZMH), Halle (DEI, ZMB), Kyffhäuser, Seeburg, Naumburg (TMB). **Leipzig:** Winkelmühle. **Magdeburg:** Arendsee (SMT). **Neubrandenburg:** Faule Ort, Naturschutzgebiet Müritzhof. **Potsdam:** Fürstenberg (TMB), Zechlin (ZMB), Zootzen. **Rostock:** Prerow, Rostock, Stralsund (DEI, ZMB). **Rügen:** Hiddensee Island (DEI, SMT), Rügen Island: Mönchgut (SMT) and Ummanz. **Schwerin:** Campow (ZMB), Schwerin (ZMB), Wendeltorf near Schwerin.

Germany, Federal (93 ♀, 51 ♂): **Baden-Würtemberg:** Enzklösterle (KS), Heidelberg (ZSM), Hochwacht (HW), Isny (NHMB), Kaiserstuhl (ZMB), Karlsruhe (KS, ZMH), Küssaberg (KS), Radolfzell (ZMH), Schwarzwald (SMT), Tiengen in Wutach Valley (KS). **Bayern:** Abensberg (ZSM), Allach (ZSM), Aschaffenburg (FIS), Balderschwang (KS), Bamberg (ZSM), Ebenhausen (ZSM), Erdweg (ZSM), Hörgersthausen near Moosburg (ZSM), Ingolstadt (ZSM), Kahl (FIS), München (FSAG, ZSM), Nürnberg (ZSM), Rotwand area (ZSM), Schliersee (ZSM), Tegernsee (ZSM). **Hamburg** (ZMH): Ochsenwärder, Warwisch. **Hessen:** Battenfeld near Biederkopf (ZMH), Gründau E Frankfurt (HW, HY), Marburg (HW, WJP). **Niedersachsen:** 2 km NW Dötlingen (VH), Dörpen: 14 km SW Papenburg (VH), Elbe Islands (VH), 5 km S Oldenburg (VH), Pevestorf: 72 km SE Lauenburg (VH), Wobeck (ZMH). **Nordrhein-Westfalen:** Ahaus (ZSM), Neheim (FSAG), Leverkusen (ZMH), Plettenberg (HW), Siegen (HW). **Rheinland-Pfalz:** lower Ahr valley (FIS), Mainz (KS), Nattenheim (FSAG), Worms (FIS). **Schleswig-Holstein:** Amrum Island (VH), Eutin (KS), Ihlkathe 2 km SE Kiel (VH), Lütjenburg (KS), Ratzeburg (ZMH), Schierensee SW Kiel (VH), Schleswig (VH).

Great Britain (92 ♀, 106 ♂; BMNH unless stated otherwise): **Berkshire:** Reading. **Buckingham:** Iver, Slough. **Devon:** Paignton. **Dorset:** Wareham. **Essex:** Brentwood, Colchester, Epping Forest. **Gloucester:** Chalford. **Hampshire:** Brockenhurst, Fleet, New Forest, Wickham. **Isle of Wight:** Sandown, Shanklin. **Kent:** Cobham, Darenth, Faversham (WJP), Goudhurst. **London:** Hampstead, Mill Hill, Mitcham Common, Norwood, Putney. **Northampton:** Ashton Wold (Oundle). **Oxford:** Goring, Oxford, Tubney near Oxford. **Somerset:** Dunster. **Suffolk:** Arger Fen, Bury St. Edmunds, Dunwich. **Surrey:** Byfleet, Esher, Horsell, Weybridge. **Sussex:** Midhurst: Ambersham Common.

Greece (2 ♀, 4 ♂): **Peloponnesus** (de Beaumont, 1965): Mega Spilaion, Pirgos, and Taygetus. **Sterea Ellas:** Karpenission (KMG). **Thessalia:** Aspropotamos near Kalabaka (KMG).

Hungary (13 ♀, 3 ♂): **Bacs-Kiskun:** Kalocsa (TMB), Tabdi (TMB). **Györ-Sopron:** Neusiedlersee (NHMV). **Somogy:** Balatonszemes (TMB). **Szolnok:** Jászbéreny (TMB). **Tolna:** Simontornya (NHMV). **Veszprem:** Tihany Peninsula on Balaton Lake (HD, TMB, WJP).

Italy (19 ♀, 8 ♂): **Emilia-Romagna:** Cattolica (RMNH). **Lombardia:** Pavia: Cignolo Po (MSNM), Sondrio: Valtellina (KS). **Piemonte:** Alpignano (GP), Colle di Sestriere in Alpi Cozie (GP), Murazzano (GP), San Benedetto Belbo 20 km S Alba (GP), Val d'Angrogna in Alpi Cozie (WJP). **Valle d'Aosta:** Bresson near St. Vincent (GP). **Venezia Giulia:** Trieste (CU, NHMV). **Trentino-Alto Adige:** Bolzano (as Bozen, NHMV), Cavalese (BB), Collalbo (de Beaumont, 1959), Ortisei (NRS), Trafoi (NHMV).

Japan (Tsuneki 1981): western Hokkaido (Esashi, Hakodate, Jozankei, Kamikawa) and central Hondo (Prefectures: Fukui, Ishikawa, Kyoto, Nagono, Niigata, Saitama, and Yamanashi). Specimens studied: 4 ♀, 4 ♂; KT, TN.

Morocco (1 ♀, 2 ♂): Asni, 1250 m alt. (paratype ♀ of *figulus barbarum,* RMNH), Fez (holotype of *fieuzeti,* IEE), Marrakech (BMNH).

Netherlands (108 ♀, 73 ♂, RMNH if not indicated otherwise): **Drenthe:** Emmen, Erm, Havelte, Sellingen, Wijster, Zuidlaren. **Gelderland:** Apeldoorn (FSAG), Barneveld, Hulshorst, Nijkerk, Putten, Renkum, Vierhouten, Wageningen (GVR, RMNH). **Groningen:** Onnen. **Limburg:** Epen (GVR), Haelen, Heerlen, Helden, Posterholt. **Noord Brabant:** Empel, Helenaveen, Neerijnen, Udenhout, Ulvenhout. **Noord Holland:** Aerdenhout, Hilversum, Laren. **Overijssel:** Heino, Wezepe. **Utrecht:** Baarn, Bilthoven, de Bilt, den Dolder. **Zuid Holland:** Delft (GVR), Hillegersberg, Leiden, Leiderdorp, Loosduinen, Oegstgeest, Rijnsburg, Rotterdam, 's Gravenhage, Warmond.

Norway (1 ♀, 1 ♂): **Buskerud:** Ål (as Aal, DEI). **Oppland:** Lom (RMNH).

Poland (35 ♀, 24 ♂): **Białystok:** Białowieża (as Bialowies, FIS, ZMB), Leńkowo near Grajewo (ZMB). **Bydgoszcz:** Bydgoszcz (as Bromberg, SMT). **Kielce:** Góry Pieprzowe near Sandomierz (CAS), Kielce (TMB), Sandomierz (CAS). **Lublin:** Kazimierz on Wisła River (WJP). **Warszawa:** Podkowa Leśna (CAS). **Wrocław:** Muszkowice near Henryków (WJP), Osola: 25 km NW Wrocław (WJP), Wrocław (CAS, WJP). **Szczecin:** Bielinek (as Bellinchen, ZMB), Międzyzdroje (as Misdroy, ZMB). **Zielona Góra:** Kostrzyń (as Cüstrin, ZMB).

Portugal (2 ♀, 2 ♂): **Douro:** Resende (RMNH). **Estramadura:** Lisboa (RMNH).

Romania (8 ♀, 9 ♂, MGA if not indicated otherwise): **Bacău:** Lacul Bicaz 20 km W Piatra Neamţ (HD). **Braşov:** Sighişoara, Turnisor near Sibiu. **Bucureşti:** Braneşti (WJP), Budeşti. **Constanţa:** Crişan, Hagieni. **Crişana:** Ineu (as Borosjenö, TMB). **Orasul Bucureşti:** Mogosoaia, Pantelimon. **Timişoara:** Eselniţa, Jupalnic near Mehedinţi, Mehadia (NHMV), Orsova (RMNH).

Spain (53 ♀, 51 ♂): **Alicante:** Alicante (KMG), Orihuela (IEE). **Avila** (SFG): Becedas, Gilbuena, Puerto Castilla, Solana de Béjar, Tremedal. **Barcelona:** Canet de Mar (FSAG). **Caceres** (SFG): Baños de Montemayor, Cabezuela del Valle, Gargantilla, La Garganta. **Cadiz:** Algeciras (NHMV). **Ciudad Real:** Ruidera (FJS). **Granada:** Salobreña (VH). **Huesca:** Arguis (RMNH), Torla (FSAG), Valle de Ordesa. **Lerida:** Bohí, Lago di San Mauricio (FSAG). **Logroño:** San Roman de Cameros (IEE). **Madrid:** El Escorial (IEE), Sierra de Guadarrama (IEE). **Salamanca** (SFG): Béjar, Cantagallo, Colmenar de Montemayor, El Cerro, La Cabeza de Béjar, Lagunilla, Montemayor del Rio, Navacarros, Palomares de Béjar, Peñacaballera, Puebla de San Medel, San Medel, Sorihuela, Valdehijaderos, Vallejera de Rio Frio. **Teruel:** Albarracin (KMG, ZSM), Libros (FSAG). **Toledo:** Toledo (RMNH, WJP). **Valencia:** La Eliana (FSAG). **Valladolid:** Olmedo (FJS, WJP), Simancas (RMNH, WJP), Valladolid (FJS, WJP), Villa Báñez (FJS), Villalba de los Alcores (FJS). **Zamora:** Montamarta (FSAG).

Sweden (43 ♀, 40 ♂, NRS if not indicated otherwise): **Dalarna:** Täktbo. **Öland:** Arontorp, Glömminge, Högsrum, Halltorps hage, Mörbylånga, Repplinge, Vickleby. **Östergötland:** St. Anna Korsnäs, Simonstorp. **Skåne:** Åhus, Hälsingborg, Haväng, Höör distr. (BMNH), Torekov (ZMK), Trolleholm, Vitemölla. **Småland:** Hagby, Jönköping, Kalmar, Kalmar Sund (Blå Jungfrun), Söderåkra. **Södermanland:** Häggenäs, Mälarhojden, Mörtö, Tullgarn, Tyresö, Tyresö – Brevik. **Uppland:** Björkö, Håbo – Tibble, Österäker, Rådmansö, Svartsjö, Värmdö, Vassunda.

Switzerland (78 ♀, 41 ♂, NHMB if not indicated otherwise): **Bern:** Adelboden, Bantiger (7 km NE Bern), Bätterkinden, Bern, Büschiwald forest (5 km SSW Bern), Gadmen, Mürren, Signau, Spiez, Wachseldornmoos bog (27 km SE Bern), Zweisimmen, Zwischenflüh (16 km SSW Thun). **Genève:** Genève (MHNG, NHMV), Genthod (NHMV), Peney (MHNG, NHMV). **Graubünden:** Chur (ZSM), Parc National Suisse (MHNG), Somvix, Versam. **Luzern:** Entlebuch Graben (CAS). **Sankt Gallen:** Vättis. **Valais:** Ausserberg (11 km W Brig), Ayel – Zinal (RMNH), Berisal (BMNH, NHMB, NHMV), Chalet à Gobet (BMNH), Champery, Eusegne (as Usegne), Evolène, Haudères, Inden, Lötschental, Martigny, Riederalp (8 km NNE Brig), Saas, Sankt Niklaus, Sierre (NHMV), Simplon (BMNH), Stalden, Verbier (BMNH), Vissoye, Zermatt. **Vaud:** Nyon (MHNG).

Turkey (6 ♀, 3 ♂): **Afyon:** Çay (FSAG). **Ankara:** Ankara (as Angora, TMB), Karagol (BMNH). **Denizli:** Sarayköy (as Seraj-Köj, TMB). **Istanbul:** Sile area (BMNH). **Konya:** Konya (JG). **Kütahya:** Karat Dagi (BMNH). **Samsun:** Köprübaşi (de Beaumont, 1967). **Tokat:** Arguslu above Niksar (BMNH). **Trabzun:** Zigana Dagi (de Beaumont, 1967).

USSR: **Armenian SSR:** Yerevan area (8 ♂, ZMMU). **Azerbaydzhan SSR** (1 ♀): Khanlar (as Helenendorf, NHMV). **Kazakh SSR:** Vostochnokazakhstanskaya obl.: foothills of Azutau Khrebet 18 km N Alekseyevka (1 ♂, VLK); Kalbinskiy Khrebet, 20 km SE Leninka (1 ♀, VLK); 15 km NW Ust'-Kamenogorsk (1 ♂, VLK). **Latvian SSR** (2 ♀, 8 ♂): Wezkukkul, 20 km S Jaunjelgava (ZMB). **Lithuanian SSR** (1 ♀, 2 ♂): Ignalina (DEI). **Russian SSR:** Belgorodskaya oblast: Valuyki (2 ♀, NHMV). Chelabinskaya oblast: Ilmenskiy Zapovednik (1 ♀, ZMMU). Gorno-Altayskaya Avtonomnaya oblast: Uymen River (2 ♂, ZMMU). Ivanovskaya oblast: Kineshma (1 ♀, ZMMU). Karelian ASSR (2 ♀, 1 ♂, HY): Salmi, Sortavala. Kuybyshevskaya oblast: Mirnyi (2 ♀, VLK). Leningradskaya oblast: Solnechnoye (as Ollila, 1 ♂, HY), Streltsovo (as Muola, 1 ♀, HY), Suursari Island (as Hogland, 1 ♂, HY). Karachayevo-Cherkesskaya oblast: Teberda-Dzhamagat (2 ♀, HD). Moskovskaya oblast: Krylatskoe near Moskva (4 ♀, 1 ♂, ZMMU), Moskva (1 ♀, ZMMU), Mytishchi (1 ♂, ZMMU), Zavety Il'icha (1 ♂, ZMMU). Orenburgskaya oblast: Kargala near Orenburg (1 ♀, ZMB). **Ukrainian SSR:** Otuzy Valley in Crimea (2 ♀, 2 ♂, ZMMU), Podgortse E Lvov (as Podhorce, 1 ♀, NHMV), Sebastopol area (1 ♂, ZMMU).

Yugoslavia (11 ♀, 6 ♂): **Croatia:** Plitvice (RMNH), Senj (VH). **Kosovo:** Peč (TMB). **Macedonia:** Mavrovska Valley (RMNH), Ohrid - Resen (RMNH). **Slovenia:** Begunje near Postojna (KS), Kranjska Gora (as Weissenfels, NHMV), Portorož (FIS), Radenci in Mura Valley (near Austrian border, as Radein, NHMV), Vipava (as Wippach, NHMV).

Records (New World) (Krombein 1951:955, 1979:1643; Finnamore 1982:115).—Quebec: Duchesnay (1 ♀, USNM), Ile Perrot (2 ♀, LEM), Lakeside (1 ♀, LEM), Levis (3 ♀, LEM), Montreal (1 ♀, CU; 2 ♂, LEM), Ste. Anne de Bellevue (3 ♀, 6 ♂, LEM), Ste. Annes (1 ♀, 3 ♂, LEM), St. Hilaire (5 ♀, LEM), St. John's Co. (1 ♀, LEM).

Ontario: Ottawa (2 ♀, 2 ♂, CNC), St. Anne's (4 ♀, CNC).

Maine: Bangor (1 ♀, MCZ).

New Hampshire: Glen House (1 ♂, USNM).

Massachusetts: Cambridge (1 ♀, USNM), Dorchester (1 ♀, MCZ), Fall River (1 ♀, USNM), no specific locality (1 ♀, WSU).

Trypoxylon minus de Beaumont

Trypoxylon figulus var. *minus* de Beaumont, 1945:478, ♀, ♂ (as *minor*, incorrect original spelling). Holotype: ♀, Switzerland: Cologny near Geneva (Mus. Zool. Lausanne). — Blüthgen, 1951:234 (var. *minor*); de Beaumont, 1958:206 (forma *minor*), 1959:30 (same); Wolf, 1959:15, 16 (*figulus minus*); Valkeila, 1961:144 (var. *minor*); de Beaumont, 1964a:290, 1964b:84 (forma *minor*), 1965:56 (same), 1967: 338 (same); Bohart and Menke, 1976:346 (ssp. *minor*); Richards, 1980:45 (var. *minor*).

Trypoxylon figulus koma Tsuneki, 1956:28, ♀, ♂. Holotype: ♀, Korea: Mt. Kodai (K. Tsuneki collection, Mishima). **New synonym.** — Bohart and Menke, 1976:346; Tsuneki, 1981: 20.

Trypoxylon figulus medium: Wolf, 1959:fig. b.

Diagnosis.—Most *minus* can be recognized by the presence of a flat, median process emerging from the anteroventral mesothoracic carina (Fig. 5B, C). However, the process is absent in a female and two males from Linz, Austria, and also one of the females from Gonfarons, France, which otherwise do not differ from the remaining *minus* examined. Unlike most *figulus,* the mesopleural setae around scrobe are shorter than the midocellar diameter. In the female, the median clypeal projection is shorter than in *medium*; unlike *figulus* and *medium,* the clypeal free margin is scarcely sinuate or evenly arcuate between the orbit and the projection (Fig. 5A). The female hindcoxal pit is circular or nearly so (Fig. 5D–F), unlike most *figulus.* The maximum length of male flagellomere X is 0.5–0.7 times its width; flagellomere XI is longer than in most *medium*: its maximum length equals 2.2–3.1 times its basal diameter. Body length 6–9 mm in female, 5–7.5 mm in male.

Variation.—In most females, the free margin of the clypeal projection is emarginate, but it is entire in a female from Finland, one from France and one from Sweden.

In most males, the maximum length of flagellomere X is 0.6–0.7 times its width, and the maximum length of flagellomere XI is 2.2–2.4 times the basal diameter. These ratios are 0.8 and 2.6, respectively, in some males from Belgium, 0.6 and 2.6 in the single male examined from Sardinia, 0.8 and 3.0 in the single male from Corsica, and 0.5 and 3.1 in the single male from Gerona, Spain.

Life History.—A female from Elender Wald, Austria (NHMV), was reared from a gall of *Andricus kollari* (Hartig). I was unable to find this locality.

Geographic Distribution (Fig. 5).—Palearctic Region between western Europe and Korea, north to about 64°N in Norway and Sweden and about 67°N in Finland, south to northern Mediterranean countries including Sardinia and Sicily, northern Turkey and southern Kazakh SSR. Unknown from Great Britain and North Africa. The absence of this species in Great Britain suggests that it reached northwestern Europe only recently, after separation of the British Isles from the continent.

Records.—Austria (41 ♀, 52 ♂, NHMV if not indicated otherwise): **Burgenland:** Breitenbrunn (JG), Donnerskirchen on Neusiedlersee (KS), Mogersdorf (JG), Mörbisch: 5 km S Rust (RMNH). **Kärnten:** Bleiberg (RMNH), Mallnitz (ZMB), Waidisch bei Ferlach (FSAG). **Niederösterreich:** Anninger, Bisamberg near Vienna, Brühl, Dornbach, Hainbach, Hainsburg

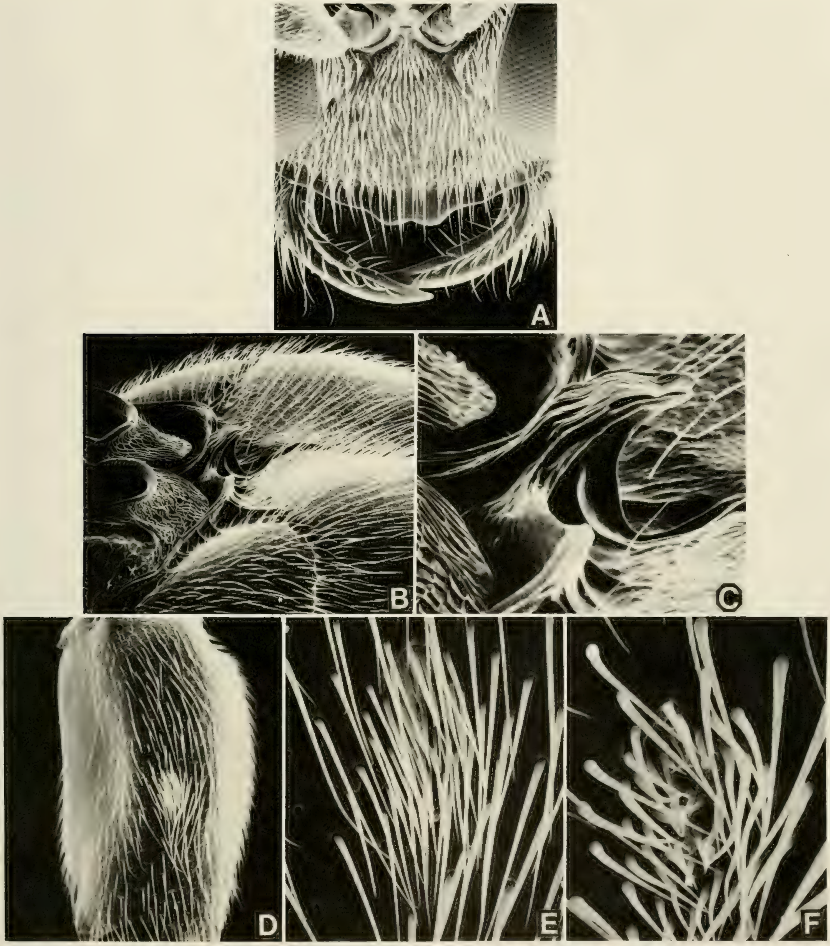


FIGURE 5. *Trypoxon minus:* A—female clypeus, B—mesothoracic venter, C—anteroventral mesothoracic process, D—female hindcoxa ventrally, D—female hindcoxal pit, vertical view, E—same, oblique view.

(ZMB), Kahlenberg near Vienna, Neunkirchen (FSAG, JG), Piesting, Purgstall (JG), Schneeberg, Traismauer, Wien (Prater). **Oberösterreich:** Almsee (NHMV), Gutau (JG), Innerbreitenau (JG), Kremsmünster (FSAG), Linz (HY, JG, NHMV), Rutzing bei Hörsching (JG), Sarleinsbach, Zeissberg bei Freistadt (FSAG, JG), Zellhof bei Bad Zell (JG). **Salzburg:** Salzburg (BMNH, FSAG). **Steiermark:** Admont (FSAG), Gleichenberg (JG), Riegersburg (JG), Tragöss-Oberort (DBB), Weinburg (JG). **Tirol:** Huben (ZMB), Innsbruck, Kals (RMNH), Stubai (WJP), Wenns (BMNH), Zwieselstein in Ötztal.

Belgium (348 ♀, 379 ♂, FSAG if not indicated otherwise): **Brabant:** Berchem-Sainte-Agathe, Groenendael, Monstreux, Rhode-Saint-Genèse, Rixensart, Tilly, 't Roth (RMNH), Woluwe-Saint-Pierre. **Hainaut:** Gilly, Gosselies, Lobbes-Calvaire, Quaregnon. **Liège:** Bleyberg, Chaudfontaine, Clermont-sur-Berwinne, Dalhem, Embourg, Esneux, Forêt de Grunhault, Fouron-Saint-Pierre, Hergenrath, Herstal, Jupille, Liège, Queue-du-Bois, Remersdael, Spa, Xhendelesse, Wandre. **Limburg:** Bassenge, Eben, Kanne, Sint Pietersberg (RMNH), Tongres, Wonck. **Luxembourg:** Bodange, Chatillon, Les Epioux. **Namur:**

FIGURE 6. *Trypoxylon minus:* geographic distribution.

Beauraing, Couvin, Felenne, Gembloux, Gesves, Jambes, La Plante, Malonne, Mont-Gauthier, Namur, Saint Marc, Willerzie, Yvoir. **West-Vlaanderen:** Sint Pieter.

Bulgaria (1 ♂): Chepalare Pass in Rhodope Mts. (ZMT).

Czechoslovakia (4 ♀, 4 ♂): **Jihomoravsky Kraj:** Vranov W Znojmo (as Frain, NHMV). **Vapadoslovensky Kraj:** Štúrovo (HD, SMT).

Denmark (2 ♀, ZMK): **Maribo:** Lolland Island: Roden Skov. **Vejle:** Klattrup.

Finland (105 ♀, 124 ♂, HY if not indicated otherwise): **Abo:** Perniö (AKM), Rymättylä (AKM), Särkisalo (AKM), Turku (AKM). **Alandia:** Eckerö (AKM, HY, ZMK), Finström (AKM), Geta (ZMK), Hammarland, Lemland. **Karelia Australis:** Virolahti. **Karelia Borealis:** Herajoki on Pielinen Lake (ZMK), Kesälahti, Kitee (AKM, HY), Polvijärvi (AKM), Tohmajärvi. **Karelia Ladogensis:** Parikkala, Simpele. **Kuusamo:** Perä Posio. **Lapponia Kemensis:** Sodankylä. **Nylandia:** Helsinki, Pernaja (as Pärnå). **Ostrobottnia Australis:** Koivulahti. **Ostrobottnia Borealis:** Räväsjärvi, Rovaniemi. **Ostrobottnia Media:** Siikajoki. **Satakunta:** Loimaa (AKM), Suoniemi. **Savonia Australis:** Lappeenranta, Rautjärvi. **Tavastia Australis:** Aitolahti, Hämeenlinna, Hattula, Janakkala, Kalvola, Kangasala, Lahti (AKM), Lammi, Luopioinen (AKM), Pälkäne, Pirkkala (as Birkkala), Somero (AKM), Tyrväntö, Vanaja, Ylöjärvi.

France (24 ♀, 17 ♂): **Basses-Alpes:** Allos (FSAG), Annot (FSAG), Colmars (FSAG), La Javie (FSAG), Peyresq (FSAG), Saint-André-les-Alpes (FSAG). **Corse:** Bonifacio (KMG), Col de Sorba (KMG). **Drome:** Dieulefit (RMNH). **Haute Savoie:** Chamonix (RMNH). **Haut-Rhin:** Rouffach (FSAG). **Loiret:** Lorris (RMNH). **Lozère:** Sainte Enimie (BMNH). **Nièvre:** Nevers (RMNH). **Puy-de-Dôme:** Beaune (FSAG, ZMK), Besse (BMNH). **Pyrenées-Orientales:** Vinça (VH). **Var:** Gonfarons (FSAG).

Germany, Democratic (33 ♀, 20 ♂, DEI if not indicated otherwise): **Berlin:** Berlin-Borgsdorf (HD). **Dresden:** Freital (SMT), Gersdorf near Kamenz (SMT), Moritzburg (SMT). **Erfurt:** Nordhausen area (HD). **Frankfurt:** Eberswalde area (DEI, HD), 20 km NW Eisenhüttenstadt (HD), Schönwalde near Berlin (HD). **Gera:** Beutnitz bei Jena. **Halle:** Halle (DEI, ZMB), Kyffhäuser (DEI, ZMB). **Karl-Marx-Stadt:** Freiberg. **Leipzig:** Dornreichenbach near Wurzen, Leipzig, Reglitz bei Schkeuditz. **Magdeburg:** Haldensleben, Stapelburg (ZMH). **Neubrandenburg:** Serrahn near Neustrelitz (HD), Teterower See (HD). **Rostock:** Rostocker Heide. **Schwerin:** Perleberg, Schwann near Güstrow.

Germany, Federal (59 ♀, 42 ♂): **Baden-Württemberg:** Enzklösterle (KS), Grötzingen (KS), Heidelberg (BMNH), Kaiserberg (ZMH), Kaiserstuhl (ZMB), Karlsruhe (KS, ZMH), Küssaberg (KS), Tübingen (KS), Windenreute near Emmendingen (ZMB). **Bayern:** Aschaffenburg (VH), Balderschwang (KS), Karlstadt am Main (KS), Lohr am Main (KS), Mainfranken (FIS), Miltenberg (FIS), München (ZSM), Oberau in foothill of Ammer Mts. (KMG), 32 km S Würzburg (RMNH). **Hessen:** Dillenburg (HW, WJP), Fulda (VH), Marburg (HW, WJP), Taunus (KS). **Rheinland-Pfalz:** Bad Münster am Stein (KS), Burgen an der Mosel (TMB), Donnersberg, Mainz (KS). **Niedersachsen:** Sage: 25 km S Oldenburg (VH). **Schleswig Holstein:** Lütjenburg (KS), Russee near Kiel (VH), Schierensee SW Kiel (VH). **Westfalen:** Plettenberg (HW), Siegen (HW).

Greece (2 ♀, 2 ♂): **Ionian Islands:** Isle de Levkas (as Lefkas, BMNH). **Sterea Ellas:** Timfristos (KMG).

Hungary (1 ♀, 1 ♂): Balaton (HD).

Italy (23 ♀, 14 ♂): **Abruzzi:** Scanno (KMG). **Emilia-Romagna:** Bologna: Pracchia (RMNH), Ronzano (NHMV); Modena: Zocca: Montetortore (NHMV). **Friuli-Venezia Giulia:** Gemona (JG), Prosecco (NHMV), Tarvisio (NHMV). **Lombardia:** Varese: Mercallo (MSNM). **Piemonte:** Borgomale (GP), Castelnuovo in Asti (GP), Chianale (GP), Condove (GP), San Benedetto Belbo ca 20 km S Alba (GP), Val d'Angrogna in Alpi Cozie (1 ♀, det. J. de Beaumont, WJP), Vinovo 10 km S Torino (GP). **Sardegna:** Aritzo (BMNH), Desulo (BMNH). **Sicilia:** Piano Battaglia (KMG). **Trentino-Alto Adige:** Colle Isarco (MSNM), Merano (as Meran, FSAG). **Valle d'Aosta:** Buthier (ZMB). **Veneto:** Padova (de Beaumont, 1959). **Venezia Giulia:** Trieste (NHMV).

Korea: **North Korea:** Mt. Kodai near 38th parallel (Tsuneki, 1956, 1981), Mt. Sombo near 38th parallel (1 ♀, 1 ♂). **South Korea:** Seoul (Tsuneki, 1956, 1981).

Netherlands (5 ♀, 9 ♂, RMNH unless indicated otherwise): **Limburg:** Elkenrade, Epen, Maastricht, Slenaken, Vijlener Bosch (GVR). **Noord Brabant:** Empel. **Zuid Holland:** Leiden.

Norway (11 ♀, 19 ♂): **Akerhus:** Oslo (as Kristiania, ZMUB). **Hordaland:** Granvin (ZMUB). **Nord Trøndelag:** Røra (FSAG). **Oppland:** Lom (RMNH). **Sogn og Fjordane:** Balestrand (ZMBU). **Vestagder:** Kristiansand (ZMUB). **Vestfold:** Herstad (ZMUB).

Poland (7 ♀, 13 ♂): **Białystok:** Białowieża (as Bialowies, ZMB). **Kraków:** Ojców (SMT), Pieniny Mts. (WJP). **Wrocław:** Karkonosze Mts. (as Riesengebirge, ZMB), Osola: 25 km NW Wrocław (WJP), Rościsławice (WJP), Sobótka: 35 km S Wrocław (WJP), Wrocław (CAS), 10 km NE Wrocław (WJP). **Rzeszów:** Jarosław (CAS).

Portugal (1 ♀): **Douro:** Resende (RMNH).

Romania (6 ♀, 3 ♂, MGA if not indicated otherwise): **București:** Ciolpani, Periş, Videle (WJP). **Constanța:** Babadag. **Ploești:** Valea Longă-Gorgota. **Timişoara:** Eşelniţa, Ogradina, Orşova.

Spain (2 ♀, 4 ♂): **Gerona:** Gerona (BMNH). **Huesca:** Sierra de Oroel (FSAG), Valle de Ordesa (FIS). **Salamanca:** Horcajo de Montemayor (SFG), Valdehijaderos (SFG).

Sweden (34 ♀, 44 ♂, NRS if not indicated otherwise): **Bohuslån:** Ljung. **Dalarna:** Ludvika, Nås, Stora Kopparberg, Täktbo. **Gästrikland:** Sandviken. **Gotland:** Fardume Träsk E Lärbro (ZMK), Visby, St. Karlsö. **Jämtland:** Undersåker. **Närke:** Örebro. **Öland:** Halltorps hage, Högsrum, Räpplinge. **Skåne:** Höör distr. (BMNH), Skäralid, northern Skåne (BMNH). **Östergötland:** Kvarsebo, Norrköping, Simonstorp. **Småland:** Barkeryd, Höreda, Järsnas, Ljungarum. **Södermanland:** Flisby, Runmarö, Tullgarn, Tyresö - Svartöcken. **Uppland:** Harparbol, Rådmansö, Stockholm, Uppsala (HY), Vassunda, Vira bruk. **Västerbotten:** Händene. **Västmanland:** Sala.

Switzerland (21 ♀, 26 ♂, NHMB if not indicated otherwise): **Bern:** Bätterkinden, Bern, Burgdorf, Grauholz forest (up to 9 km NNE Bern), Wachseldornmoos bog (27 km SE Bern). **Engadin:** Zuoz (AWE). **Genève:** Genève Cologny (BMNH), Genthod (NHMV), Peney (MHNG). **Graubünden:** Parc National Suisse (de Beaumont, 1958), Somvix. **Tessin:** Lugano (FSAG). **Valais:** Binntal (15 km NE Brig), Grimentz (FSAG, RMNH), St. Luc (RMNH), Simplon (BMNH), Zermatt (RMNH). **Vaud:** Nyon (MHNG). **Zürich:** Wädenswil.

Turkey (1 ♀, 2 ♂): **Artvin:** Artvin, Berta (BMNH). **Istanbul:** Belgrat Orman (de Beaumont, 1967). **Samsun:** Bafra (BMNH).

USSR: **Georgian SSR:** Bakuriani (1 ♀, ZMMU). **Kazakh SSR:** Chimkent, 2000 m (1 ♂, WJP); Razdolnyi area, 50°43′N, 81°06′E (1 ♂, VLK), Zapovednik Aksu-Dzhabagly (1 ♀, ZMMU). **Kirghiz SSR:** Arkit in Chatkalskiy Khrebet (1 ♂, ZMMU). **Russian SSR:** Karelian ASSR: ozero Tumas (as Kolatselka, 1 ♀, HY). Kemerovskaya oblast: 60 km SE Novokuznetsk (1 ♂, VLK).

Leningradskaya oblast: Kondratyevo W Vyborg (as Säkkijärvi, 1 ♀, HY). Moskovskaya oblast: Mytishchi (1 ♂, ZMMU). Permskaya oblast: Nizhnyaya Kurya, 15 km W Perm (3 ♀, 2 ♂, WJP). **Ukrainian SSR:** Crimea: Krymskiy Zapovednik (1 ♂, ZMMU).

Yugoslavia (4 ♀, 3 ♂): **Croatia:** Plitvice (RMNH), Skrad (GP). **Slovenia:** Bled (RMNH), Cerknica (KS), Logatec (as Loitsch, ZMH), Opčina Mtn. on Italian border E Triest (NHMV). **Serbia:** Draževac (FSAG).

Trypoxylon medium de Beaumont

Trypoxylon figulus var. *medium* de Beaumont, 1945:477, ♀, ♂ (as *media*, incorrect original spelling). Holotype: ♀, Switzerland: Martigny (Mus. Zool. Lausanne). — Blüthgen, 1951: 234 (var. *media*); de Beaumont, 1958:206 (forma *media*), 1959:30 (same); Wolf, 1959:15, 16 (*figulus medium*); Valkeila, 1961:144 (var. *media*); de Beaumont, 1964a:290, 1964b:84 (forma *media*), 1965:56 (same), 1967:338 (same); Bohart and Menke, 1976:346 (ssp. *medium*); Lomholdt, 1976:267 (*figulus media*); Richards, 1980:45 (var. *media*); Tsuneki, 1981:19 (*medium*).

Trypoxylon figulus minus var. *rubi* Wolf, 1959:15, ♂. ! Lectotype, ♂, Federal Germany: Plettenberg (coll. H. Wolf, Plettenberg), **present designation.** Synonymized by de Beaumont, 1964:291.

Trypoxylon figulus minus: Wolf, 1959:fig. c.

Diagnosis.—There is no single character by which *medium* can be distinguished from both *figulus* and *minus.* The anteroventral mesothoracic carina is either straight or sinuate and curved posterad mesally, but unlike that of most *minus* it is not expanded into a process. Unlike those of most *figulus,* the mesopleural setae around the scrobe are shorter than the midocellar diameter. In the female, the clypeal free margin is evenly concave between the orbit and median projection (Fig. 7A), unlike that of *minus* and most *figulus,* and the setae of the hindcoxal pit form a curious channel-like structure visible only under high magnifications (Fig. 7C, D) and which has not been found in the other two species. The hindcoxal pit is circular (Fig. 7B) instead of oblong (as it is in most *figulus*). The maximum length of male flagellomere X equals 0.75–0.9 of its basal diameter (the highest ratios are observed in specimens in which the flagellomere XI is the longest); the maximum length of flagellomere XI is usually 2.0–2.2 times its basal diameter (2.2–3.6 in *figulus* and *minus*). However, the flagellomere XI length is 2.4 times its basal diameter in some specimens, e.g., in a male from Horsell, England (KMG), or a male from Uilac, Romania; such specimens differ externally from *figulus* in having a shorter mesopleural vestiture and a longer flagellomere X. Gonoforceps with ventroexternal expansion at about midlength (Fig. 7E, F); expansion absent in *figulus* and *minus.* Body length 6.5–12 mm in female, 6.0–8.5 mm in male.

Life History.—Several specimens of *medium* (seen by me) were reared from *Rubus* twigs (Wolf, 1959). A male was reared from an old gall of the chloropid fly *Lipara lucens* Meigen containing a vacated nest of the bee *Hylaeus pectoralis* Förster (England, Hampshire, Browndown, G. R. Else collector, BMNH).

Geographic Distribution (Fig. 8).—Western and central Palearctic Region between Great Britain and eastern Kazakh SSR, north to southern England and beyond the Arctic Circle in Finland, south to northern Mediterranean countries including Mallorca, Crete, and Cyprus, as well as Turkey, Syria, Israel, and northern Iran. Unknown from Iberian Peninsula and North Africa.

Records.—Austria (30 ♀, 20 ♂, NHMV if not indicated otherwise): **Burgenland:** Andau (RMNH), Jois (JG), Donnerskirchen an Neusiedlersee (KS), Neusiedl (KS, NHMV, ZMB), Panzergraben an Neusiedlersee (JG), Winden (JG), Zurndorf (AWE, RMNH). **Niederösterreich:** Bisamberg near Vienna, Deutsch Altenburg (ZMB), Donauauen near Vienna (ZMH), Hainburg (ZMB), Herzograd (JG), Marchfeld (JG), Oberweiden (DBB), Piesting, Schneeberg, Stammersdorf (DBB), Wien-Türkenschanze. **Oberösterreich:** Gutau (JG). **Salzburg:** Katchenberghöhe (VH), Salzburg (BMNH). **Tirol:** Galtür (BMNH), Huben (ZMB), Innsbruck, Kraspes (DEI), 1 km SW Zwieselstein. **Voralberg:** Bielerhöhe.

Belgium (11 ♀, 17 ♂, FSAG): **Antwerpen:** Geel. **Liège:** Liège, Montzen, Spa, Wandre. **Limburg:** Bree, Eben, Lummen. **Luxembourg:** Chatillon, Les Epioux, Torgny. **Namur:** Eprave, Ferage, Mont-Gauthier.

Bulgaria (1 ♀): Ruse (SMT).

Cyprus (3 ♀, 6 ♂): Amathus (FSAG, RMNH), Paphos (KMG).

Czechoslovakia (1 ♀, 2 ♂): **Jihočesky Kraj:** Prachatice (as Prachatitz, NHMV). **Vapadoslovensky Kraj:** Štúrovo (SMT).

Denmark (11 ♀, 8 ♂, ZMK, if not indicated otherwise): **Bornholm:** Arnager. **Frederiksborg:** Hulerød, Humblebæk (S Helsingør), Tisvilde Hegn. **Hjørring:** Fauerholt Hede (ca 10 km W Frederikshavn), Skoven on Læse Island. **Maribo:** Kristianssæde Skov on Lolland Island. **Randers:** Glatved Strand and Kalø on Djursland Peninsula, Mols Bjerge. **Ribe:** Børsmose, Ho Plantage. **Svendborg:** Keldsnor on Langeland Island. **Thisted:** Bagsø at Nors (ca 7 km NW Thisted). **Tønder:** Rømø Island (RMNH), Stensbæck Plantage.

Finland (18 ♀, 15 ♂, HY if not indicated otherwise): **Abo:** Perniö (AKM), Rymättylä (AKM). **Alandia:** Finström (AKM), Hammarland. **Karelia Australis:** Virolahti. **Karelia Borealis:** Nurmes. **Kuusamo:** Kuusamo (ZMK). **Lapponia Inarensis:** Ivalo. **Nylandia:** Hyvinkää. **Ostrobottnia Media:** Paavola. **Tavastia Australis:** Hämeenlinna, Hattula, Janakkala, Pälkäne, Somero (AKM), Vanaja.

France (24 ♀, 8 ♂, FSAG if not indicated otherwise): **Aisne:** Liesse. **Alpes Maritimes:** Aurons (AWE). **Aube:** bois de Lignières. **Aveyron:** Creissels. **Basses-Alpes:** Annot, Montagne de Lure (ZMK), Peyresque. **Dordogne:** Paunat. **Drôme:** Dieulefit (RMNH). **Haute-Loire:** Pont de Sumène. **Haut-Rhin:** Rouffach. **Hautes-Alpes:** Saint-Véran. **Hérault:** Canet (BMNH).

FIGURE 7. *Trypoxylon medium:* A—female clypeus, B—female hindcoxa ventrally, C—female hindcoxal pit, vertical view, D—same, oblique view, E—male genitalia (arrow: area shown in F), F—same, process of gonoforceps.

Landes: Mont-de-Marsan (MHNG), Parentis (KMG), St. Girons - Plage (RMNH). **Moselle:** Orny, Sierck. **Pyrenées-Orientales:** La Llagonne - Mont Louis (VH). **Var:** Saint-Tropez, Valescure (KMG). **Vaucluse:** Carpentras (RMNH).

Germany, Democratic (15 ♀, 6 ♂): **Berlin:** Berlin (BMNH, DEI, ZMB), Spandau (ZMB). **Cottbus:** Luckau (DEI). **Dresden:** Gersdorf near Kamenz (SMT). **Frankfurt:** Buckow (ZMB), Eberswalde area (DEI), Störitzsee near Berlin (DEI). **Halle:** Bad Frankenhausen near Kyffhäuser (HD), Halle (DEI), Kattenburg near Kyffhäuser (HD), Kyffhäuser (DEI). **Potsdam:** Gross Machnow (ZMB).

Germany, Federal (25 ♀, 34 ♂): **Baden-Württemberg:** Federsee (KS), Kaiserberg (ZMH), Kaiserstuhl (VH, ZMB), Karlsruhe (ZMH), Radolfzell (ZMH). **Bayern:** Balderschwang (KS), Kreuth in Oberbayern (ZMB), Mainfranken (FIS), Miltenberg (FIS), Obersdorf in Allgau (ZMB), Sondershausen (ZMH). **Hessen:** Dillenburg (HW, WJP), Marburg (HW). **Niedersachsen:** Dörpen: 14 km SW Papenburg (VH), Norderney Island

FIGURE 8. *Trypoxylon medium:* geographic distribution.

(VH). **Nordrhein-Westfalen:** Krefeld (DEI), Plettenberg (including lectotype and 2 paralectotypes of *rubi*, HW, WJP), Siegen (HW). **Rheinland-Pfalz:** Bad Münster am Stein (KS), Mainz (KS).

Great Britain (53 ♀, 44 ♂, BMNH if not indicated otherwise): **Buckingham:** Slough. **Devon:** Bovey Tracey, Braunton. **Dorset:** Chideock, Wareham. **Gloucester:** Stroud (Rodborough). **Hampshire:** Basingstoke, Bramdean, Browndown, Fareham, Hurn, Stockbridge. **Isle of Wigt:** Alum Bay, Sandown, St. Helen's. **Kent:** Cobham, Darenth, Pluckley (KMG). **London:** Mill Hill, Ruislip (KMG), Uxbridge. **Oxford:** Goring. **Surrey:** Chobbham (KMG), Ewell (DBB), Horsell. **Sussex:** Findon, Midhurst (Ambersham Common), Singleton (The Trundle).

Greece (1 ♀, 1 ♂): **Crete:** Kato Metokhi (ZMB). **Peloponnesus:** Mega Spilaion (de Beaumont, 1965). **Sterea Ellas:** Kifissia (KMG).

Hungary (2 ♀, 1 ♂): **Pest:** Ocsa (TMB). **Tolna:** Simontornya (NHMV).

Iran (1 ♀): Gorgan, Shaskola Forest (JG).

Israel (3 ♀): Baniass (KMG), Eshtaol: Kesalon Valley (KMG).

Italy (19 ♀, 7 ♂): **Emilia-Romagna:** Modena: Zocca: Montetortore (NHMV). **Lazio** (Frosinone): Pontecorvo (NHMV), Roma (4 ♀, det. J. de Beaumont, WJP). **Liguria:** Genova (MSNM), San Remo (GP). **Lombardia** (Varese): Mercallo (MSNM). **Piemonte:** San Benedetto Belbo ca 20 km S Alba (GP). **Trentino-Alto Adige:** Bolzano (as Bozen, NHMV), Cavalese (BB), Merano (as Meran, ZSM), Predazzo (ZMB). **Veneto:** Colli Euganei: Montegrotto Terme (WJP), Garda (FSAG), Jesolo (FSAG), Lido di Venezia (de Beaumont, 1959). **Venezia Giulia:** Trieste (ZMH).

Netherlands (14 ♀, 10 ♂, RMHN if not indicated otherwise): **Drenthe:** Emmen, Exloo, Mantinge. **Gelderland:** Ede (GVR), Kootwijk, Hulshorst. **Limburg:** Heerlen. **Noord Brabant:** Griendtsveen, Helenaveen, Udenhout, Waalwijk. **Noord Holland:** Hilversum. **Utrecht:** den Dolder.

Norway (4 ♀, 5 ♂): **Hordaland:** Granvin (ZMUB). **Sogd og Fjordane:** Balestrand (ZMUB). **Sør-Trøndelag:** Osen district (FSAG).

Poland (1 ♂): **Szczecin:** Międzyzdroje (as Misdroy, ZMB).

Romania (9 ♀, 18 ♂, MGA if not indicated otherwise): **Braşov:** Uilac. **Bucureşti:** Valea Rosie near Olteniţa. **Constanţa:** Babadag (RMNH), Caraorman, Crişan, Gorgova in Danube Delta (HD), Periprava, Valu lui Traian. **Oradea:** Oradea (RMNH). **Ploeşti:** Valea lui Bogdon near Sinaia.

Spain (1 ♀): Mallorca (DEI).

Sweden (22 ♀, 10 ♂, NRS): **Äsele Lappmark:** Saxnäs. **Blekinge:** Ronneby. **Bohuslan:** Ljung. **Dalarna:** Falun. **Gotland:** Fardume, Fårö, Stånga. **Hälsingsland:** Järvsö. **Jämtland:** Storlien. **Öland:** Högby, Mörbylånga, Vickleby. **Skåne:** Ivö, Stenshuvud. **Småland:** Kalmar Sund (Blå Jungfrun). **Uppland:** Bogesund, Danderyd. **Västergötland:** Österplana hed. **Västmanland:** Skinnskatteberg.

Switzerland (20 ♀, 20 ♂, NHMB if not indicated otherwise): **Bern:** Bern, Biel. **Genève:** Bois d'Onex (MHNG), Genthod (NHMB, RMNH), Peney (MHNG). **Graubünden:** Chur (ZSM), Parc National Suisse (de Beaumont, 1958), Scanfs, Somvix. **Valais:** Binntal (15 km NE Brig), Grimentz (RMNH), Lötschental, Martigny (BMNH), Saar Fee (BMNH), Sierre (NHMV), Simplon (BMNH), Zermatt (RMNH). **Vaud:** Nyon (MHNG).

Syria (1 ♂): Damascus (NHMV).

Turkey (4 ♀, 9 ♂): **Amasya:** Amasya (BMNH). **Antakya:** Antakya (de Beaumont, 1967). **Antalya:** Antalya (BMNH), Finike (de Beaumont, 1967), Finike-Kaş road (BMNH). **Bursa:** Uludag (BMNH). **Kastamonu:** Kastamonu area (BMNH). **Mersin:** Gözne (BMNH), Mut (JG). **Mugla:** near Köycegiz (BMNH), Marmaris (BMNH). **Samsun:** Samsun area (BMNH).

USSR: **Armenian SSSR:** Noyembryan (3 ♂, ZMMU). **Georgian SSR** (2 ♀, ZMMU): Leselidze, Yermolovskoye near Gagra. **Kazakh SRR** (7 ♀, 14 ♂, VLK if not indicated otherwise): Almaatinskaya oblast: 12 km W Alma Ata; Ili river 60 km E Ili (now Kapchagai); Kargalinka, 5 km SW Alma Ata; Malaya Almaatinka River in Zailiyskiy Alatau (ZMMU), 25 km S Turgen village in Zailiyskiy Alatau. Semipalatinskaya oblast: 30 km SE Georgyevka; Tarbagatai Khrebet foothills 6 km N Irinovka (which is 47°09′N, 81°53′E); 12 km N Zharma. Vostochnokazakhstanskaya oblast: Baighym Canyon in Narymskiy Khrebet; Kalbinskiy Khrebet 20 km SW Leninka; Kendyrlik river 15 km E Zaysan; 5 km N Oktyabrskiy in Ulbinskiy Khrebet; 15 km NE Ust'-Kamenogorsk; 15 km SSW Ziryanovsk; 28 km SSE Ziryanovsk. **Russian SSR:** Bashkirskaya Avtonomnaya oblast: Kazmash (1 ♂, ZMMU). Belgorodskaya oblast: Valuyki (1 ♂, NHMV). Leningradskaya oblast: Primorsk (as Koivisto, 1 ♀, AKM). Saratovskaya oblast: Kuznetsk (1 ♀, ZMMU). **Ukrainian SSR:** Crimea (1 ♀, 2 ♂, ZMMU): Karadag, Sebastopol.

Yugoslavia (6 ♀, 1 ♂): **Croatia:** Poreč (FSAG), Puli (as Pola, NHMV), Rab Island (as Arbe, TMB). **Kosovo:** Brezovica in Šar Mts. (TMB), Peč (TMB). **Serbia:** Draževac (FSAG), Šid (FSAG). **Slovenia:** Portorož (FIS).

LITERATURE CITED

BOHART, R. M., AND A. S. MENKE. 1976. Sphecid wasps of the world: a generic revision. University of California Press, Berkeley, Los Angeles, London. i–ix + 695 pp.

BLÜTHGEN, P. 1951. Neues oder Wissenswertes über mitteleuropäische Aculeaten und Goldwespen II. (Hym.). Bonner Zool. Beitr. 2:229–34.

CRESSON, E. T. 1928. The types of Hymenoptera in the Academy of Natural Sciences of Philadelphia other than those of Ezra T. Cresson. Mem. Amer. Ent. Soc. 5:1–90.

DAY, M. 1979. The species of Hymenoptera described by Linnaeus in the genera *Sphex, Chrysis, Vespa, Apis* and *Mutilla*. Biol. J. Linn. Soc. 2:45–84.

DE BEAUMONT, J. 1945. Notes sur les Sphecidae (Hym.) de la Suisse. Première série. Mitt. Schweiz. Ent. Ges. 19:467–81.

———. 1957 (1956). Hyménoptères récoltés par une mission Suisse au Maroc (1947). Sphecidae 4. Bull. Soc. Sci. Nat. Phys. Maroc 36:139–64.

———. 1958. Ergebnisse der wissenschaftlichen Untersuchungen des schweizerischen Nationalparks, 6 (N. F.), 40. Les Hyménoptères Aculéates du Parc National Suisse et des régions limitrophes: 145–233, 1 map.

———. 1959. Sphecidae italiens de l'Institut National d'Entomologie de Rome (Hymenoptera). Fragm. Ent. 3:1–46.

———. 1964a. Notes sur les Sphecidae (Hym.) de la Suisse. Deuxième série. Mitt. Schweiz. Ent. Ges. 36:289–302.

———. 1964b. Insecta Helvetica. Fauna 3. Hymenoptera: Sphecidae. Imprimerie La Concorde, Lausanne. 169 pp.

———. 1965. Les Sphecidae de la Grèce (Hym.). Mitt. Schweiz. Ent. Ges. 38:1–65.

———. 1967. Hymenoptera from Turkey. Sphecidae, I. With Appendix. Sphex Linne, Subgenus *Palmodes* Kohl par P. Roth. Bull. Brit. Mus. (Nat. Hist.) Ent. 19:251–382.

Finnamore, A. 1982. The Sphecoidea of southern Quebec (Hymenoptera). Lyman Ent. Mus. Res. Lab. Mem. 11:1–348.

Fox, W. J. 1891. On the species of *Trypoxylon* inhabiting America north of Mexico. Trans. Amer. Ent. Soc. 18:136–48, pl. III.

Giner Marí, J. 1959. Himenópteros del Marruecos frances. Fams. Sphecidae, Psammocharidae y Mutillidae (s. 1.). Eos 35:385–403.

Higgins, L. G. 1963. Entomologia Carniolica: J. A. Scopoli, 1763. J. Soc. Bibliogr. Nat. Hist. 4:167–96.

Jurine, L. 1807. Nouvelle méthode de classer les Hyménoptères et les Diptères. J. J. Paschoud, Genève. 320 pp., 14 pl.

Kohl, F. F. 1883. Die Fossorien der Schweiz. Mitt. Schweiz. Ent. Ges. 6:647–84.

Krombein, K. V. 1951. Subfamily Trypoxyloninae, p. 954–957. *In,* C. W. F. Muesebeck, K. V. Krombein and H. K. Townes. Hymenoptera of America north of Mexico. Synoptic Catalog, United States Department of Agriculture. Agriculture Monograph No. 2. Washington, D.C. 1420 pp.

———. 1979. Superfamily Sphecoidea, p. 1573–1740. *In,* K. V. Krombein, P. D. Hurd, D. R. Smith and B. D. Burks. Catalog of Hymenoptera in America north of Mexico, Volume 2. Apocrita (Aculeata). Smithsonian Institution Press, Washington, D.C. i–ix + 1199–2209.

Latreille, P. A. 1802. Histoire naturelle générale et particulière des Crustacés et des Insectes, 3. Imprimerie de F. Dufart, Paris. 467 pp.

Linnaeus, C. 1758. Systema Naturae, 10th Edition, 1. Laurentii Salvii, Holmiae. 823 pp.

Lomholdt, O. 1975–1976. The Sphecidae (Hymenoptera) of Fennoscandia and Denmark. *In,* Fauna Entomologica Scandinavica, 4, part 1:224 (1975), part 2:225–452 (1976). Scandinavian Science Press, Klampenborg, Denmark.

Pate, V. S. L. 1943. On some Holarctic sphecoid wasps (Hymenoptera: Aculeata). Bull. Brooklyn Ent. Soc. 38: 14–16.

Richards, O. W. 1980. Handbooks for identification of British insects, 6, Part 3(b): Scolioidea, Vespoidea and Sphecoidea. Hymenoptera Aculeata, Roy. Ent. Soc. London, London, 118 pp.

Rogenhofer, A., und K. W. von Dalla Torre. 1882. Die Hymenopteren in I. A. Scopoli's Entomologia Carniolica und auf den dazugehörigen Tafeln. Verh. Zool. Bot. Ges. Wien 31:593–604.

Sandhouse, G. A. 1940. A Review of the Nearctic wasps of the genus *Trypoxylon* (Hymenoptera: Sphecidae). Amer. Midland Nat. 24:133–76.

Scopoli, A. 1763. Entomologia Carniolica. Typis Ioannis Thomae Trattner, Vindobonae. 420 pp. (see also Higgins, 1963).

Tsuneki, K. 1956. Die Trypoxylonen der nordöstlichen Gebiete Asiens (Hymenoptera, Sphecidae, Trypoxyloninae). Mem. Fac. Liberal Arts, Fukui Univ., Ser. II, Nat. Sci. No. 6:1–42, pl. I–IV.

———. 1981. Revision of the *Trypoxylon* species of Japan and northeastern part of the Asiatic continent, with comments on some species of Europe (Hymenoptera, Sphecidae). Spec. Publ. Japan Hymenopt. Assoc. 17:1–92.

Valkeila, E. 1961. Beiträge zur Kenntnis der nordeuropäischen Grabwespen (Hym., Sphecoidea). Ann. Ent. Fennici 27:141–46.

vander Linden, P. L. 1829. Observations sur les Hyménoptères d'Europe de la famille de Fouisseurs, deuxième partie, Bembecides, Larrates, Nyssoniens, Crabronites. Nouv. Mém. Acad. Roy. Sci. Bel. Let. Bruxelles 5:1–125.

Wolf, H. 1959. Über einige westdeutsche Bienen und Grabwespen (Hym. Apoidea, Sphecoidea). Mitt. Deutsch. Ent. Ges. 18:11–16.

PROCEEDINGS
OF THE
CALIFORNIA ACADEMY OF SCIENCES

Vol. 43, No. 11, pp. 141-158, 19 figs., 1 table
January 17, 1984

DESCRIPTION AND OSTEOLOGY OF *THRYSSOCYPRIS,* A NEW GENUS OF ANCHOVYLIKE CYPRINID FISHES, BASED ON TWO NEW SPECIES FROM SOUTHEAST ASIA

By

Tyson R. Roberts

California Academy of Sciences, Golden Gate Park,
San Francisco, California 94118

and

Maurice Kottelat

Naturhistorisches Museum, Augustinerstrasse 2,
CH-4001, Basel, Switzerland

Abstract: ***Thryssocypris*** **new genus comprises two new species, the generic type-species *T. smaragdinus* from the Kapuas River in Kalimantan Barat (Indonesian western Borneo) and *T. tonlesapensis* from the lower Mekong basin in Kampuchea and Vietnam. Extremely compressed and anchovylike, *Thryssocypris* differs from all other cyprinids in having a non-protrusible upper jaw with the posterior half of its margin formed solely by the maxilla, and a pair of elongate, slitlike supraethmoidal laterosensory trenches. Osteological study reveals features of the Weberian apparatus, gill arches, pelvic girdle, and terminal radials of the dorsal and anal fins that have not been reported previously in cyprinids. The two new species differ in proportions and fin positions, in numbers of anal fin rays, scales, and vertebrae, and in coloration. The relationships of the new genus to other cyprinids require further study.**

Introduction

Two recently discovered, anchovylike, insectivorous cyprinid fishes, one from the Kapuas River in western Borneo (Kalimantan Barat, Indonesia) and the other from the lower Mekong basin in Kampuchea and Vietnam, are closely related to each other and represent a highly specialized new genus. We do not know of any previously described species referable to this genus.

Five specimens of the Bornean species were obtained at a single locality during an ichthyological survey of the Kapuas River in 1976, and we have been unable to locate any additional material of this species. Nine specimens of the Mekong species were obtained by F. d'Aubenton during a survey of the Tonle Sap in 1961, and at least one hundred specimens by W. J. Rainboth during a University of Michigan fisheries survey in the Mekong Delta in 1974. This species also does not seem to have been collected previously. The species differ so markedly in head size and other characters that they were not immediately recognized as congeneric. However, closer comparison, including osteological study, revealed that they agree in numerous characters not found, or at least not reported, in any other cyprinids and that they clearly do belong in the same genus.

Cyprinidae is the largest family of freshwater fishes, and we are very far from a phyletic classification of the genera or even a reasonable division of the family into taxonomic categories above the generic level. A great deal of work remains to be done in order to provide adequate definitions for cyprinid genera, many of which, as currently understood, are polyphyletic and must be split up before a phyletic classification can be achieved. Since many distinctive cyprinid genera are relatively rare, and live specimens virtually unobtainable, classification must be based mainly on information that can be extracted from preserved specimens. Osteological accounts of distinctive genera, especially if extensively illustrated in a standardized format (e.g., that of *Brycon* by Weitzman 1962) provide perhaps the most ready source of information for use in phyletic classification. Unfortunately, there is a dearth of such accounts. In addition to describing this new genus and its two species, therefore, we present an account of its osteology.

MATERIAL AND METHODS

Material of the two species described herein is deposited in the following institutions: California Academy of Sciences (CAS), Museum of Zoology of the University of Michigan (UMMZ), Smithsonian Institution (USNM), Museum national d'Histoire naturelle, Paris (MNHN), Museum d'Histoire naturelle de Genève (MHNG), Museum Zoologicum Bogorense, Bogor, Indonesia (MZB). The osteological account is based on a 53.2-mm paratype of *T. smaragdinus* and a 46.0-mm paratype of *T. tonlesapensis,* which were cleared and stained in alcian blue and alizarin. Additional osteological observations were made on radiographs of the other four type specimens of *T. smaragdinus* and 12 of the largest *T. tonlesapensis.* Although our osteological figures are based mainly on *T. smaragdinus,* our remarks generally relate to the osteology of both species. While it is not always so in fishes prepared with alcian and alizarin, in our material of *T. smaragdinus* and *T. tonlesapensis,* except for the distal ends of the intermuscular bones, it seems that all skeletal elements stained with alcian are true cartilage; all stained with alizarin are true bone. In the figures bone is indicated by stipple, cartilage by simple diagonal hatching, and fenestrae or foramina opening into intracranial spaces by cross-hatching. In all of the figures the scale bar equals 1 mm.

We draw attention to a few reservations concerning the osteology. The parietal laterosensory canal bony tubules and supraoccipital crest were badly damaged in the 53.2-mm specimen illustrated and were drawn on the basis of reconstruction and comparison with whole, unstained specimens. The shape of the posteriormost portions of the prevomer and parasphenoid and their relationships to other elements were not observed with certainty in the specimen illustrated and may be in error. In particular, the appearance of the prevomer may be due to breakage rather than to mere separation. We did not detect an intercalar, an element sometimes absent in Cyprinidae, but are uncertain of its absence in the present instance. Otoliths were not removed so that the crania could be preserved intact, and thus they are not described or figured.

Thryssocypris, new genus

TYPE-SPECIES.—*Thryssocypris smaragdinus* Roberts and Kottelat, new species.

DIAGNOSIS.—Small (largest specimen 63.8 mm), anchovylike cyprinids with highly compressed head and body; barbels absent; exceptionally large olfactory organ; well-developed hyaline eyelid; elongate, moderately upturned, and very narrow terminal jaws; acutely pointed snout, slightly to strongly projecting anterior to upper jaw; low dorsal and anal fins, with falcate margins, originating in posterior half of body; abdomen rounded, without keel. *Thryssocypris* differ from all other known cyprinid genera in the following characters: 1) upper jaw entirely nonprotrusible, without rostral cap or even vestigial groove of rostral cap, with posterior half of border formed solely by maxilla; 2) cephalic laterosensory system with elongate, slitlike supraethmoidal or rostral canal medial to nasal canal, supraorbital canals similarly slitlike, not enclosed in bony tubules on frontal bone, and an elongate dermosphenotic canal enclosed in a bony tubule fused for entire length to dorsal surface of sphenotic bone; 3) ventral portion of gill arches highly specialized, ceratobranchials 1–4 with proximal portions abruptly narrowed and ending in elongate cartilaginous extensions, hypobranchial one minute and hypobranchials 2–3

FIGURE 1. *Thryssocypris smaragdinus*, 49.4-mm holotype (MZB 3435).

absent, and basibranchials extremely slender; 4) Weberian apparatus with lateral process of centrum 2 extremely elongate and strongly curved posteriorly dorsal to tripus, extending laterally equally as far as fully formed pleural rib of fifth vertebra; 5) ischiac process of pelvic girdle with elongate and extremely slender anterior and posterior processes; and 6) posteriormost pterygiophore of dorsal and anal fins with a deeply bifurcate radial projecting considerably beyond base of posteriormost fin rays.

Regarding the diagnostic characters listed above: 1) a few other cyprinids have nonprotrusible upper jaws (e.g., the North American *Exoglossum* and *Parexoglossum*), but in these and all other cyprinids known to us the maxilla is entirely or almost entirely excluded from the gape by the premaxilla; 2) some other cyprinids apparently have laterosensory canals in the supraethmoidal region (e.g., *Luciosoma*), but the position and shape of these canals is quite different from those in *Thryssocypris*, and they are not slitlike. Lekander (1949) reported rostral laterosensory organs in some European cyprinids, but these are more anterior (near snout tip) and are joined by a commissure (absent in *Thryssocypris*). Supraorbital canals in Cyprinidae are usually enclosed in bony tubules on the dorsal surface of the frontal bone. A dermosphenotic laterosensory canal is present in most cyprinids, but usually occurs in a short segment of bony tubule or on a small laminar dermosphenotic bone that is completely separate and superficial to the sphenotic bone; 3) in all other cyprinids we have examined or know about the gill arches have ceratobranchials 1–4 uniformly wide and hypobranchials one to three present; 4) many cyprinids have a very large lateral process on centrum two, but in most instances it projects directly laterally from the vertebral column, or in some instances is strongly curved posteriorly but projects ventrally to the tripus (rather than dorsally to it as in *Thryssocypris*); 5–6) the unusual condition of the ischiac process and of the terminal radials in the dorsal and anal fins is unlike anything we know of or have seen reported in any other cyprinids.

A more detailed account of the osteology of *Thryssocypris* is given following the species descriptions. Some additional characters of the genus are given here. Lateral line complete, moderately curved downward anteriorly. Gill rakers

FIGURE 2. *Thryssocypris tonlesapensis*, 50.6-mm holotype (MNHN 1982–1032).

TABLE 1. QUANTITATIVE CHARACTERS IN *Thryssocypris*.

Character	*T. smaragdinus*	*T. tonlesapensis*
Counts		
Gill rakers on first gill arch[1]	0+7	0+8
Pharyngeal teeth (left/right)[1]	1+5/5+1	2+5/5+2
Dorsal fin rays	9½(1),10½(3)	9½(3),10½(9)
Anal fin rays	12½(1),13½(2),14½(1)	15½(12),16½(6)
Pectoral fin rays	11–12	10–12
Pelvic fin rays	7–8	7–8
Procurrent caudal fin rays	9+9	9+8–9
Scales in lateral series	36–39	43–46
Scale rows above + below lateral line	5+3	6+3
Median predorsal scales	25?–27?	26–31
Circumferential scales	18–20	18–21
Circumpeduncular scales	14–15	16–17
Abdominal + caudal = total vertebrae	21+17 = 38(2),21+18 = 39(3)	21+22 = 43(12),21+23 = 44(1)
Proportions (times in standard length)		
Head	3.8–4.1	4.9–5.3
Snout	12.0–12.5	15.4–16.9
Olfactory organ	18.4–22.4	33.6–34.7
Eye	15.5–17.0	19.2–24.8
Lower jaw[1]	7.9	10.7
Pharyngeal bone[1]	11.4	20.0
Body depth	5.1–5.5	6.2–6.8
Body width	9.9–11.1	12.2–14.3
Caudal peduncle depth	11.4–12.0	10.6–11.5
Pectoral fin	5.7–6.1	6.0–7.0
Pelvic fin	9.0–10.0	8.9–9.7
Preanal length	1.3–1.4	1.5–1.6
Other		
Inclination of jaws	25°	30–35°

[1] From cleared and stained specimens.

small, short, and somewhat stubby, leading edge of lower limb of first gill arch with seven to eight rakers, upper limb with none to one. Pharyngeal teeth uncinate, in two rows, 1–2+5/5+2–1. Scales large, 36–46 in lateral series, approximately correlated in number with vertebrae, which total 38–44. Quantitative characters of the genus are summarized in Table 1.

Dorsal and ventral profiles of head and body anterior to dorsal and anal fins uniformly and gently curved (not forming an angle at occiput or pectoral fin origin). Dorsal and ventral surface of body anterior to median fins rounded from side to side. Body moderately tapered caudally (markedly tapered in some cheline cyprinids). No indication of a cranial flexure. Morphological features related to ability of head to tilt upwards in relation to vertebral column (evidently a feeding adaptation in Asian cyprinids such as *Macrochirichthys, Salmostoma, Oxygaster,* and *Chela*) are absent. Epaxial musculature does not invade cranial roof, angle of occiput is relatively acute, and parasphenoid relatively horizontal.

Scales on dorsum, sides (including lateral line scale series), caudal peduncle, and abdomen morphologically similar, except that scales of lateral line series have simple tubule for laterosensory canal, horizontally oriented, originating at or near focus and extending for half or more than half length of posterior field. Shape modified oval; anterior, dorsal, and ventral margins slightly convex, posterior margin rounded or even slightly pointed (especially in median scale rows and near bases of paired and median fins), sometimes weakly scalloped. Dorsal and ventral fields more or less sharply set off from anterior field but grading smoothly into posterior field. Radii present on all fields, but best developed on anterior and posterior fields. Radii on anterior field 8–15, horizontally oriented (parallel to each other). Radii

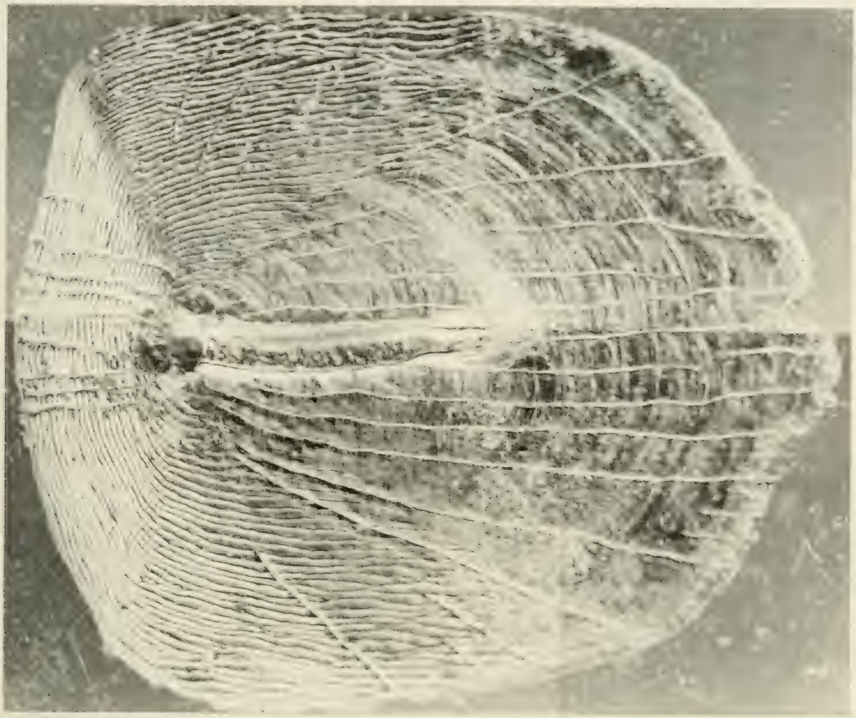


FIGURE 3. *Thryssocypris smaragdinus*, 49.7 mm, twenty-third scale in lateral line scale row (Nomarski interference contrast optics).

on posterior field 22–30 or more, slightly divergent from horizontal, more widely separated than those on anterior field. Radii on anterior and posterior fields originating near focus. Radii on dorsal and ventral fields similar, few in number, widely divergent, and variable in length, originating remote from focus, nearly parallel to uppermost and lowermost radii in posterior field, with which they seem to form a continuous series, and entirely divergent from radii in anterior field. Circuli well defined and evenly spaced in anterior, dorsal, and ventral fields, but discontinued or indistinct on posterior field. Circuli of anterior field vertical, of dorsal and ventral fields horizontal; circuli of dorsal and ventral fields meeting at right angles with circuli of anterior field at interfield margins, and bisecting growth lines of posterior field at a sharp angle. Growth lines, readily observable in posterior field, much more numerous and more nearly circular in arrangement than circuli.

Multicellular horny projections, or tubercles (also known as breeding tubercles), absent from body and fins, and perhaps also from head. Numerous minute conical projections toward tip of snout, on upper lip, and on lacrimal area of head (especially near ventrolateral margin of infraorbital 1) appear to be tubercles. Tubercles frequently occur on dorsal surface of pectoral fins, on scales, and on mandible in many cyprinids, especially in males, but are absent from these places in *Thryssocypris*.

ETYMOLOGY.—From the Greek *thrissos*, a herring or anchovy, and *cypris*, a small minnow.

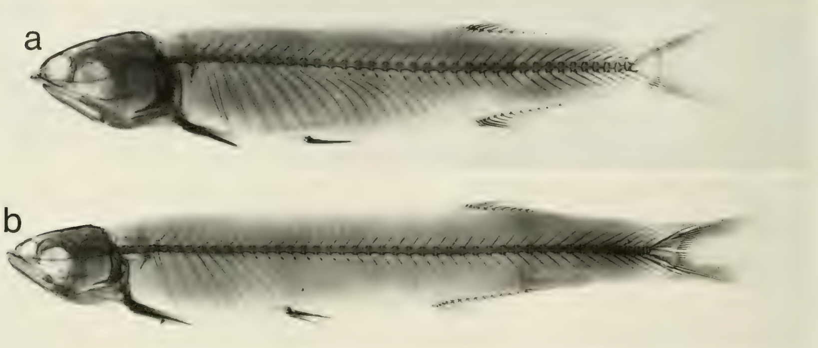


FIGURE 4. *Thryssocypris,* radiographs. a, *T. smaragdinus,* 49.4 mm (holotype); b, *T. tonlesapensis,* 52.0 mm (paratype, CAS 50946). Note obvious differences between species but also basically identical morphology of skulls.

Thryssocypris smaragdinus, new species
(Figures 1, 3a, 4–9, 10b, 11–19)

HOLOTYPE.—MZB 3435, 49.4 mm, mainstream of upper Kapuas River, 6 km w of Putussibau, Kalimantan Barat, Indonesia, lat. 0°50.5′N, long. 112°52′E. Seining in late afternoon and at dusk, on gently sloping open beach with coarse sand to fine gravel bottom and moderate current. 9 Aug. 1976.

PARATYPES.—CAS 49314, 3: 46.8–54.0 mm, and USNM 230243, 1: 49.7 mm, collected with holotype.

DIAGNOSIS.—*Thryssocypris smaragdinus* is most readily distinguished from *T. tonlesapensis,* its only congener, by much larger head, larger eye, larger pharyngeal bone, and fewer anal fin rays, scales, and vertebrae. These and other quantitative characters differing in the two species are summarized in Table 1. In *T. smaragdinus,* anal fin origin on a vertical with dorsal fin origin (versus anal fin origin far in advance of dorsal fin origin in *T. tonlesapensis*). Snout tip projects strongly beyond upper jaw in four of the five specimens of *T. smaragdinus* (including the holotype), thus differing strikingly from *T. tonlesapensis,* in which it projects but very slightly. In one paratype of *T. smaragdinus* (USNM 230243, 49.7 mm), however, the snout tip projects little more than in *T. tonlesapensis.* Some additional differences between the two species are indicated in the color descriptions below and in the osteological account following.

In life *T. smaragdinus* are brilliant emerald green on the upper half of the head and body and bright silvery below. Preserved specimens exhibit a wide longitudinal band, narrowest anteriorly, extending from head to caudal fin, and lying entirely in dorsal half of body. Middle of caudal peduncle and caudal fin base with dark round spot level with longitudinal band. Melanophores absent from all fins except for a few small scattered ones on interradial membranes of dorsal and caudal fins. Melanophores almost entirely absent on ventral half of body. Dorsal half of body with numerous fine melanophores or chromatophores in addition to those of longitudinal band, but not forming noticeable patterns such as rows parallel to posterior margin of scales. Dorsal midline of body with two or three thin longitudinal rows of melanophores. Dorsal surface of head, especially dorsal to nasal organs, deeply pigmented with numerous large melanophores. Inner surface of opercle dusky.

Gut contents of 53.2-mm paratype comprise moderately numerous triturated remains of aquatic coleopteran and dipteran larvae, and some adult winged dipterans. No other food items observed.

ETYMOLOGY.—From the Greek *smaragdinos,* emerald green.

Thryssocypris tonlesapensis, new species
(Figures 2, 3b, 10a)

HOLOTYPE.—MNHN 1982–1032, 50.6 mm, Prek Tamen, at or near Snoc Trou, Kampuchea, 9 Nov. 1961.

PARATYPES.—MNHN 1982–1033, 3: 44.7–50.3 mm, MHNG 2119.63–64, 2: 45.5–46.0 mm, CAS 50946, 2: 48.4–52.1 mm, collected with holotype; MNHN 1982–1034, 1: 52.3 mm, Prek Tasom, at or near Snoc Trou, Kampuchea, June 1961; UMMZ

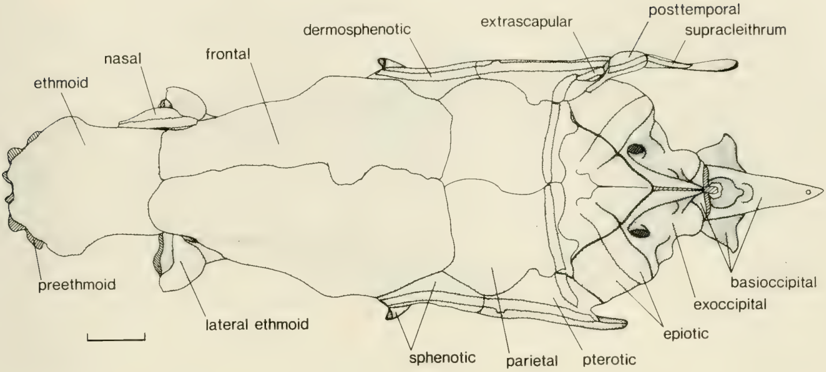


FIGURE 5. *Thryssocypris smaragdinus*, 53.2 mm, cranium (dorsal view).

210277, 1: 43.4 mm, Mekong River at w end of Con Phong (or Con Ho?) Island 2–5 km w of My Tho, Vietnam, 18 July 1974; UMMZ 210278, 1: 45.7 mm, Mekong River at Con Ho Island, My Tho, Vietnam, 19 June 1974; UMMZ 210279, 58: 20.4–60.1 mm, fish market at Vinh Long, Vietnam, 22 June 1974; UMMZ 210280, 36: 29.2–63.8 mm, fish market at Can Tho, Phong Dinh Province, Vietnam, 23 June 1974.

DIAGNOSIS.—Characters distinguishing *T. tonlesapensis* from *T. smaragdinus* are given in the diagnosis of *T. smaragdinus*, in Table 1, in the description of coloration and other remarks below, and in the osteological account following. The species is immediately distinguished from *T. smaragdinus* by its much smaller head, more numerous scales (44–46 in lateral line series versus 36–39), and more numerous anal fin rays (15½–16½ versus 12½–14½). The very striking difference in size of the pharyngeal jaws of *tonlesapensis* (Fig. 4), the linear dimensions of which are only about half as great as in *T. smaragdinus*, is much greater than would be expected if this difference were due only to the difference in head size, since the head is only about 20% longer in *T. smaragdinus*.

Coloration of live *T. tonlesapensis* has not been observed. Specimens observed in fish markets by W. J. Rainboth were entirely silvery. Color pattern of preserved specimens is similar in its basic features to that of *T. smaragdinus*, including the longitudinal band and basicaudal spot, but differing in some details: longitudinal band lower, nearly midlateral in position (confined to dorsal half of body in *T. smaragdinus*); melanophores on dorsal half of body tending to form rows parallel to posterior margins of scales; and inside of opercle clear instead of dusky.

Guts of numerous specimens are moderately to very full of insects, mostly aquatic larvae; no other food items observed.

ETYMOLOGY.—From Tonle Sap, the enormous permanent backwater of the lower Mekong, into which the Prek Tamen and Prek Tasom flow.

OSTEOLOGY

Although the two species of *Thryssocypris* differ strikingly in skull size and there are obvious differences in the axial skeleton and median fin skeletons related to differences in vertebral number and anal fin position and ray number, their osteology is very similar in most respects (Fig. 4). Some osteological differences between the two species are noted in the following account, which is based on both species, even though the drawings (except Fig. 10a) are of *T. smaragdinus*.

CRANIUM (Figs. 5–8, 10).—Roof of cranium entire, without fontanel, strongly convex transversely for its entire length. Frontals with narrow, flangelike, nearly horizontal lateral margins, and a transverse shallow depression or groove overlying tectum cranii or epiphyseal bar. Sphenotic as well as pterotic bones contribute substantially to cranial roof, with moderately developed sphenotic and pterotic projections or spines. Ethmoid (or supraethmoid) very large,

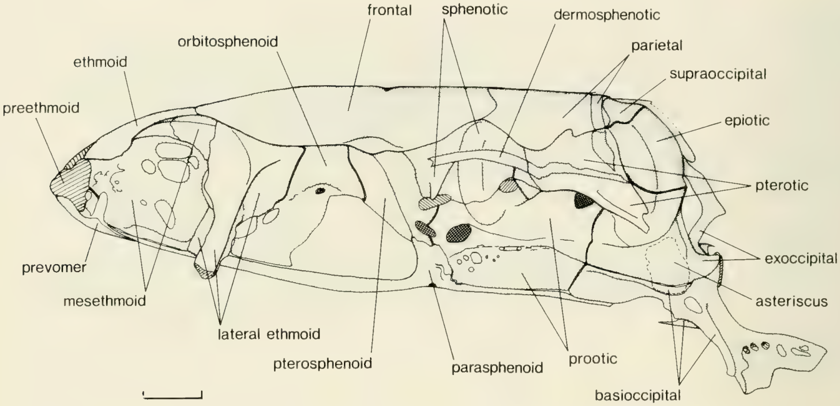


FIGURE 6. *Thryssocypris smaragdinus*, 53.2 mm, cranium (lateral view).

completely covering mesethmoid so that it does not contribute to dorsal surface of ethmoid region. Preethmoids cartilaginous. Dilatator fossae indistinct. Posttemporal fossae absent.

In most cyprinids the cranium tends to be dorsally flattened, or even transversely concave. In rasborines and bariliines the cranium tends to be barrel-shaped (Gosline 1975), with a convex dorsum, as in *Thryssocypris*. The sphenotic is usually entirely or almost entirely excluded from the dorsal roof of the cranium, a noted exception occurring in *Esomus* (Ramaswami 1955), which in other respects differs very much from *Thryssocypris*. In Cyprinidae the ethmoid is usually much shorter than in *Thryssocypris*, broader than long, and with its anterior margin broadly and deeply indented medially to receive the kinethmoid (*Thryssocypris* has only a very small indentation anteriorly; see Fig. 5).

In chelines (Howes 1979) the cranium is more

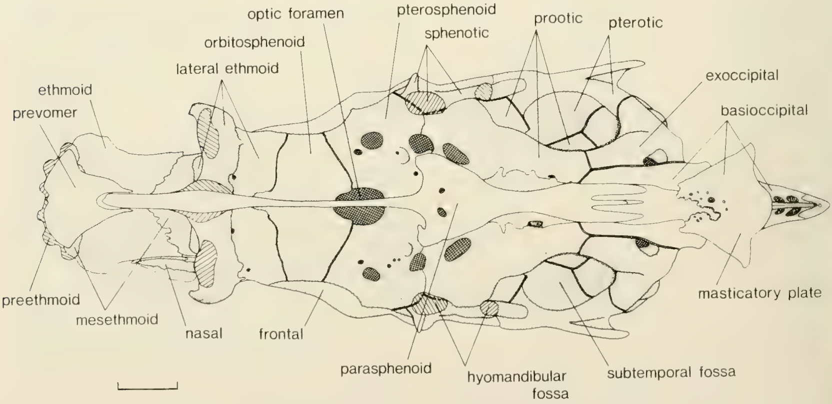


FIGURE 7. *Thryssocypris smaragdinus*, 53.2 mm, cranium (ventral view).

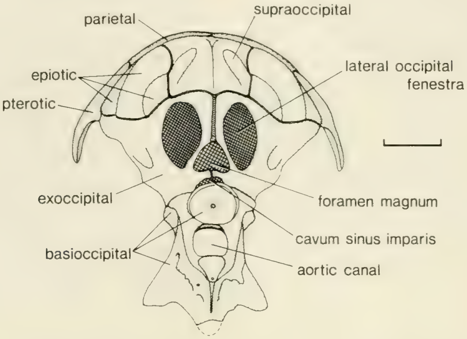


FIGURE 8. *Thryssocypris smaragdinus*, 53.2 mm, cranium (occipital view).

or less flat or even concave dorsally, the mesethmoid forms a shelflike projection extending anteriorly to the ethmoid, the anterior half of the parasphenoid is oriented at an angle of about 20° to 30° from the horizontal, the supraoccipital crest tends to be dorsal in position, and the occiput is elongated and gently sloping. In all of these respects chelines differ from *Thryssocypris*.

JAWS (Figs. 9–11).—Jaws elongate, upturned, and very narrow. Premaxilla only half as long as maxilla, maxilla alone forming margin of posterior half of upper jaw (maxilla entirely excluded or almost entirely excluded from gape in all other cyprinids). In *T. smaragdinus* maxilla with two ascending or ethmoid processes, each with a cartilaginous cap, anterior process moderately elongate or pedicellate, posterior process short (Fig. 11); in *T. tonlesapensis* maxilla with only a single

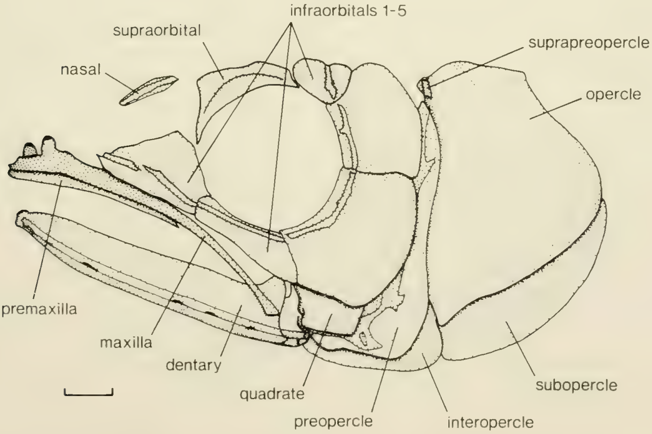


FIGURE 9. *Thryssocypris smaragdinus*, 53.2 mm, jaws and facial bones (lateral view).

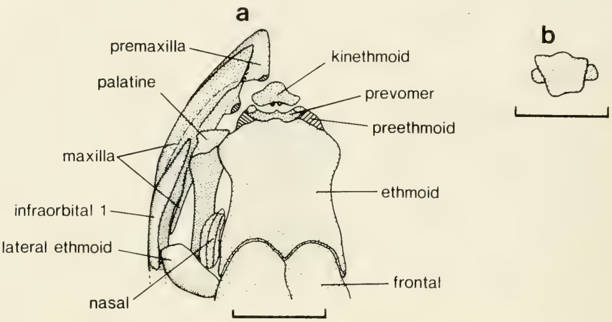


FIGURE 10. a, *Thryssocypris tonlesapensis*, 46.0 mm, ethmoid region of skull (dorsal view); b, *Thryssocypris smaragdinus*, 53.2 mm, kinethmoid bone (dorsal view).

ethmoid process, short and broad based (nonpedicellate), and with a cartilaginous cap (Fig. 10). Anterior half of maxilla with a medially directed shelf arising from its dorsal margin, coextensive with and largely overlapping lateral surface of premaxilla. Maxilla with a slender, posteriorly curved, broad-based projection arising near middle of its dorsal surface and extending medially to infraorbital number one, to which it is firmly attached by connective tissue, thus contributing to immobilization of upper jaw. Only posterior half of maxilla free from snout and capable of limited movement. Posterior portion of maxilla, separated from infraorbitals by a shallow groove, simple, elongate, and flexible; extends to proximal end of dentary. Lower jaw slightly shorter than upper jaw, elongate and very narrow, completely included within gape when mouth is closed. Symphysis of lower jaw without pronounced dorsal or ventral knobs, although vestigial or rudimentary dorsal symphyseal knob may be present, especially in *T. tonlesapensis*. Dorsal margin of dentary with a slight elevation just behind symphysis in *T. tonlesapensis*; in *T. smaragdinus* elevation absent or barely noticeable. Dentary and angular with coronoid processes short, vertically oriented, and separate, that of dentary arising very near proximal end (coronoid process of dentary frequently very large, usually arising near middle of dentary, and not

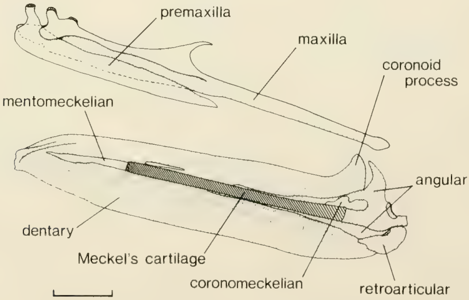


FIGURE 11. *Thryssocypris smaragdinus*, 53.2 mm, jaws (medial view).

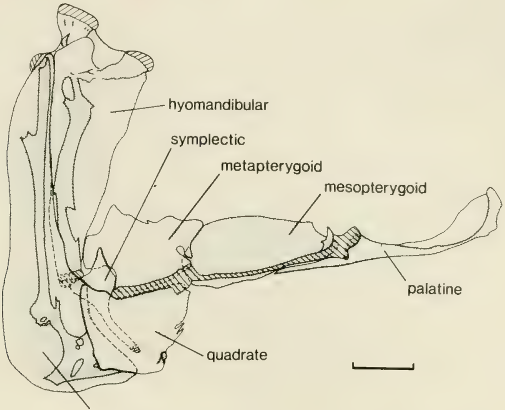


FIGURE 12. *Thryssocypris smaragdinus*, 53.2 mm, suspensorium (lateral view).

separate from angular in most cyprinids; angular without distinct coronoid process in most cyprinids). Free ventromedian margins of dentary nearly straight for entire length, those of opposite sides in contact or closely approximated (ventromedian margin of dentary frequently highly modified in shape in cyprinids, as in *Danio* and its relatives, and dentaries of opposite sides usually more or less widely separated in cyprinids, including genera with comparably elongate and narrow lower jaws such as *Macrochirichthys, Salmostoma,* and *Securicula*).

The poorly developed condition of the single ethmoid process on the maxilla of *T. tonlesapensis* is suggestive of the condition in chelines, but because the jaws of *Thryssocypris* are otherwise very unlike those of chelines and because *T. smaragdinus* has well-developed ethmoid processes, this resemblance is probably due to independent reduction (possibly related to small size of the head as well as nonprotrusibility of the jaws).

Development of large dorsal symphyseal knobs on each dentary (and sometimes almost equally prominent ventral symphyseal knobs) is characteristic of most chelines, and small dorsal symphyseal knobs occur in many cyprinids, including *Rasbora* and *Barilius.* In forms with dorsal symphyseal knobs the symphysis of the upper jaw is frequently indented for their reception; there is no comparable indentation in the upper jaw of *Thryssocypris.*

INFRAORBITAL AND NASAL BONES (Fig. 9).—Infraorbital series complete, with five large, lamellar infraorbital bones each bearing a simple bony tubule for infraorbital laterosensory canal and, together with supraorbital bone, forming an almost complete ring around eye. Posterior border of supraorbital indented where concave anterior margin of infraorbital 5 fits snugly against it; slender, pointed, anteroventral projection of supraorbital nearly contacts dorsal margin of infraorbital 1. Nasal bone moderately elongate, with a narrow lamellar portion on either side of bony tubule for nasal laterosensory canal.

Among Asian minnows with elongate, upturned jaws and compressed bodies, a complete infraorbital series in which all five infraorbitals have well-developed lamina is typical of rasborines and bariliines and unusual in chelines (Gosline 1975). In Cyprinidae the primitive number of infraorbitals, exclusive of the dermosphenotic (sometimes counted as an infraorbital), is five. Occasionally a greater number occurs, but this is usually (perhaps invariably) due to fragmentation of more or less tubular infraorbitals in which the lamellar component is greatly reduced or absent.

SUSPENSORIUM (Fig. 12).—Palatine arch nearly horizontal. Hyomandibular and preopercle ver-

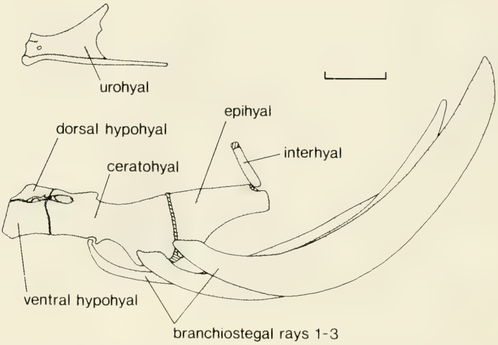


FIGURE 13. *Thryssocypris smaragdinus,* 53.2 mm, hyoid bar and urohyal (lateral view).

tical. Lateral abductor process of hyomandibular dorsally directed, originating just below hyomandibular articulation with cranium. Metapterygoid-quadrate fenestra absent or greatly reduced and almost entirely occluded by peculiarly expanded distal end of symplectic. Anteroventral limb of preopercle extremely short. Quadrate nearly square, with strong posteroventral extension seen in many or most cyprinids, and without a foramen immediately posterior to articular facet for lower jaw. Ectopterygoid apparently absent in *T. smaragdinus*; present but reduced in *T. tonlesapensis.* Palatine bone with a well-developed posteroventral extension underlying lateral ethmoid articular facet. An elongate, continuous palatine cartilage connects palatine bone to mesopterygoid anteriorly and to metapterygoid and quadrate posteriorly. At its anterior end, between palatine bone and mesopterygoid, this cartilage forms a large, saddlelike facet articulating with ventral surface of lateral ethmoid. Opercle generalized in shape, deeper than long, its posterior margin rounded, dilatator process weakly developed. Suprapreopercle short, tubular, fused to anterodorsal corner of opercle.

In chelines the palatine bar is usually upturned like the strongly upturned jaws, and is thus obliquely oriented. Many cyprinids, including some chelines and bariliines, have a well-developed metapterygoid-quadrate fenestra, and most have the quadrate with a well-developed posteroventral process, a preopercle with a prominent anteroventral portion, and a large, broad ectopterygoid. In *T. smaragdinus* the elongate ventral portion of the mesopterygoid extends narrowly below the palatine cartilage where the ectopterygoid normally occurs, but examination with direct and transmitted light failed to reveal an ectopterygoid. In *T. tonlesapensis* the mesopterygoid does not extend ventral to the palatine cartilage, and a very thin, elongate ectopterygoid is present. Most chelines (Howes 1979) and *Luciobrama* (Howes 1978) have a foramen in the quadrate immediately posterior to its articulation with the lower jaw. Chelines and some other cyprinids tend to have a stout, fingerlike dilatator process forming the elevated anterodorsal corner of the opercle. Some cyprinids have a free suprapreopercle and some lack this element altogether. Fusion of the suprapreopercle with the opercle occurs frequently but is known only in the Cyprinidae. The cyprinid suprapreopercle is always a simple bony tube enclosing the uppermost portion of the preopercular laterosensory canal, never with a laminar portion (sometimes greatly enlarged) as in characoids.

HYOID BAR AND UROHYAL (Fig. 13).—Hyoid bar generalized for Cyprinidae, with three branchiostegal rays as in all members of the family, and no unusual features. First branchiostegal ray articulated to ventral surface of ceratohyal, which has a notch in margin at point of articulation; second branchiostegal ray broadly articulated to lateral face of ceratohyal; third broadly articulated to lateral face of epihyal. Basihyal dorsoventrally compressed, its anterior third cartila-

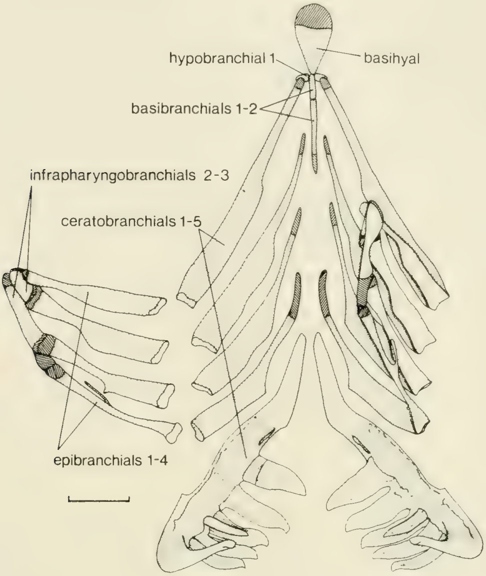


FIGURE 14. *Thryssocypris smaragdinus*, 53.2 mm, gill arches and pharyngeal jaws (dorsal view, with upper half of arches on left side deflected to reveal ventral surface).

ginous and with a broadly rounded anterior margin (basihyal elongate and narrow for its entire length in at least some chelines). Interhyal tubular and moderately elongate (flattened and laterally expanded in some chelines and cultrines). Urohyal with posteroventral process not greatly expanded, its distal end simple in *T. smaragdinus* and with a very small notch in *T. tonlesapensis*. (Urohyal greatly modified in some bottom dwelling cyprinoids including cyprinids; posteroventral process very deeply forked in *Luciobrama* and at least some chelines.)

GILL ARCHES AND PHARYNGEAL JAWS (Fig. 14).—Gill arches (main features described above under generic diagnosis) basically similar in *T. smaragdinus* and *T tonlesapensis*. Narrow proximal portion of ceratobranchials not quite so long as in *T. smaragdinus*, but equally strongly narrowed and with peculiar cartilaginous proximal ends as large as in *T. smaragdinus*. Basibranchials two in *T. smaragdinus*, three in *T. tonlesapensis*, extremely slender in both species. Ceratobranchial 5 (tooth-bearing pharyngeal bone) uniformly slender, its length more than five times its width, gracefully arched. External ala elongate but extremely narrow, its origin marked by a small, strongly angular projection opposite base of middle tooth in major tooth row. Ventral edentulous limb slightly shorter, and dorsal edentulous limb slightly longer, than dentigerous portion. Symphyseal half of ventral edentulous limb abruptly narrowed and set at angle to rest of bone, so its orientation is nearly horizontal. Pharyngeal teeth uncinate (conical with recurved tips), in two rows; those of inner or major row uniformly decreasing in size from front to back, those of minor or outer row substantially smaller than those of major row.

Like most cyprinids *Thryssocypris* has but two infrapharyngobranchials, here interpreted as infrapharyngobranchials 2–3. They exhibit the characteristic two-plus-two relationship with

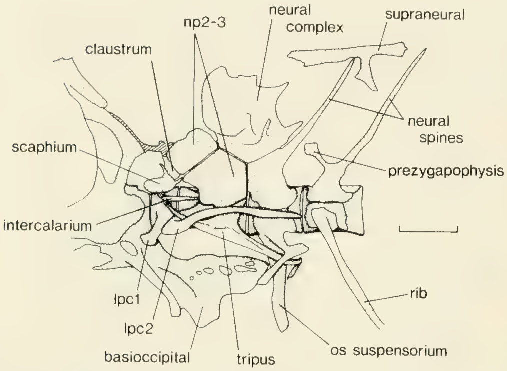


FIGURE 15. *Thryssocypris smaragdinus,* 53.2 mm, Weberian apparatus (lateral view) (1pc1,2 = lateral processes of centrum 1 and centrum 2; np2,3 = neural plates of centrum 2 and centrum 3).

epibranchials 1–2 and 3–4 which seems to be characteristic of all cyprinoids. Epibranchials 1–2 are united by cartilaginous joints to the distal end of infrapharyngobranchial 2, and epibranchials 3–4 are similarly joined to infrapharyngobranchial 3. Thus the proximal ends of infrapharyngobranchials 1 and 2 approximate each other, and there is a slight but distinct gap between epibranchials 1–2 and epibranchials 3–4. This peculiar orientation, which seems not to have been noted previously, has been observed without exception in numerous cyprinoids examined by us. Although the orientation is highly specialized compared to the primitive one-to-one relationship between the infrapharyngobranchials and epibranchials observed in characoids and most lower teleosts, it is apparently primitive for cyprinoids. A curiously similar two-plus-two arrangement is present in numerous siluroids examined, including *Diplomystes,* but the relationships of the infrapharyngobranchials to the epibranchials appears not to be exactly the same. Further investigation should be done to determine whether this condition in cyprinoids and siluroids indicates a common ancestor for these two groups. In any event this specialized condition is too widespread among cyprinids to be of any use in assessing phyletic relationships of *Thryssocypris.*

In some cyprinoids (mainly bottom feeders, such as *Labeo* and *Osteochilus,* with inferior, suctorial mouths) the basibranchial bones appear to be shaped and articulated in such a fashion as to permit them to slide over and under each other, thus indicating that the ventral half of the branchial basket is capable of anteroposterior contraction and expansion. In *Thryssocypris* the elongate, slender, and straight basibranchial bones are firmly joined end to end, indicating that the branchial basket is incapable of such contraction and expansion movements.

WEBERIAN APPARATUS (Fig. 15).—Similar generally to Weberian apparatus of *Opsariichthys* (Fink and Fink 1981; Fig. 14). Neural complex vertical (not strongly posteriorly sloped as in many chelines and cultrines), widely separated from occiput. Occiput attached to anterodorsal surface of Weberian apparatus by a thin median strip of cartilage extending from posterodorsal median margins of exoccipitals to claustrum and neural process of centrum number two. Lateral process of centrum 2 exceptionally elongate and strongly curved posteriorly, extending dorsally to tripus and laterally as far as major curvature of fully formed pleural rib of vertebra 5. Fourth pleural rib and parapophysis (bearing os suspensorium) without a prominent anterodorsally projecting lateral process (present in *Opsariichthys*). Intercalarium simple, slender, and elongate, horizontally oriented, without ascending or articular

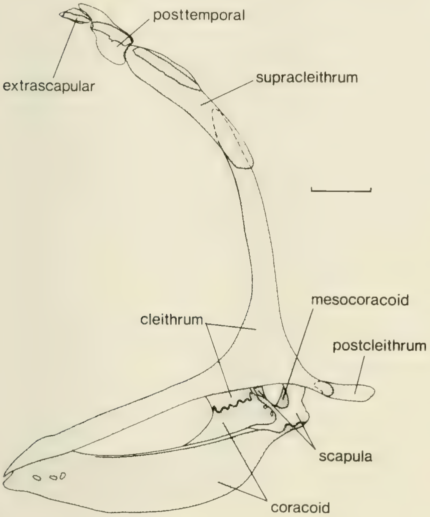


FIGURE 16. *Thryssocypris smaragdinus*, 53.2 mm, pectoral girdle, left half (lateral view).

processes. Centra 2 and 3 fused to each other, at least ventrally (centra 2–3 separate in *Opsariichthys* but partially or completely fused in many cyprinids).

Endochondral union of Weberian apparatus with cranium is characteristic of cyprinoids and is not found in other ostariophysans (Fink and Fink 1981). Reduction and loss of ascending and articular processes of intercalarium in other ostariophysans, especially siluroids, is reported by Fink and Fink (1981:328). In *Opsariichthys* relatively large gaps occur between neural arches 2–3 and the vertebral column, and between neural arches 3 and 4; these gaps are greatly reduced in *Thryssocypris* (that between neural arches 3 and 4 is completely occluded). The element here termed neural arch of centrum 2 is the anteriormost supraneural according to Fink and Fink (1981).

Fusion of centra 2 and 3 is possibly a primitive character for all Cyprinidae. We propose a hypothesis that this condition evolved only once and that the mosaic distribution of cyprinid genera with fused and with separate centra 2–3 is due to repeated secondary failure to fuse and reversion to the fused condition, rather than to truly independent evolution of fusion between these centra in phyletically diverse lines (the hypothesis seemingly favored by Greenwood et al. [1966:385] and Fink and Fink [1981:331]). Centra 2–3 are fused in the primitive siluroid *Diplomystes*, centra 2–4 and sometimes also 5 in all other siluroids (Hassur 1970). Whether fusion of centra 2–3 evolved independently in siluroids or indicates their phyletic relationship to cyprinoids has not been resolved satisfactorily (compare Roberts 1973 with Fink and Fink 1981). The centra of the Weberian apparatus are all separate in all characoids, gymnotoids, and gonorynchs. In any event this character is unlikely to be relevant in considerations of the closer phyletic relationships of *Thryssocypris*.

PECTORAL GIRDLE (Fig. 16).—Pectoral girdle morphologically generalized, slender, with a single extrascapular (two extrascapulars in some cyprinids), dorsal and anteroventral limbs of cleithrum slender, postcleithrum moderately elongate (slightly more elongate in *T. tonlesapensis* than in *T. smaragdinus*). Coracoid with a strongly developed lateral shelf, but not ventrally expanded; coracoid foramen broad. (Coracoid is ventrally expanded, sometimes enormously so, in most chelines and cultrines. In some, coracoid foramen reduced or even occluded.) In chelines (Howes 1979), postcleithrum frequently (always?) arclike, very slender and elongate, and with distal end projecting downwards, quite unlike the postcleithrum in *Thryssocypris*. In *Thryssocypris* the pectoral fin, although slightly larger proportionately in *T. tonlesapensis* than in *T. smaragdinus*, is not notably enlarged, nor is the simple outer ray thickened or otherwise modified. The pectoral axial flap (attached to the postcleithrum) is simple, moderately elongate, and not overlain by peculiarly shaped scales. In all of these respects the pectoral fin of chelines and cultrines tends to be modified.

PELVIC GIRDLE (Fig. 17).—Pubic bone deeply bifurcate anteriorly (as in most cyprinoids); lateral pubic projection nearly twice as long as medial. Ischiac process highly modified, with extremely elongate anterior and posterior projections. In *T. smaragdinus* anterior ischiac projection about half as long as posterior projection; in *T. tonlesapensis* anterior projection

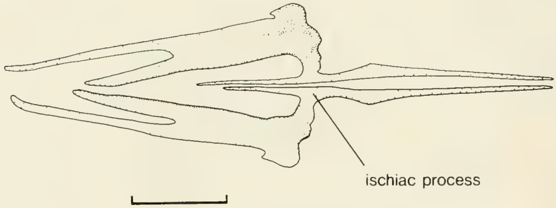


FIGURE 17. *Thryssocypris smaragdinus*, 53.2 mm, pelvic girdle (ventral view).

twice as long as posterior one, extending anteriorly as far as distal end of medial pubic projection. Origin of ischiac process opposite distal end of pleural rib of vertebra number 9 in *T. smaragdinus*, and of pleural rib of vertebra 11 or 12 in *T. tonlesapensis*.

AXIAL SKELETON.—Supraneurals 4–6 in number, commencing immediately posterior to neural complex of Weberian apparatus (not greatly enlarged or articulated to each other as in some chelines). In *T. smaragdinus* vertebrae 5–20 and in *T. tonlesapensis* 5–16 with enlarged prezygapophyses. *Thryssocypris smaragdinus* with well-developed dorsal ribs attached to anterior half of centrum on vertebrae 11–24; *T. tonlesapensis* without dorsal ribs (dorsal ribs unreported in any Cyprinidae until now). Pleural ribs of vertebrae 5–10 with broad, laminar proximal ends attached to comparably broad parapophyses; remaining pleural ribs with proximal ends slender, weakly attached to slender parapophyses. In *T. smaragdinus* proximal portion of pleural ribs on vertebrae 6–7 with spurlike, posteriorly directed projections (absent in *T. tonlesapensis*).

The counts of abdominal, caudal, and total vertebrae in *Thryssocypris* (Table 1) are close or identical to counts reported in several species of *Barilius* by Howes (1980: table 1).

DORSAL AND ANAL FINS (Fig. 18).—Dorsal and anal fin rays uniformly slender, nonserrate, first two dorsal and first three anal fin rays simple. Last complete pterygiophore bears two (counted as one and a half) fully formed, branched rays; bases of ray halves of anterior of these two rays overlap and lie externally to ray halves of posterior ray.

In the anal fin the bifurcate terminal radial (see generic diagnosis) is the medial radial of the last pterygiophore, which is complete. In the dorsal fin the situation is more complicated, and the

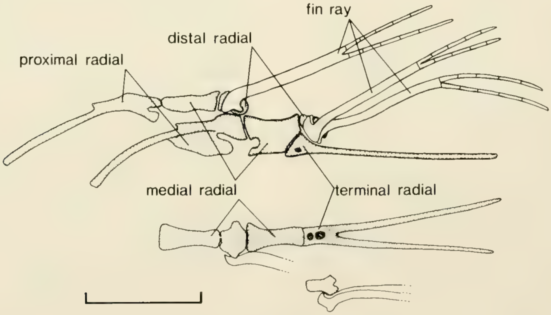


FIGURE 18. *Thryssocypris smaragdinus*, 53.2 mm, posteriormost fin rays and pterygiophores in dorsal fin (lateral view above, dorsal view below).

homology of the bifurcate terminal radial with the proximal, medial, and distal radials is unclear. In *T. smaragdinus* the bifurcate terminal radial constitutes by itself the terminal pterygiophore, articulating endochondrally only with the medial radial of the preceding pterygiophore. In *T. tonlesapensis* an additional element is present ventral to the bifurcate terminal radial; the dorsal margin of this element articulates with the ventral margins of the bifurcate terminal radial and of the preceding medial and proximal radials, and its homology also is unclear.

INTERMUSCULAR BONES.—Intermuscular bones well-developed, epineurals extending entire length of body, epipleurals commencing at vertebra 12. Proximal ends of anteriormost two or three epineurals attached to exoccipital in a small depression or fossa (shown in Fig. 8) near its posterolateral margin and on a level with foramen magnum. Distal ends of posteriormost two or three epineurals and epipleurals multifid (mostly bifid or trifid). Epineurals and epipleurals forked anteriorly with expanded laminae posteriorly.

In chelines and cultrines the anteriormost epineurals tend to insert much higher on the cranium (Howes 1979) than in *Thryssocypris.*

CAUDAL SKELETON (Fig. 19).—Generalized in nearly all respects, with a single epural; one or two uroneurals; parhypural fused to ural centrum, with an exceptionally large, elongate hypurapophysis; six hypurals, separate from each other, with hypurals 1–2 fused to ural complex centrum.

In most lower teleosts with the primitive principal caudal fin ray formula of 10+9, including all characoids and all Cyprinidae, the caudal fin skeleton tends to be highly conservative, retaining a relatively generalized or primitive morphology, including the primitive complement of six hypurals (exclusive of the parhypural). There is a maximum of three epurals, and perhaps invariably at least one epural. Presumably three is the primitive number of epurals in teleosts including ostariophysans, but reductions to two and one and subsequent reversion to three seem to have occurred repeatedly, particularly often in ostariophysans including Cyprinidae. Thus the single epural in *Thryssocypris* is not likely to be helpful in assessing its relationships to other cyprinids.

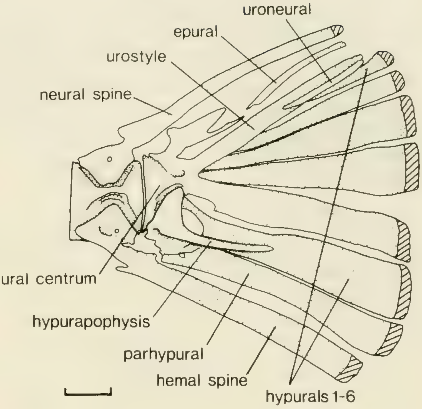


FIGURE 19. *Thryssocypris smaragdinus*, 53.2 mm, caudal fin skeleton (lateral view).

It should be noted that previous works on ostariophysan caudal skeletons report seven hypurals (e.g., Weitzman 1962; Roberts 1969). Following Monod (1968) the element previously considered as hypural one is here termed the parhypural. The parhypural bears the hypurapophysis which serves as origin of the main muscles for adduction of the upper caudal fin lobe. Thus the hypurals formerly numbered 2–7 are now hypurals 1–6. This new nomenclature has been used by most authors dealing with ostariophysan caudal skeletons subsequent to Monod (1968) including Lundberg and Baskin (1969) and Fink and Fink (1981).

CONCLUSION

The discovery of *Thryssocypris* provides another example of the extraordinary diversity of Cyprinidae, especially in Southeast Asia, and of the close biogeographic relationship between the Kapuas and Mekong basins.

Upon first examining *Thryssocypris* we thought that it might be a specialized *Barilius* or at least closely related to that genus. Lacking osteological information on most other cyprinid genera we are not prepared to discuss its relationships at this time except to note that it does not seem to be related to the chelines (sensu Howes 1979). The specialized characters in *Thryssocypris* that seem most unusual or highly derived and therefore likely to indicate phyletic relationships have not been reported in any other cyprinids. These include the peculiar morphology of ceratobranchials and absence of hypobranchials 2–3, shape of jaw bones, elongate anterior and posterior projections of ischiac process, and bifid terminal radials in median fins.

Acknowledgments

For making available material of *Thryssocypris* in their care we wish to thank J. Daget and F. d'Aubenton and W. J. Rainboth. The study was also facilitated in various ways by the following persons: G. J. Howes, Michael A. Hearne, W. N. Eschmeyer, Daphne Dunn, and Vincent Lee. The Kapuas ichthyological survey was sponsored by the Smithsonian Tropical Research Institute, Indonesian National Research Council, and Museum Zoologicum Bogorense. This paper is part of a project to report on the fishes of the Kapuas basin supported by National Science Foundation grant DEB77-24759.

Literature Cited

Fink, S. V., and W. L. Fink. 1981. Interrelationships of ostariophysan fishes (Teleostei). Zool. J. Linn. Soc. 72(4): 297–353.

Gosline, W. A. 1975. The cyprinid dermosphenotic and the subfamily Rasborinae. Occ. Pap. Mus. Zool. Univ. Michigan, no. 673, 13 pp.

Greenwood, P. H., D. E. Rosen, S. H. Weitzman, and G. S. Myers. 1966. Phyletic studies of teleostean fishes, with a provisional classification of living forms. Bull. Amer. Mus. Nat. Hist. 131(4):339–456.

Hassur, R. L. 1970. Studies on the osteology of catfishes, order Siluriformes. Ph.D. dissertation, Stanford Univ., 133 pp.

Howes, G. J. 1978. The anatomy and relationships of the cyprinid fish *Luciobrama macrocephalus* (Lacepède). Bull. Brit. Mus. (Nat. Hist.), zool. ser. 34(1):1–64.

———. 1979. Notes on the anatomy of *Macrochirichthys macrochirus* (Valenciennes) 1844, with comments on the Cultrinae (Pisces, Cyprinidae). Bull. Brit. Mus. (Nat. Hist.), zool. ser. 36(3):147–200.

———. 1980. The anatomy, phylogeny and classification of bariliine cyprinid fishes. Bull. Brit. Mus. (Nat. Hist.), zool. ser. 37(3):129–198.

Lekander, B. 1949. The sensory line system and the canal bones in the head of some Ostariophysi. Acta Zool. 30:1–131.

Lundberg, J. G., and J. N. Baskin. 1969. The caudal skeleton of the catfishes, order Siluriformes. Amer. Mus. Nov. no. 2399, 49 pp.

Monod, T. 1968. Le complex urophore des téléostéens. Mém. Inst. fr. Afr. noire 81:1–705.

Ramaswami, L. S. 1955. Skeleton of cyprinoid fishes in relationship to phylogenetic studies: 7. The skull and Weberian apparatus of Cyprininae (Cyprinidae). Acta Zool. 36:199–242.

Roberts, T. R. 1969. Osteology and relationships of characoid fishes, particularly the genera *Hepsetus, Salminus, Hoplias, Ctenolucius,* and *Acestrorhynchus.* Proc. California Acad. Sci. 36(15):391–500.

———. 1973. Interrelationships of ostariophysans, pp. 373–395 in P. H. Greenwood, R. S. Miles, and C. Patterson (eds.), Interrelationships of Fishes, London, Academic Press.

Weitzman, S. H. 1962. The osteology of *Brycon meeki,* a generalized characid fish, with an osteological definition of the family. Stanford Ichth. Bull. 8:1–77.

PROCEEDINGS
OF THE
CALIFORNIA ACADEMY OF SCIENCES

Vol. 43, No. 12, pp. 159-177, 32 figs. July 12, 1984

STUDIES ON NEBRIINI (COLEOPTERA: CARABIDAE), V. NEW NEARCTIC *NEBRIA* TAXA AND CHANGES IN NOMENCLATURE

By

David H. Kavanaugh

Department of Entomology, California Academy of Sciences,
Golden Gate Park, San Francisco, California 94118

Abstract: This paper introduces new Nearctic *Nebria* taxa and changes in nomenclature. Names are provided for 10 new species and 3 new subspecies (type locality in parentheses): *Nebria altisierrae* (Olmsted Point, Yosemite National Park, California), *N. campbelli* (Mount Baker, Whatcom County, Washington), *N. wallowae* (West Fork Wallowa River, Wallowa County, Oregon), *N. jeffreyi* (South Fork McCoy Creek, Harney County, Oregon), *N. haida* (Mount Needham, Graham Island, Queen Charlotte Islands, British Columbia), *N. louiseae* (Skedans, Louise Island, Queen Charlotte Islands, British Columbia), *N. gebleri albimontis* (Birch Creek, Mono County, California), *N. labontei* (West Fork Wallowa River, Wallowa County, Oregon), *N. calva* (Mount Baldy, Apache County, Arizona), *N. sierrablancae* (Sierra Blanca, Lincoln County, New Mexico), *N. piute sevieri* (Parowan Creek, Iron County, Utah), *N. steensensis* (South Fork McCoy Creek, Harney County, Oregon), and *N. trifaria pasquineli* (Lefthand Creek, Boulder County, Colorado). For each, diagnostic combination of characters and notes on geographical distribution are provided and distinguishing features are illustrated. Changes in status are proposed for the following names (second name in each pair considered valid): *Nebria intermedia* Van Dyke = *N. crassicornis intermedia* Van Dyke; *N. sonorae* Kavanaugh = *N. acuta sonorae* Kavanaugh; *N. fragilis* Casey = *N. arkansana fragilis* Casey; *N. trifaria piute* Erwin and Ball = *N. piute piute* Erwin and Ball; and *N. trifaria utahensis* Kavanaugh = *N. piute utahensis* Kavanaugh. New synonymies proposed include: *Nebria arkansana uinta* Kavanaugh = *N. arkansana fragilis* Casey; *N. fragilis teewinot* Kavanaugh = *N. arkansana fragilis* Casey; and *N. trifaria tetonensis* Erwin and Ball = *N. trifaria trifaria* LeConte.

Introduction

For several years, I have been working on a monographic treatment of genus *Nebria* Latreille for the Nearctic Region. During that time, I have provided names for several new species and numerous new subspecies, designated lectotypes, and proposed certain nomenclatural changes (Kavanaugh 1979 and 1981). Validation of these new names and clarification of the status of existing names were needed to permit their proper use in various other reports by the author and several colleagues. Since 1981, additional specimens and data have been acquired. Study of this new material has revealed 13 hitherto unknown taxa (10 species and 3 subspecies) as well as several nomenclatural problems with previously described taxa.

The purpose of this report, which serves as a final presentation of nomenclatural matters preliminary to submission of the monographic treatment, is to provide names for the new taxa and to present formally the needed nomenclatural changes. The latter include both new synonymies and other changes in status of names. As before, these names are needed immediately for use in other manuscripts; and data and discussions presented for each name are limited to little more than the minimum required by the International Code of Zoological Nomenclature. More detailed information for all taxa, including those presented here as new, will be provided in the monograph.

MATERIALS AND METHODS

This report is based on examination of 1136 adult *Nebria* specimens, representing taxa described here as new, and over 80,000 additional specimens, representing previously described *Nebria* taxa, used for comparative purposes. Recognition of new synonymies and changes in status of taxa are based on study of this total specimen resource pool.

Following is a list of acronyms used in the text. These refer to collections from which specimens have been received and/or in which paratype specimens have been deposited. Curators responsible for collections during the course of my study are also listed; and I here acknowledge with sincere thanks their assistance in providing specimens for study on loan.

ANSP—Academy of Natural Sciences, Philadelphia, Pennsylvania 19103; W. W. Moss.
BCPM—British Columbia Provincial Museum, Victoria, British Columbia V8V 1X4; R. A. Cannings.
CArm—C. Armin, 191 West Palm Avenue, Reedley, California 93654 (specimens deposited in CAS).
CAS—California Academy of Sciences, San Francisco, California 94118; D. H. Kavanaugh, H. B. Leech.
CNC—Canadian National Collection of Insects, Biosystematics Research Institute, Ottawa, Ontario K1A 0C6; R. de Ruette, A. Smetana.
CUB—University of Colorado, Boulder, Colorado 80302; H. Rodeck.
CUIC—Cornell University, Ithaca, New York 14850; L. L. Pechuman.
DEUN—University of Nebraska, Lincoln, Nebraska 68503; B. C. Ratcliffe.
EAMa—E. A. Martinko, University of Kansas, Lawrence, Kansas 66044 (specimens deposited in CAS).
FMNH—Field Museum of Natural History, Chicago, Illinois 60605; H. Dybas, L. Watrous.
JRLa—J. R. La Bonte, 710 NW 11th, Corvallis, Oregon 97330.
KSUC—Kansas State University, Manhattan, Kansas 66502; H. D. Blocker.
LACM—Los Angeles County Museum of Natural History, Los Angeles, California 90007; C. L. Hogue.
MCZ—Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts 02138; J. F. Lawrence, A. F. Newton, Jr.
MSU—Michigan State University, East Lansing, Michigan 48823; R. L. Fischer.
OSUC—Ohio State University, Columbus, Ohio 43210; C. A. Triplehorn.
PJJo—P. J. Johnson, 1408 28th Street SE, Auburn, Washington 98002.
QCIM—Queen Charlotte Islands Museum, Skidegate, British Columbia V0T 1S0; N. Gessler and T. Gessler.
ROM—Royal Ontario Museum, Toronto, Ontario M5S 2C6; G. B. Wiggins.
RTBe—R. T. Bell, University of Vermont, Burlington, Vermont 05401.
UAFA—University of Arkansas, Fayetteville, Arkansas 72701; R. T. Allen.
UASM—University of Alberta, Strickland Museum, Edmonton, Alberta T6G 2E3; G. E. Ball.
UMMZ—University of Michigan, Ann Arbor, Michigan 48104; R. D. Alexander.
USNM—United States National Museum, Smithsonian Institution, Washington, D.C. 20560; T. L. Erwin.
UWEM—University of Wisconsin, Madison, Wisconsin 53706; L. J. Bayer.
ZMLS—Zoological Institute, University of Lund, Lund, Sweden; C. H. Lindroth, R. Danielsson.

Methods used in the present study, including measurement and dissection techniques and criteria for ranking taxa as species or subspecies, have been described in a previous paper (Kavanaugh 1979).

NEW *NEBRIA* SPECIES AND SUBSPECIES

The order of presentation of new species and subspecies below reflects a new classification of Nearctic *Nebria,* which will be provided in a monographic treatment of the genus now in preparation for publication. Except as noted, all specimens listed (by locality) in sections about geographical distribution have been designated as paratypes.

Nebria altisierrae, new species

(Figures 2, 15, 31)

Nebria virescens; KAVANAUGH 1978:345 (in part).

HOLOTYPE, ♂, in CAS, labelled: "U.S.A., California, Yosemite N. P., Sierra Nevada, Olmsted Point, 1.5 mi. sw. Tenaya Lk. on Tioga Rd., 2560m, 8 Nov. 1976 D. H. Kavanaugh"/"D. H. Kavanaugh Collection" [orange label]/"Holotype Nebria altisierrae n. sp. det. D. H. Kavanaugh 1983" [red label]/"California Academy of Sciences Type No. 14338." PARATYPES: five (four ♂ and one ♀), also deposited in CAS.

TYPE-LOCALITY.—Olmsted Point, 2560 m, Sierra Nevada, Yosemite National Park, California.

DIAGNOSTIC COMBINATION.—Head uniformly dark, without pale spots on vertex; labium with paraglossae distinct as short, pointed lateral lobes on apical margin of ligula; pronotum (Fig. 2) semiovoid, relatively short and moderately wide, ratio pronotal width to elytral width less than or equal to 0.75, basal sinuation of lateral margin absent or short and very shallow, basal angles not or only moderately denticulate, midlateral seta present; elytra with silhouette subrectangular, not narrowed basally, humeri (Fig. 15) not or only faintly carinate; metepisternum impunctate; hind tarsus with all tarsomeres glabrous dorsally, fourth tarsomere truncate ventrally with medial and lateral apicoventral setae symmetrical in length and position; specimen from locality in Sierra Nevada of California (Fig. 31).

Derivation of Taxon Name.—The species epithet is a combination of the Latin word for "high" (=*altus*) and a shortened form of "Sierra Nevada," in reference to the High Sierra region inhabited by members of this species.

Geographical Distribution.—Figure 31. Known only from high elevations in the Sierra Nevada of California, from Tuolumne County south to Sequoia National Park. I have studied specimens from the following localities:

United States of America

California: Sequoia National Park, Alta Meadow ([2740 m]) [Aug.] (2; CAS); Tuolumne County, Blue Canyon Lake ([3110 m]) [July] (1; CAS); Yosemite National Park, Olmsted Point (1.5 miles SW of Tenaya Lake [2560 m]) [Nov.] (3; CAS).

Nebria campbelli, new species

(Figures 3, 16, 31)

Nebria virescens; Kavanaugh 1978:345 (in part).

Holotype, ♂, in CAS, labelled: "U.S.A., Wash., Whatcom Co., Cascade Range, ne. slope Mt. Baker, Kulshan Ridge, 1460m–1520m, 11 Aug. 74 D. H. Kavanaugh"/ "D. H. Kavanaugh Collection" [orange label]/ "Holotype Nebria campbelli n. sp. det. D. H. Kavanaugh 1983" [red label]/ "California Academy of Sciences Type No. 14339." Paratypes: two (one ♂ and one ♀) deposited in CAS and CNC.

Type-Locality.—Mount Baker, 1460–1520 m, Cascade Range, Whatcom County, Washington.

Diagnostic Combination.—Head uniformly dark, without pale spots on vertex; labium with paraglossae distinct as short, pointed lateral lobes on apical margin of ligula; pronotum (Fig. 3) semiovoid, relatively long and narrow, basal sinuation of lateral margin short and moderately deep, basal angles markedly denticulate laterally, midlateral seta present; elytra with silhouette narrowed basally, nearly subovoid, humeri (Fig. 16) markedly carinate; metepisternum impunctate; hind tarsus with all tarsomeres glabrous dorsally, fourth tarsomere truncate ventrally with medial and lateral apicoventral setae symmetrical in length and position.

Derivation of Taxon Name.—I take pleasure in naming this species in honor of my friend and colleague J. Milton Campbell, who collected the only known female specimen of this species.

Geographical Distribution.—Figure 31. Known only from the northern end of the Cascade Range and its flanking ranges, from Manning Provincial Park in southern British Columbia to Mount Baker in northern Washington. I have studied specimens from the following localities:

Canada

BRITISH COLUMBIA: Manning Provincial Park (Three Brothers Mountain [2130 m]) [July] (1; CNC).

United States of America

WASHINGTON: Okanogan County, Pasayten Wilderness (Bunker Hill Lookout [2120 m]) (1; CAS); Whatcom County, Mount Baker (NE slope on Kulshan Ridge [1520 m]) [Aug.] (1; CAS).

Nebria wallowae, new species

(Figures 4, 17, 24, 31)

Holotype, ♂, in CAS, labelled: "U.S.A., Oregon, Wallowa County, Wallowa Mts., West Fork Wallowa River, 2070–2130m, 10 July 1982 Stop #82–16 D.H. & J. L. Kavanaugh colls."/ "D. H. Kavanaugh Collection" [orange label]/ "Holotype Nebria wallowae n. sp. det. D. H. Kavanaugh 1983" [red label]/ "California Academy of Sciences Type No. 14347." Paratypes: 87 (36 ♂ and 51 ♀), deposited in CAS, CNC, JRLa, UASM, and USNM.

Type-Locality.—West Fork Wallowa River, 2070–2130 m, Wallowa Mountains, Wallowa County, Oregon.

Diagnostic Combination.—Pronotum (Fig. 4) with lateral explanation broad throughout, basal sinuation of lateral margin moderately deep, basal angles rectangular or slightly acute, moderately projected posteriorly, midlateral seta absent; elytra with silhouette subovoid, slightly narrowed basally, humeral angles not markedly rounded or obtuse, humeral carinae moderately developed, slightly projected anteriorly; hindwing full-sized, with reflexed apex distal to stigma; hind coxae bi- or plurisetose basally; middle tibiae dorsally concave or sulcate (at least near middle), with brush of dorsal setae moderately and densely developed; third to fifth visible abdominal sterna each with two or more pairs of posterior paramedial setae; median lobe of male (Fig. 17) long, very slender; bursa copulatrix of female (Fig. 24) with very small bursal sclerite; specimen from locality in Wallowa Mountains of Oregon (Fig. 31).

Derivation of Taxon Name.—This species is named for the Wallowa Mountains.

Geographical Distribution.—Figure 31. Known only from the Wallowa Mountains of northeastern Oregon. I have studied specimens from the following localities:

United States of America

Oregon: Wallowa County, Glacier Lake (meadow below [2440 m]) [Sep.] (2; JRLa), Mirror Lake area ([2350 m]) [July] (5; CNC), West Fork Wallowa River (0.25 to 0.5 miles NE of Frazier Lake [2040–2190 m], and small side stream [1980 m]) [July] (81; CAS, JRLa).

Nebria jeffreyi, new species

(Figures 5, 31)

Holotype, ♂, in CAS, labelled: "U.S.A., Oregon, Harney County, Steens Mountains, South Fork McCoy Creek, 2290–2560m, 14 July 1982, Stop #82–22, D. H. & J. L. Kavanaugh colls."/ "D. H. Kavanaugh Collection" [orange label]/ "adult specimen used in laboratory rearing of immature stages"/ "Holotype Nebria jeffreyi n. sp. det. D. H. Kavanaugh 1983" [red label]/ "California Academy of Sciences Type No. 14342." Paratypes: 35 (11 ♂ and 24 ♀), deposited in CAS, JRLa, PJJo, UASM, and USNM.

Type-Locality.—South Fork McCoy Creek, 2390–2560 m, Steens Mountains, Harney County, Oregon.

Diagnostic Combination.—Pronotum (Fig. 5) with lateral explanation broad throughout, apical angles very broad and rounded, basal angles rectangular, basal sinuation of lateral margin moderately deep, midlateral seta absent; elytra with silhouette subrectangular, not narrowed basally, humeral angles not markedly rounded or obtuse, humeral carinae absent or only slightly developed, not projected anteriorly; hind coxae bi- or plurisetose basally; middle tibiae dorsally concave or sulcate (at least near middle), with brush of dorsal setae moderately and densely developed; third to fifth visible abdominal sterna each with two or more pairs of posterior paramedial setae; specimen from locality in Steens Mountains of Oregon (Fig. 31).

Derivation of Taxon Name.—I take great pleasure in naming this species in honor of my son, Jeffrey L. Kavanaugh, who assisted me in collecting the first known specimens of this species.

Geographical Distribution.—Figure 31. Known only from the Steens Mountains of southcentral Oregon. I have studied specimens from the following localities:

United States of America

Oregon: Harney County, Little Blitzen River ([2560 m]) [July] (10; PJJo), South Fork McCoy Creek ([2390–2560 m]) [July] (26; CAS, JRLa).

Nebria haida, new species

(Figures 6, 31)

Holotype, ♂, in CAS, labelled: "Canada, British Columbia, Queen Charlotte Islands, Graham Island, 1.8 km N of Mt. Needham, 700m–780m, 18 July 1981, Stop #81–37, D. H. Kavanaugh collector"/ "D. H. Kavanaugh Collection" [orange label]/ "Queen Charlotte Islands Expedition—1981" [row of asterisks] "D. H. Kavanaugh Calif. Acad. Sciences"/ "Holotype Nebria haida n. sp. det. D. H. Kavanaugh 1983" [red label]/ "California Academy of Sciences Type No. 14341." Paratypes: 151 (68 ♂ and 83 ♀), deposited in BCPM, CAS, CNC, QCIM, UASM, and USNM).

Type-Locality.—1.8 km N of Mount Needham, 700–780 m, Graham Island, Queen Charlotte Islands, British Columbia.

Diagnostic Combination.—Size medium: standardized body length of male 9.0 to 10.5 mm, of female 9.4 to 10.8 mm; head relatively large and wide; pronotum (Fig. 6) relatively long and slender, with lateral explanation broad throughout, apical angles short, relatively broad and slightly rounded, basal angles rectangular, basal sinuation of lateral margin long, moderately deep, midlateral seta absent; elytra with silhouette subovoid, long and slender, distinctly narrowed basally, humeral angles not markedly rounded or obtuse, humeral carinae absent or only slightly developed, not projected anteriorly, intervals markedly convex; legs long, slender, femora and tibiae piceous; hind coxae bi- or plurisetose basally; middle tibiae dorsally concave or sulcate (at least at middle), with brush of dorsal setae moderately and densely developed; third to fifth visible abdominal sterna each with two or more pairs of posterior paramedial setae; specimen from locality in Queen Charlotte Islands, British Columbia (Fig. 31), from above treeline in alpine area.

Derivation of Taxon Name.—This species is named in honor of the Haida people, traditional inhabitants of the Queen Charlotte Archipelago.

Geographical Distribution.—Figure 31. Known only from high elevations in the Queen Charlotte Islands, British Columbia. I have studied specimens from the following localities:

Canada

British Columbia: Queen Charlotte Islands: Graham Island, Mount Needham (1.0 km [790–910 m] and 1.8 km [700–780 m] N) [July] (148; CAS); Moresby Island, Mount Moresby (northwest-facing cirque [910–1070 m]) [July] (4; CAS).

Nebria louiseae, new species

(Figures 7, 31)

Holotype, ♂, in CAS, labelled: "B. C., Q. C. I. Louise Is., Skedans 11.VI.1981 R. A. Cannings"/ "Holotype Nebria louiseae n. sp. det. D. H. Kavanaugh 1983" [red label]/ "California Academy of Sciences Type No. 15005." Paratypes: four ♀, deposited in BCPM, CAS, and CNC.

Type-Locality.—Skedans, Louise Island, Queen Charlotte Islands, British Columbia.

Diagnostic Combination.—Size large: standardized body length of male 10.4 mm, of female 10.6 to 11.0 mm; head relatively large and wide; pronotum (Fig. 7) relatively long and slender, with lateral explanation broad throughout, apical angles moderate in length, relatively narrow and pointed, basal angles rectangular, basal sinuation of lateral margin long, moderately deep, midlateral seta absent; elytra with silhouette subovoid, long and slender, distinctly narrowed basally, humeral angles not markedly rounded or obtuse, humeral carinae absent or only slightly developed, not projected anteriorly, intervals markedly convex; legs long, slender, femora and tibiae piceous; hind coxae bi- or plurisetose basally; middle tibiae dorsally concave or sulcate (at least at middle), with brush of dorsal setae moderately and densely developed; third to fifth visible abdominal sterna each with two or more pairs of posterior paramedial setae; specimen from locality in Queen Charlotte Islands, British Columbia (Fig. 31), from upper sea beach area.

Derivation of Taxon Name.—This species is named for Louise Island, on which the type locality is found.

Geographical Distribution.—Figure 31. At present known only from Louise Island, Queen Charlotte Islands. I have studied specimens from the following locality:

Canada

British Columbia: Queen Charlotte Islands: Louise Island, Skedans [June] (5; BCPM).

Nebria gebleri albimontis, new subspecies

(Figures 1, 8, 18, 25, 32)

Holotype, ♂, in CAS, labelled: "U.S.A., California, Mono County, White Mts., Birch Creek, 3290m–3410m, 8 July 1980 D. Giuliani collector"/ "Collection of California Academy of Sciences, San Francisco, Calif."/ "Holotype Nebria gebleri albimontis n. ssp. det. D. H. Kavanaugh 1983" [red label]/ "California Academy of Sciences Type No. 14340." Paratypes: four (two ♂ and two ♀), also deposited in CAS.

Type-Locality.—Birch Creek, 3290–3410 m, White Mountains, Mono County, California.

Diagnostic Combination.—Head dark, with a pair of pale paramedial spots on vertex; antennal scape (Fig. 1) short, moderately thick; pronotum (Fig. 8) with basal angles markedly acute, distinctly divergent posteriorly, margination of apical angles and anterior one-third of lateral margin very narrow, midlateral and basolateral setae present; elytra without metallic reflection, elytral silhouette subrectangular, hindwing full-sized; median lobe of male (Fig. 18) with preapical area markedly bulbous left dorsolaterally; bursa copulatrix of female (Fig. 25) with spermathecal chamber small, narrow in dorsal aspect; specimen from locality in White Mountains of California (Fig. 32).

Derivation of Taxon Name.—The subspecific epithet is a combination of the Latin words for "white" (=*albus*) and "mountain" (=*mons*), in reference to the White Mountains.

Geographical Distribution.—Figure 32. Known only from the type locality in the White Mountains of eastern California. I have studied specimens from the following locality:

United States of America

California: Mono County, Birch Creek ([3290–3410 m]) [July] (5; CAS).

Nebria labontei, new species

(Figures 9, 32)

Holotype, ♂, in CAS, labelled: "U.S.A., Oregon, Wallowa County, Wallowa Mts., West Fork Wallowa River, 2040–2190m, 11 July 1982, D. H. & J. L. Kavanaugh Stop #82–17"/ "D. H. Kavanaugh Collection" [orange label]/ "adult specimen used in laboratory rearing of immature stages"/ "Holotype Nebria labontei n. sp. det. D. H. Kavanaugh 1983" [red label]/ "California Academy of Sciences Type No. 14343." Paratypes: 57 (29 ♂ and 28 ♀), deposited in CAS, JRLa, UASM, and USNM.

Type-Locality.—West Fork Wallowa River, 2040–2190 m, Wallowa Mountains, Wallowa County, Oregon.

Diagnostic Combination.—Size very large: standardized body length of male greater than 11.5 mm, of female greater than or equal to 12.0 mm; head moderate in size, dark, with a pair of pale paramedial spots on vertex; pronotum (Fig. 9) broad, markedly cordate, midlateral and basolateral setae present; elytra with brilliant red metallic reflection, elytral silhouette distinctly subovoid, narrowed basally with lateral margins distinctly rounded, intervals flat; specimen from locality in Wallowa Mountains of Oregon (Fig. 32).

Derivation of Taxon Name.—I am pleased to name this species in honor of my friend and fellow collector, James R. LaBonte, who collected the first known specimen of this extraordinary species.

Geographical Distribution.—Figure 32. Known only from the Wallowa Mountains of northeastern Oregon. I have studied specimens from the following localities:

United States of America

OREGON: Wallowa County, Glacier Lake (meadow below [2440 m]) [Sep.] (1; JRLa), West Fork Wallowa River (0.25 to 0.5 miles NE of Frazier Lake [2040–2190 m]) [July] (57; CAS, JRLa).

Nebria calva, new species

(Figures 10, 19, 26, 32)

Holotype, ♂, in CNC, labelled: "Ariz: Apache Co Mt. Baldy, 10–11000′ SW of Springerville 13.VII.79, S & J Peck spruce-fir forest"/ "Holotype Nebria calva n. sp. det. D. H. Kavanaugh 1983" [red label]. Paratypes: 10 (7 ♂ and 3 ♀), deposited in CAS and CNC.

Type-Locality.—Mount Baldy (SW of Springerville), 3050–3350 m, Apache County, Arizona.

Diagnostic Combination.—Head moderate in width and size, dark, with a pair of pale paramedial spots on vertex; pronotum (Fig. 10) with midlateral and basolateral setae present; elytra with faint but distinct metallic (violet) reflection, elytral silhouette subovoid, markedly narrowed basally, intervals moderately flat; median lobe of male (Fig. 19) with apex straight in ventral aspect; bursa copulatrix of female (Fig. 26) with very small bursal sclerite; specimen from locality in eastcentral Arizona (Fig. 32).

Derivation of Taxon Name.—The species epithet is formed from the Latin word for "bald" (=*calvus*), in reference to the type locality, Mount Baldy.

Geographical Distribution.—Figure 32. Known only from Mount Baldy in eastern Arizona. I have studied specimens from the following locality:

United States of America

Arizona: Apache County, Mount Baldy (SW of Springerville [3050–3350 m]) [July] (11; CNC).

Nebria sierrablancae, new species

(Figures 11, 20, 27, 32)

Nebria trifaria catenata; Kavanaugh 1978:431 (in part).

Holotype, ♂, in CNC, labelled: "N. M. Lincoln Co. Sierra Blanca 10500′ 18.VII.1969 A. Smetana"/ "Holotype Nebria sierrablancae n. sp. det. D. H. Kavanaugh 1983" [red label]. Paratypes: 25 (10 ♂ and 15 ♀), deposited in CAS, CNC, and CUIC.

Type-Locality.—Sierra Blanca, 3200 m, Lincoln County, New Mexico.

Diagnostic Combination.—Body color uniformly rufous; head relatively large in relation to pronotum, with a pair of pale paramedial spots on vertex; pronotum (Fig. 11) with lateral margin markedly sinuate basally, slightly to moderately angulate at middle, apical angles narrow and bluntly pointed, midlateral and basolateral setae present; elytra with faint metallic (violet) reflection, elytral silhouette subovoid, narrowed basally, intervals moderately flat; median lobe of male (Fig. 20) with apex deflected left laterally in ventral aspect; bursa copulatrix of female as in Fig. 27; specimen from locality in Capitan Mountains or Sierra Blanca of central New Mexico (Fig. 32).

Derivation of Taxon Name.—This species is named for Sierra Blanca, the type locality.

Geographical Distribution.—Figure 32. Known only from Sierra Blanca and the Capitan Mountains of central New Mexico. I have studied specimens from the following localities:

United States of America

New Mexico: Lincoln County, Capitan (1; CUIC), Sierra Blanca (Sierra Blanca Ski Area [3200–3510 m]) [July] (25; CNC).

Nebria piute sevieri, new subspecies

(Figures 12, 21, 28, 32)

Nebria trifaria trifaria, auctorum—Erwin and Ball 1972:93 (in part)—Kavanaugh 1978:430 (in part).

Holotype, ♂, in CAS, labelled: "U.S., Utah, Iron Co., Markagunt Plateau, 13.5 mi. s. Parowan, Hwy. 143, Parowan Cr., 9200′, 21 June 71 D H Kavanaugh & E A Martinko"/ "D. H. Kavanaugh Collection" [orange label]/ "71–224" [orange label]/ "Holotype Nebria piute sevieri n. ssp. det. D. H. Kavanaugh 1983" [red label]/ "California Academy of Sciences Type No. 14344." Paratypes: 230 (107 ♂ and 123 ♀), deposited in ANSP, CAS, CNC, KSUC, MCZ, OSUO, UASM, and USNM. All specimens studied have been designated as paratypes except for the single (female) specimen from Clay Springs, Navajo County, Arizona. At present, I believe that this specimen is mislabelled. However, form of the bursa copulatrix in this specimen differs markedly from that in other females of *N. piute sevieri*. This may be a teratological example, or, if the specimen is correctly labelled, it may represent a distinct form not yet adequately sampled. My identification of the specimen as belonging to this subspecies is therefore tentative, pending additional fieldwork in Arizona.

Type-Locality.—Parowan Creek (13.5 miles S of Parowan), 2800 m, Markagunt Plateau, Iron County, Utah.

Diagnostic Combination.—Body color uniformly rufopiceous or black; head moderate in width and size in relation to pronotum, with a pair of pale paramedial spots on vertex; antennal scape markedly narrowed basally; pronotum (Fig. 12) with lateral margin moderately sinuate basally, rounded at middle, apical angles relatively broad and rounded, midlateral and basolateral setae present; elytra without metallic reflection, elytral silhouette elongate, subovoid or nearly ovoid, narrowed basally, intervals moderately flat; median lobe of male (Fig. 21) very thick basal to apical orifice, with apex moderate in length and broad in lateral aspect, deflected left laterally in ventral aspect; bursa copulatrix of female (Fig. 28) with bursal sclerite large, narrow in dorsal aspect; specimen from locality in southwestern Utah, east of Tushar Mountains and Midget Crest and west of Henry Mountains (Fig. 32).

Derivation of Taxon Name.—This subspecies is named for the Sevier River and Sevier Plateau, important physiographic features of the region occupied by members of this species.

Geographical Distribution.—Figure 32. Known at present only from the montane region between Salina, Utah, and Cedar Breaks National Monument and east to the Boulder Mountains. I have studied specimens from the following localities:

United States of America

Utah: Garfield County, Cottonwood Peak (38.5 miles SW of Antimony at Cottonwood Creek [2440 m]) [July] (72; CAS), Mount Dutton (23.4 miles SW of Antimony at North Fork Deep Creek [3120 m]) [July] (18; CAS); Iron County, Cedar Breaks National Monument ([3200 m]) [June–Aug.] (36; CAS, OSUC), Cedar Canyon (Coal Creek [2650 m]) [June] (6; CAS), The Mammoth ([3050 m]) [July] (17; ANSP, CAS, CNC, KSUC, MCZ, UASM, USNM), Parowan Creek (13.5 miles S of Parowan [2800 m]) [June] (10; CAS); Kane County, Long Valley Junction [Aug.] (12; CAS); Sevier County, Monroe Peak (8.6 [2640 m] and 12.4 [2990 m] miles SE of Monroe) [July] (3; CAS), Mount Marvine (0.1 miles N of Johnson Valley Reservoir at Sevenmile Creek [2590 m]) [Aug.] (10; CAS); Wayne County, Bluebell Knoll (31 miles S of Torrey [2440–3050 m]) [July] (46; CAS, USNM).

Doubtful Records:

United States of America—Arizona: Navajo County, Clay Springs [Sep.] (1; CAS).

Nebria steensensis, new species

(Figures 12, 22, 29, 32)

Holotype, ♂, in CAS, labelled: "U.S.A., Oregon, Harney County, Steens Mountains, South Fork McCoy Creek, 2390–2560m, 14 July 1982, Stop #82–22 D. H. & J. L. Kavanaugh colls."/ "D. H. Kavanaugh Collection" [orange label]/ "Holotype Nebria steensensis n. sp. det. D. H. Kavanaugh 1983" [red label]/ "California Academy of Sciences Type No. 14345." Paratypes: 106 (52 ♂ and 54 ♀), deposited in CAS, JRLa, PJJo, UASM, and USNM.

Type-Locality.—South Fork McCoy Creek, 2390–2560 m, Steens Mountains, Harney County, Oregon.

Diagnostic Combination.—Body color uniformly black; head moderate in width and size in relation to pronotum, with a pair of pale paramedial spots on vertex; antennal scape slightly narrowed basally; pronotum (Fig. 13) with lateral margin very deeply sinuate basally, rounded at middle, apical angles relatively broad and rounded, basal angles rectangular, midlateral and basolateral setae present; elytra without metallic reflection, elytral silhouette subovoid, narrowed basally, intervals moderately flat; median lobe of male (Fig. 22) moderate in thickness basal to apical orifice, with distinct, projected ridge on right lateral surface, apex deflected left laterally in ventral aspect; bursa copulatrix of female (Fig. 29) with bursal sclerite small; specimen from locality in Steens Mountains of Oregon (Fig. 32).

Derivation of Taxon Name.—The species is named for the Steens Mountains.

Geographical Distribution.—Figure 32. Known only from the Steens Mountains of south-central Oregon. I have studied specimens from the following localities:

United States of America

Oregon: Harney County, Fish Creek Gorge ([2190 m]) [July] (1; PJJo), Kiger Headwall ([2680 m]) [Aug.] (1; PJJo), Little Blitzen River ([2560 m]) [July] (16; PJJo), Pate Lake ([2260 m]) [July] (1; PJJo), South Fork McCoy Creek ([2390–2560 m]) [July] (88; CAS, JRLa).

Nebria trifaria pasquineli, new subspecies

(Figures 14, 23, 30, 32)

Nebria trifaria coloradensis; Erwin and Ball 1972:96 (in part).
Nebria trifaria trifaria; Kavanaugh 1978:430 (in part).

Holotype, ♂, in CAS, labelled: "Lefthand Cr., 5 mi. E. Ward, Colo. Bould. Co. 20 July 68"/ "D. H. Kavanaugh Collection" [orange label]/ "Holotype Nebria trifaria pasquineli n. ssp. det. D. H. Kavanaugh 1983" [red label]/ "California Academy of Sciences Type No. 14346." Paratypes: 407 (224 ♂ and 183 ♀), deposited in ANSP, CArm, CAS, CNC, CUB, DEUN, EAMa, FMNH, KSUC, LACM, MCZ, MSU, ROM, RTBe, UAFA, UASM, UMMZ, USNM, UWEM, and ZMLS.

Type-Locality.—Lefthand Creek (5 miles E of Ward), Front Range, Boulder County, Colorado.

Diagnostic Combination.—Body color uniformly black; head moderate in width and size in relation to pronotum, with a pair of pale paramedial spots on vertex; antennal scape slightly arcuate, only slightly narrowed basally; pronotum (Fig. 14) with lateral margin moderately sinuate basally, rounded at middle, apical angles relatively broad and rounded, basal angles rectangular or slightly obtuse, midlateral and basolateral setae present; elytra without metallic reflection, moderately dull, microsculpture moderately impressed, elytral silhouette subovoid, elongate, narrowed basally, intervals moderately flat, fifth interval interrupted, moderately or markedly catenate (with 3 to 10 catenations, restricted to apical one half or also on basal one-half of interval); median lobe of male (Fig. 23) slender basal to apical orifice, without ridge on right lateral surface, apex moderate in thickness and length and bent dorsally in lateral aspect, deflected left laterally in ventral aspect, apical orifice short, slightly constricted; bursa copulatrix of female (Fig. 30) with bursal sclerite small, narrow; specimen from locality in eastern ranges of Southern Rocky Mountains of central or northcentral Colorado or southeastern Wyoming (Fig. 32).

Derivation of Taxon Name.—This subspecies is named for Pasquinel, the enigmatic, indomitable French trapper in James A. Michener's epic novel, *Centennial.* The mountains traveled and loved by this fictional character are within the geographical range of this taxon and, in fact, include the type locality.

Geographical Distribution.—Figure 32. Known only from the easternmost ranges of the Southern Rocky Mountains, from the Medicine Bow and Sierra Madre Ranges of southeastern Wyoming south to the Rampart Range of southcentral Colorado. I have studied specimens from the following localities:

United States of America

Colorado: (3; ANSP, KSUC, LACM); Boulder County, [Aug.] (1; CUB), Arapahoe Pass ([2740–3050 m]) [Aug.] (5; RTBe), Jenny Lake ([3200 m]) [July] (1; CArm), Lake Isabelle ([3170 m]) [July] (7; CArm), Jasper Lake ([3260 m]) [Aug.] (1; CArm), Lefthand Creek (5 miles E of Ward [2530 m]) [July–Aug.] (80; CArm, CAS), Little Royal Gorge [Aug.] (1; CUB), Long Lake ([3140 m]) [July, Sep.] (6; CArm), Mitchell Lake ([3290 m]) [July] (7; CArm, CUB), Rainbow Lakes (10 miles SW of Ward [3350 m]) [Aug.] (1; CNC), Red Rock Lake ([2900 m]) [Aug.] (6; CArm), South St. Vrain Creek ([3050 m]) [July] (1; CUB), Yankee Doodle Lake ([3140 m]) [July] (1; CArm); Clear Creek County, Leavenworth Valley (Argentine Road [2740–3350 m], Waldorf Mine [3540 m]) [June–July] (20; ANSP, CAS, CNC, DEUN, FMNH, MCZ, ROM, UMMZ, USNM, ZMLS), Mount Evans (Echo Lake [3230 m], Summit Lake [3960 m]) [July] (3; CAS, CNC), Silver Plume ([2740–3050 m]) [June] (6; ANSP, CAS, MCZ, UWEM); El Paso County, Gold Camp Road (9 miles W of Broadmoor at South Cheyenne Creek [2650–2740 m]) [July–Aug.] (50; CAS, EAMa); Gilpin County, Rollinsville area [July] (1; CArm); Jackson County, Cameron Pass ([3140 m]) [Aug.] (1; UASM); Larimer County, Bennett Creek [May–July] (18; RTBe), Browns Lake Trail [Aug.] (1; RTBe), Buckhorn Creek [July] (2; RTBe), Cameron Pass ([3050 m]) [June, Aug.] (6; MSU, RTBe, UASM, USNM), Crown Point Road (at Bennett Springs [2290–2350 m], at Crown Point Trail [3140–3200 m], 40 miles W of Bellevue [2740 m]) [June–Aug.] (20; CAS, RTBe, UASM, USNM), Monument Gulch [July] (18; RTBe), North Fork Cache la Poudre River [June] (2; RTBe), Zimmerman Lake [Aug.] (5; RTBe), West Fork Sheep Creek (16 miles W of Teds Place [3050 m]) [Aug.] (3; CNC); Park County, Kenosha Pass [July] (1; CAS); Rocky Mountain National Park, Blue Lake [July] (3; RTBe), Chasm Lake (stream below) [Aug.] (3; CArm), Endovalley Campground [Aug.] (4; RTBe), Fall River ([2620 m]) [Aug.] (1; UASM), Hang Lake [Aug.] (1; RTBe), Lake Hiayaha [Aug.] (3; UAFA), Longs Peak ([3050–3350 m] and Boulder Field [3840 m], Larkspur Creek) [July–Aug.] (27; CArm, CAS), Thunder Lake ([3080 m] and Thunder Lake Trail [2500–3350 m]) [June] (2; CArm); Routt County, Walton Creek (above Dumont Lake [2900–2960 m]) [Aug.] (3; CAS); Teller County, Divide (8 miles S on Cripple Creek Road [2900 m]) [July] (2; CNC). WYOMING: Albany County, Brooklyn Lane ([3200 m]) [July] (18; CAS), Centennial [Aug.] (1; MSU), Douglas Creek (1 mile SSE of Keystone [2440 m]) [July] (16; CAS), Laramie Peak (south slope at Friend Creek [2440 m]) [July] (20; CAS), Little Brooklyn Lake ([3120 m]) [July] (8; CAS), Snowy Range Pass ([3200 m]) [June] (8; UASM); Carbon County, South Brush Creek (20 miles SE of Saratoga [2470 m]) [July] (1; CAS), Hidden Treasure Gulch (11.5 miles WSW of Encampment [2870 m]) [July] (2; CAS), Silver Lake ([3170 m]) [July] (2; USNM), Slaughterhouse Gulch (11 miles SW of Encampment [2870 m]) [July] (6; CAS).

Specimens Without Locality Data: (1; USNM).

Nomenclatural Changes

Since my last two reports on Nearctic *Nebria* (Kavanaugh 1979 and 1981), additional specimens and data about geographical and habitat distribution have also accumulated for previously described taxa. Study of these specimens and data, re-examination of some previously studied materials, and re-evaluation of species and subspecies concepts developed in previous reports (Kavanaugh 1978, 1979, and 1981) lead me to propose the nomenclatural changes presented below. More complete discussions of proposed synomymies and changes in status of names will be presented in a forthcoming monography of Nearctic *Nebria.*

Nebria intermedia Van Dyke, 1949:49 [=*Nebria crassicornis intermedia* Van Dyke—New Status].

Analysis of the pattern of geographical variation shown by samples representing *Nebria crassicornis* Van Dyke (1925:121) and *N. intermedia* Van Dyke throughout their ranges suggests that these taxa represent allopatric forms that are clearly differentiated but not to a degree typical of closely related, sympatric species. I suggest that they be considered subspecies of a single species, *N. crassicornis.*

Nebria sonorae Kavanaugh, 1981:438 [=*Nebria acuta sonorae* Kavanaugh—New Status].

My description of *N. sonorae* was based on only one male and two female specimens. These specimens were only slightly, but consistently, different from specimens of *Nebria acuta acuta* Lindroth in several characters of external structure. However, form of the aedeagus of the male specimen (chosen as holotype) was so different from that of *N. acuta acuta* males that I had no doubt concerning specific distinctiveness of the two taxa.

Several additional male specimens of *N. sonorae* recently collected and studied all have aedeagi with form typical of *N. acuta acuta* males. I now conclude that the aedeagus of the holotype male of *N. sonorae* is not typical for that taxon and, further, that the two forms are conspecific. However, differences in external structural characters between specimens of *N. sonorae* and *N. acuta acuta* are both consistent and sufficient to support their status as allopatric subspecies of a single species.

Nebria fragilis Casey, 1924:21 [=*Nebria arkansana fragilis* Casey—New Status].
Nebria arkansana uinta Kavanaugh, 1979:102 [=*Nebria arkansana fragilis* Casey—New Synonymy].
Nebria fragilis teewinot Kavanaugh, 1979:103 [=*Nebria arkansana fragilis* Casey—New Synonymy].

Males of *Nebria arkansana arkansana* Casey and *N. a. edwardsi* Kavanaugh differ distinctly from males of "*Nebria fragilis* Casey" in form of aedeagus and in several characters of external structure. Male specimens from the Uinta and northern Wasatch Mountains of northern Utah share aedeagal form with males of the two *N. arkansana* subspecies just mentioned, yet differ from them slightly in characters of external structure. I therefore recognized (Kavanaugh 1979) these specimens as representing a distinct subspecies of *N. arkansana,* namely *N. a. uinta.* Male specimens from the Teton, Wind River, and adjacent Mountains in western Wyoming share aedeagal form with males of *N. fragilis*; but, again, they differ from the latter in several characters of external structure and color. Based on these similarities and differences, I recognized (Kavanaugh 1979) the Wyoming specimens as representing a distinct subspecies of *N. fragilis,* namely *N. f. teewinot.* The resulting pattern of geographical distribution was one in which the range of all subspecies of both *N. arkansana* and *N. fragilis* were mutually allopatric, although ranges of *N. arkansana uinta* and *N. fragilis fragilis* were essentially parapatric in northcentral Utah.

Since 1979 I have studied additional material from areas that previously represented gaps between the allopatric ranges of described subspecies, and I re-examined specimens studied earlier. These studies have shown that samples of males from localities in presumed gaps, as well as some samples from localities bordering these gaps, are mixed in aedeagal form and intermediate in characters of external structure in relation to respective allopatric forms. Such findings lead me to conclude that *N. arkansana* and *N. fragilis* are conspecific. Specimens representing *N. arkansana uinta, N. fragilis fragilis,* and *N. f. teewinot* all share a combination of structural features which distinguish them from members of other *N. arkansana* subspecies. I therefore suggest that these forms (and respective intermediates between them) together represent a single, distinct subspecies of *N. arkansana* for which the name *N. arkansana fragilis* has priority. A reconstruction of the historical development of the complex pattern of geographical variation within this subspecies will be presented in the monograph now in preparation.

Nebria trifaria tetonensis Erwin and Ball, 1972:95 [=*Nebria trifaria trifaria* LeConte—New Synonymy].

Based on an almost continuous series of samples (all collected after 1972) from the area between respective type localities for *N. trifaria trifaria* and *N. trifaria tetonensis,* I suggest that these two nominal taxa represent simply the extremes of continuous clinal variation in those characters previously used to distinguish their members.

Nebria trifaria piute Erwin and Ball, 1972:95 [=*Nebria piute piute* Erwin and Ball—New Status].

Members of *Nebria piute* and *N. trifaria* LeConte differ from each other at least as much as other closely related, but sympatric, species in characters of both external structure and genitalia (of both males and females). I therefore suggest that they represent distinct species.

Nebria trifaria utahensis Kavanaugh, 1979: 110 [=*Nebria piute utahensis* Kavanaugh—New Status].

Based on form of aedeagus of males and bursa copulatrix of females, *N. utahensis,* described as a subspecies of *N. trifaria* LeConte, should instead be considered a subspecies of *N. piute,* along with *N. piute sevieri* n.ssp. described above.

Literature Cited

Casey, T. L. 1924. Additions to the known Coleoptera of North America. Memoirs on the Coleoptera, 11:1–347.

Erwin, T. L., and G. E. Ball. 1972. Classification of the ovipennis and trifaria groups of *Nebria* Latreille (Coleoptera: Carabidae: Nebriini). Proceedings of the Biological Society of Washington, 85:77–108.

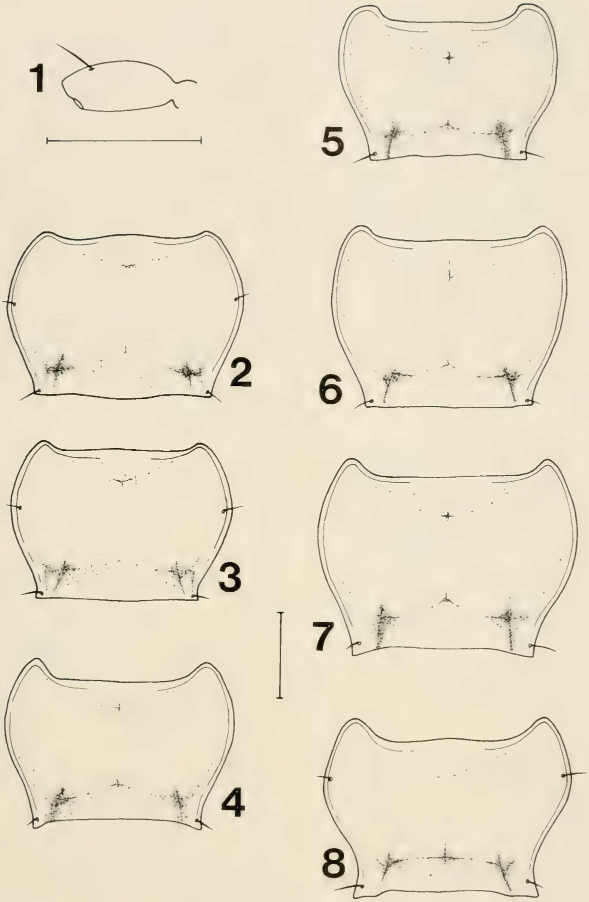
Kavanaugh, D. H. 1978. The Nearctic species of *Nebria* Latreille (Coleoptera: Carabidae: Nebriini): classification, phylogeny, zoogeography, and natural history. Unpublished Ph.D. dissertation. Department of Entomology, University of Alberta. xlviii + 1041 pp.

———. 1979. Studies on the Nebriini (Coleoptera: Carabidae), III. New Nearctic species and subspecies, nomenclatural notes, and lectotype designations. Proceedings of the California Academy of Sciences, 42:87–133.

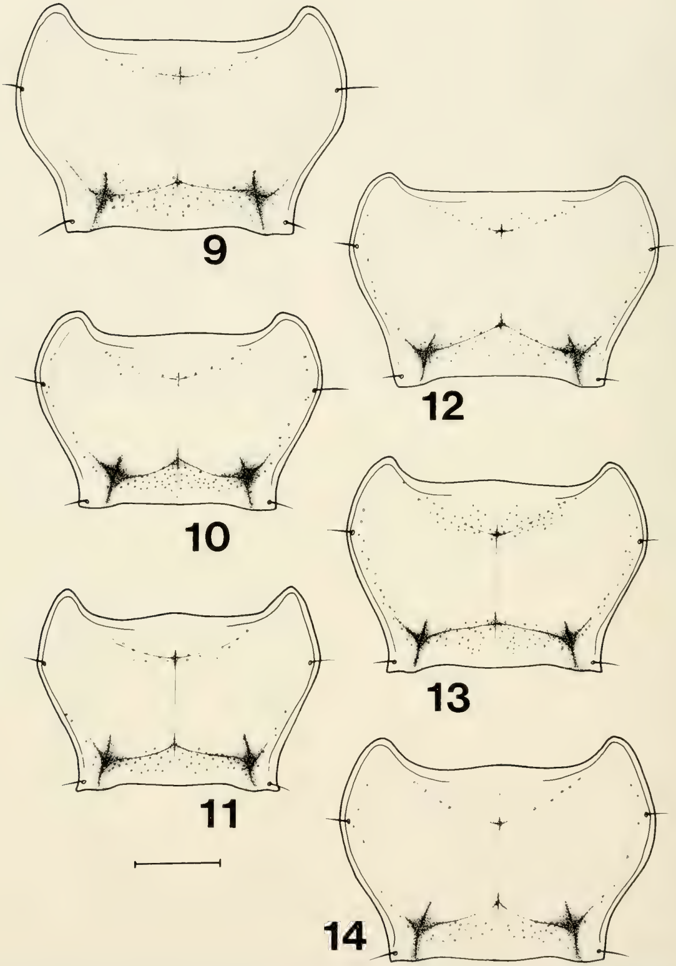
———. 1981. Studies on the Nebriini (Coleoptera: Carabidae), IV. Four new *Nebria* taxa from western North America. Proceedings of the California Academy of Sciences, 42:435–442.

Van Dyke, E. C. 1925. Studies of western North American Carabinae with descriptions of new species. The Pan-Pacific Entomologist, 1:111–125.

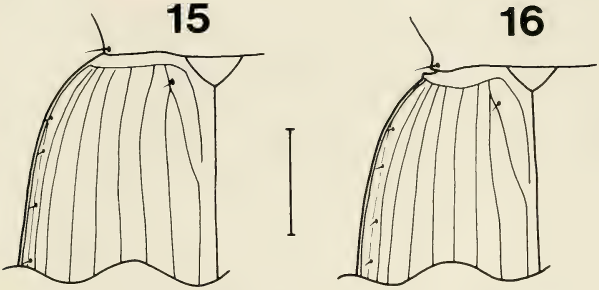
———. 1949. New species of North American Coleoptera. The Pan-Pacific Entomologist, 25:49–56.



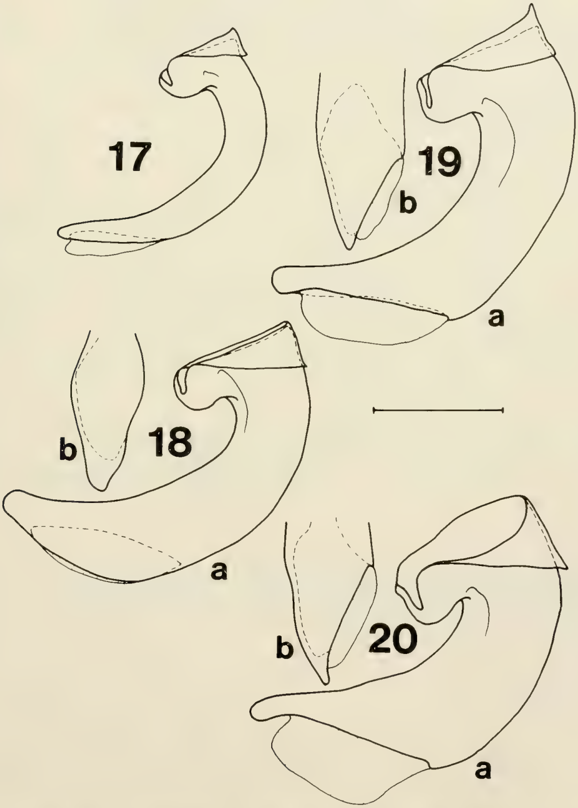
FIGURES 1–8. Fig. 1. Right antennal scape, dorsal aspect, *Nebria gebleri albimontis* n.ssp. (Birch Creek, California); scale line = 1.0 mm. Figs. 2–8. Pronotum, dorsal aspect; scale line = 1.0 mm. 2. *Nebria altisierrae* n.sp. (Olmsted Point, California). 3. *Nebria campbelli* n.sp. (Mount Baker, Washington). 4. *Nebria wallowae* n.sp. (West Fork Wallowa River, Oregon). 5. *Nebria jeffreyi* n.sp. (South Fork McCoy Creek, Oregon). 6. *Nebria haida* n.sp. (Mount Needham, Queen Charlotte Islands, British Columbia). 7. *Nebria louiseae* n.sp. (Skedans, Queen Charlotte Islands, British Columbia). 8. *Nebria gebleri albimontis* n.ssp. (Birch Creek, California).



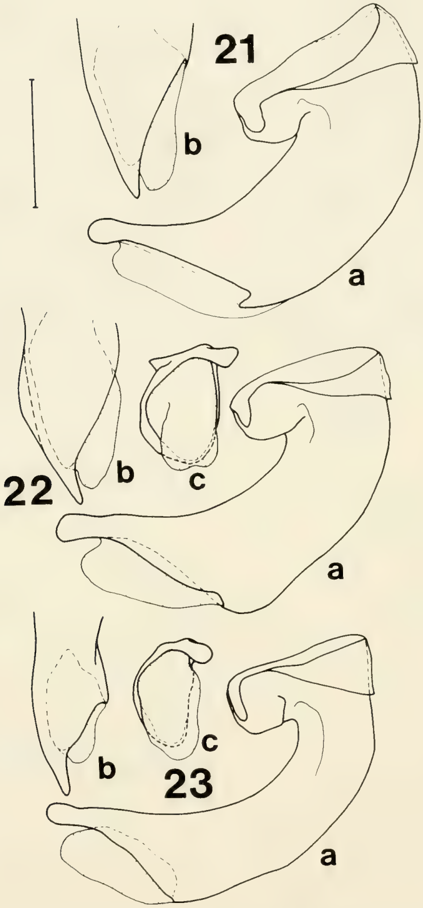
FIGURES 9–14. Pronotum, dorsal aspect; scale line = 1.0 mm. 9. *Nebria labontei* n.sp. (West Fork Wallowa River, Oregon). 10. *Nebria calva* n.sp. (Mount Baldy, Arizona). 11. *Nebria sierrablancae* n.sp. (Sierra Blanca, New Mexico). 12. *Nebria piute sevieri* n.ssp. (Parowan Creek, Utah). 13. *Nebria steensensis* n.sp. (South Fork McCoy Creek, Oregon). 14. *Nebria trifaria pasquineli* n.ssp. (Lefthand Creek, Colorado).



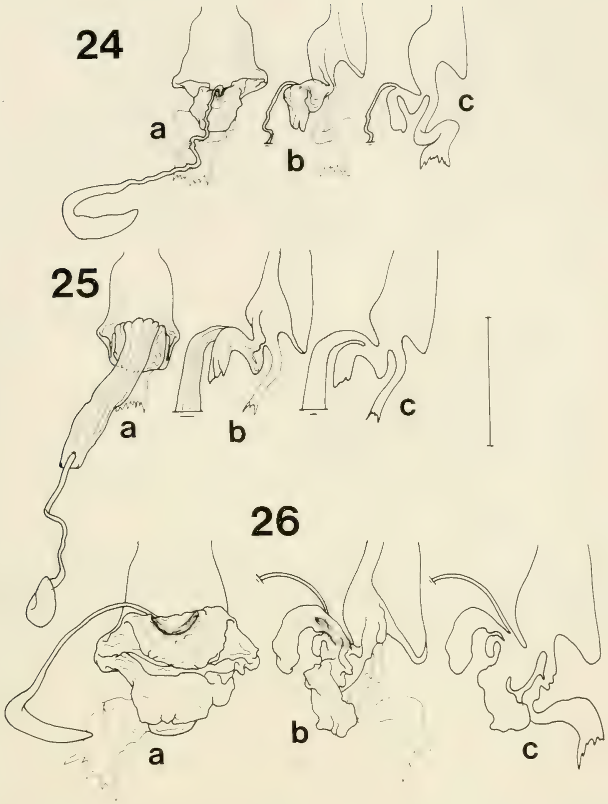
FIGURES 15–16. Basal region of left elytron, dorsal aspect; scale line = 1.0 mm. 15. *Nebria altisierrae* n.sp. (Olmsted Point, California). 16. *Nebria campbelli* n.sp. (Mount Baker, Washington).



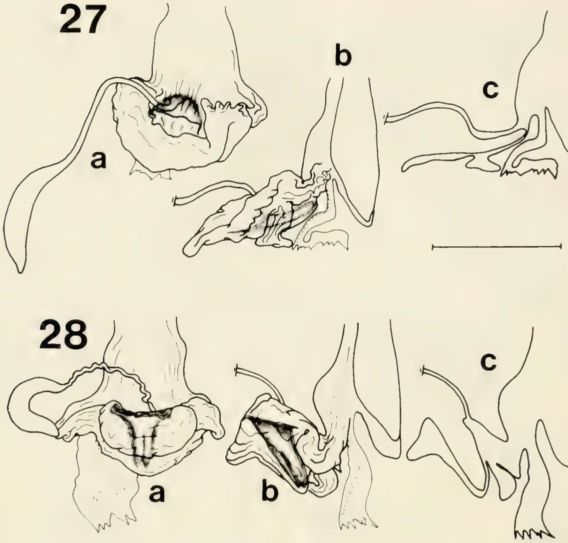
FIGURES 17–20. Median lobe of male genitalia, left lateral aspect (or a = left lateral aspect, b = ventral aspect); scale line = 1.0 mm. 17. *Nebria wallowae* n.sp. (West Fork Wallowa River, Oregon). 18. *Nebria gebleri albimontis* n.ssp. (Birch Creek, California). 19. *Nebria calva* n.sp. (Mount Baldy, Arizona). 20. *Nebria sierrablancae* n.sp. (Sierra Blanca, New Mexico).



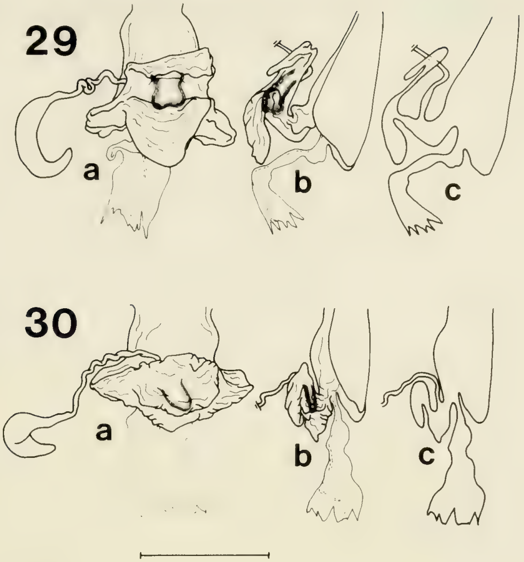
FIGURES 21–23. Median lobe of male genitalia (a = left lateral aspect, b = ventral aspect, c = apical aspect); scale line = 1.0 mm. 21. *Nebria piute sevieri* n.ssp. (Parowan Creek, Utah). 22. *Nebria steensensis* n.sp. (South Fork McCoy Creek, Oregon). 23. *Nebria trifaria pasquineli* n.ssp. (Lefthand Creek, Colorado).



FIGURES 24–26. Bursa copulatrix of female (a. dorsal aspect; b. left lateral aspect; c. mid-sagittal outline, left lateral aspect); scale line = 1.0 mm. 24. *Nebria wallowae* n.sp. (West Fork Wallowa River, Oregon). 25. *Nebria gebleri albimontis* n.ssp. (Birch Creek, California). 26. *Nebria calva* n.sp. (Mount Baldy, Arizona).



FIGURES 27–28. Bursa copulatrix of female (a. dorsal aspect; b. left lateral aspect; c. mid-sagittal outline, left lateral aspect); scale line = 1.0 mm. 27. *Nebria sierrablancae* n.sp. (Sierra Blanca, New Mexico). 28. *Nebria piute sevieri* n.ssp. (Parowan Creek, Utah).



FIGURES 29–30. Bursa copulatrix of female (a. dorsal aspect; b. left lateral aspect; c. mid-sagittal outline, left lateral aspect); scale line = 1.0 mm. 29. *Nebria steensensis* n.sp. (South Fork McCoy Creek, Oregon). 30. *Nebria trifaria pasquineli* n.ssp. (Lefthand Creek, Colorado).

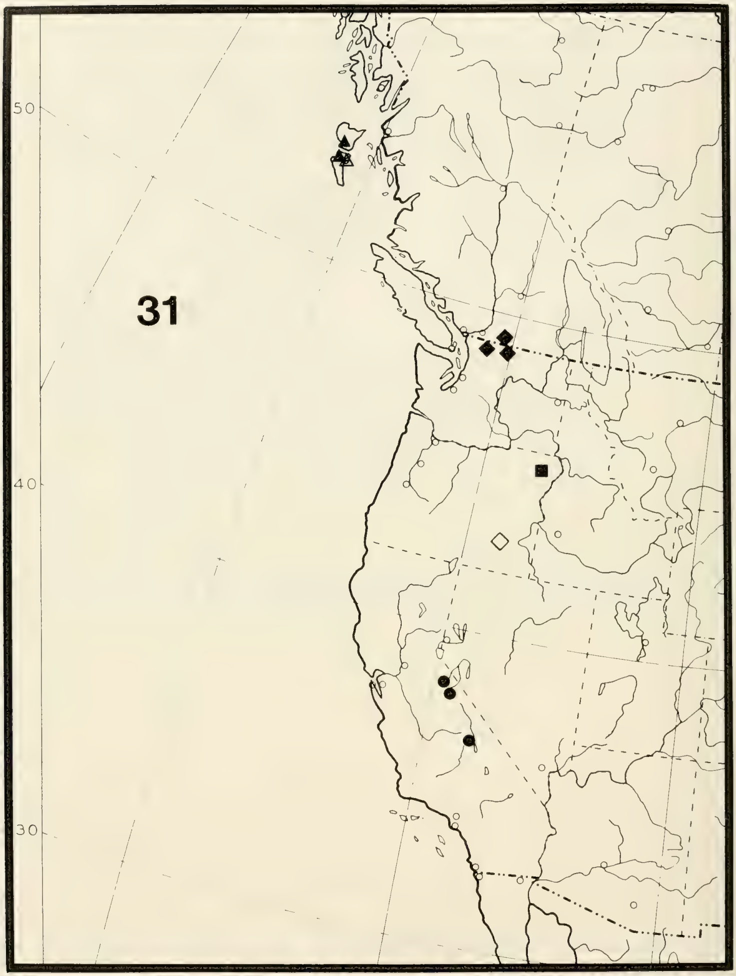


Figure 31. Map of geographical distributions: *Nebria altisierrae* n.sp. = solid circle; *Nebria campbelli* n.sp. = solid diamond; *Nebria wallowae* n.sp. = solid square; *Nebria jeffreyi* n.sp. = open diamond; *Nebria haida* n.sp. = solid triangle; *Nebria louiseae* n.sp. = open triangle.

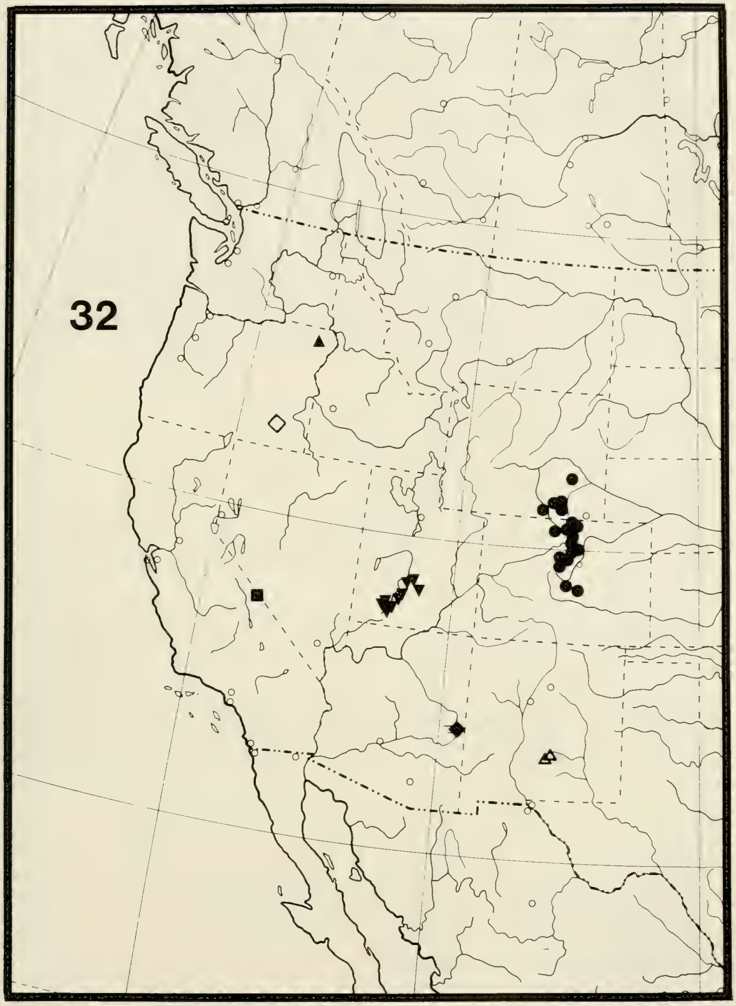


FIGURE 32. Map of geographical distributions: *Nebria gebleri albimontis* n.ssp. = solid square; *Nebria labontei* n.sp. = solid triangle; *Nebria calva* n.sp. = solid diamond; *Nebria sierrablancae* n.sp. = open triangle; *Nebria piute sevieri* n.ssp. = inverted solid triangle; *Nebria steensensis* n.sp. = open diamond; *Nebria trifaria pasquineli* n.ssp. = solid circle.

PROCEEDINGS
OF THE
CALIFORNIA ACADEMY OF SCIENCES

Vol. 43, No. 13, pp. 179-220, 22 figs., 2 tables. July 12, 1984

SKELETAL ANATOMY AND CLASSIFICATION OF THE NEOTENIC ASIAN SALMONIFORM SUPERFAMILY SALANGOIDEA (ICEFISHES OR NOODLEFISHES)

By
Tyson R. Roberts
California Academy of Sciences, Golden Gate Park, San Francisco, California 94118

Abstract: The distinctive, largely cartilaginous skeletal anatomy of the Asian icefishes or noodlefishes is described and figured from cleared specimens stained with alcian and alizarin. This information, together with examination of types and other material in North American and European museums, leads to the following revised classification of these neotenic Salmoniformes:

Salangoidea new superfamily (coordinate with Osmeroidea, Salmonoidea)
  Salangidae
  Protosalanginae: *Protosalanx chinensis*
  Salanginae: *Salanx (Salanx) ariakensis, S. (S.) cuvieri, S. (Hemisalanx) prognathus, S. (Leucosoma) reevesi*
  Salangichthyinae new subfamily: *Neosalanx andersoni, N. brevirostris, N. jordani, N. reganius, Salangichthys ishikawae, S. microdon*
  Sundasalangidae: *Sundasalanx microps, S. praecox*

The introduction includes a summary of salangoid natural history and a key for their identification. The systematic account includes all primary and secondary synonyms of genera and species recognized. New information is presented on pectoral girdle morphology in teleosts, relationships of salangoids and other salmoniforms, and breeding tubercles, meristic variation, and neoteny in salangoids.

INTRODUCTION

The slender, soft-bodied, and transparent or translucent salmoniform fishes of the family Salangidae inhabit the sea coasts, rivers, and lakes of East Asia including Japan from Sakhalin, Vladivostok, and the Amur River south to northern Vietnam (Tonkin). The greatest concentration of genera and species is in China and Korea. Of 11 species herein recognized, eight occur in China, eight or nine in Korea, and four in Japan. Only *Salangichthys microdon* occurs along the outer coast of Korea and in Siberia, and only *Salanx reevesi* and *Neosalanx brevirostris* have been reported as far south as Tonkin (or Haiphong).

Members of the Salangidae have almost always been referred to in English as icefishes. In Japanese, however, they are usually referred to as *shirauwo* (whitefishes) and rarely as *hiagio* (icefishes). In Russian they are usually referred to as *lapsha-ryba* or noodlefish, and an equivalent name exists in Chinese, *mien-tiao-yu* (麵條魚). They have been referred to as *Nudelfische* in German, but noodlefishes, a highly appropriate and distinctive name, seems not to have appeared in English except in a translation of a Russian work (Berg 1962:480). The flesh is tasty, whether cooked as a soup, eaten with vinegar or scrambled eggs, or fried (Okada 1955:60). The species most commonly eaten in Japan is *Salangichthys microdon,* and in China probably *Neosalanx brevirostris* or *N. jordani. Protosalanx* and *Salanx* are also consumed, but I doubt that tiny *Sundasalanx* has ever been dined upon.

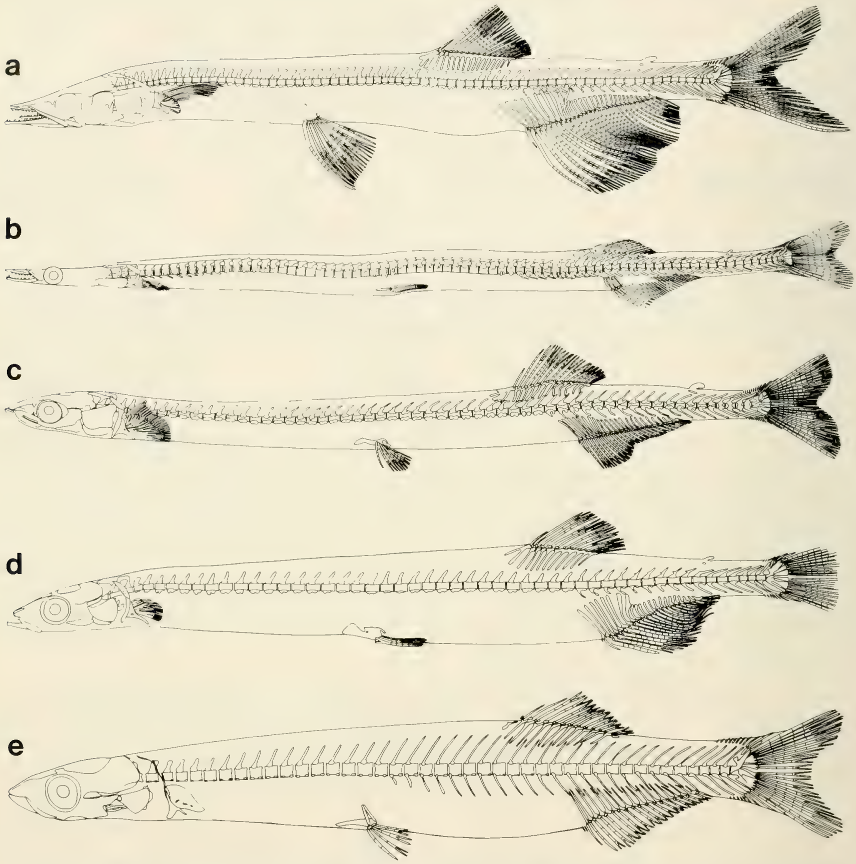


FIGURE 1. Axial skeleton. (a) *Protosalanx chinensis,* CAS-SU 6306, 85.5-mm adult male; (b) *Salanx cuvieri,* CAS-SU 32454, 61.7-mm juvenile sex undetermined; (c) *Salangichthys ishikawae,* CAS 6780, 74-mm adult female; (d) *Neosalanx jordani,* CAS 52028, 38.3-mm adult male; (e) *Sundasalanx microps,* CAS 44220, 17-mm adult sex undetermined.

Despite their standing as a delicacy—sufficient for them to be imported by the Chinese and Japanese communities of San Francisco and served in the city's sushi bars—relatively little is known about the systematics and biology of noodlefishes. An impression of their morphological diversity can be obtained from Figures 1 and 2.

The present study was undertaken in connection with the discovery of some minute, scaleless, and transparent fishes during my fieldwork in the Malay Peninsula (1971, 1973) and on the Kapuas River in Kalimantan Barat, Indonesia (1976). When first found, although in fresh water, they were living close to the sea and were mistaken for elopoid leptocephali, which they resemble only superficially. In the Kapuas River, however, they were living 800 km upriver in the midst of a rich riverine fish fauna dominated by Ostariophysi and with no elopoids. The observation that the maxillary bones curved inwards below

TABLE 1. REPRODUCTIVE BIOLOGY OF SALANGOIDS (Wakiya and Takahasi 1937, Okada 1960, Senta 1973a, b, Roberts 1981, and pers. obs.).

	Smallest mature male (mm)	Largest male (mm)	Largest female (mm)	Diameter egg (mm)	Fecundity	Remarks
Protosalanx chinensis	82	168	146	1.15	—	Breeds January–February (Korea)
Salanx ariakensis	—	—	147	0.75	—	Breeds October–November (Korea)
Salanx cuvieri	—	—	144	—	—	—
Salanx prognathus	100	111	119	0.85	—	Breeds April–May
Salanx chinensis	130	130	153	—	—	—
Neosalanx andersoni	79	100	95	—	—	Breeds April–May (Korea)
Neosalanx brevirostris	—	64	60	0.7	—	—
Neosalanx jordani	34	56.5	59.5	0.5	—	Breeds March–May
Neosalanx reganius	—	56	58	0.9	—	Breeds February–March
Salangichthys ishikawae	—	71	74	0.95	—	Breeds April–May
Salangichthys microdon	65	90	100	0.91–0.99	1300–2700	Breeds March–May
Sundasalanx microps	—	—	—	—	—	Largest specimen (sex unknown) 19.9 mm
Sundasalanx praecox	14.9	18.3	17.3	0.20–0.25	50	Both sexes ripe in June

the head led to an hypothesis that they are salangoids, and observations of their skeletal anatomy and particularly the suspensorium confirmed this (Roberts 1981). These fishes differ in a number of respects from Salangidae and constitute a separate family, Sundasalangidae, with one genus, and two or more species, one in the Malay Peninsula and one or two in the Kapuas River (Roberts 1981). *Sundasalanx* also occur in the Mekong basin, as reported herein. This is the only truly tropical genus in the entire order Salmoniformes. *Sundasalanx praecox,* with males and females sexually ripe at only 14.9 mm, is the smallest member of the order, and provides a striking example of a minute secondary freshwater fish living in the midst of a rich freshwater ichthyofauna dominated by primary freshwater Ostariophysi.

Interest in Sundasalangidae and its relationships led me to examine other salangoids but my observations and drawings quickly became too extensive to incorporate in the original description of the new taxa; hence the present monograph.

Food Habits

All salangoids, including tiny *Sundasalanx,* appear to be predators. The largest species, *Protosalanx chinensis* and *Salanx reevesi,* both with well-developed teeth on the tongue and jaws, apparently feed mainly on fishes. *Salangichthys microdon* taken in the Takahashi River had fed on larvae of the goby *Chaenogobius* sp. and on the mysid shrimp *Neomysis* sp. (Senta 1973b). Other species of Salanginae and Salangichthyinae feed mainly on small crustacea (in marine environments) or on insects (in fresh water). *Sundasalanx* are known only from fresh water and feed on tiny insects (Roberts 1981).

Reproduction

While some species are primarily marine or at least brackish water inhabitants (e.g., *Protosalanx chinensis*), and many spend part of their lives in the sea, others are restricted to fresh water or have populations which presumably repeat their life cycle without leaving fresh water. Basic information on salangoid reproductive biology is summarized in Table 1. Fecundity ranges from several thousand eggs in Protosalanginae and Salanginae (no precise numbers available) down to only about 50 in Sundasalangidae.

The external egg membrane is adhesive, eggs becoming attached to any solid object at the spawning site. Wakiya and Takahasi (1937, pl. 21) published drawings of the basal portion of the adhesive strands on the eggs of *Protosalanx chinensis, Salanx ariakensis* and *S. prognathus, Salangichthys microdon* and *S. ishikawae,* and *Neosalanx jordani.* The eggs illustrated are presumably ovarian, since the adhesive strands are not detached. For photomicrographs of the

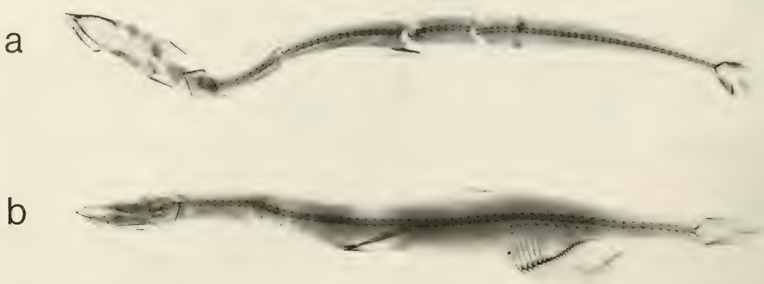


FIGURE 2. Radiographs. (a) *Salanx cuvieri,* MNHN 9900, 112 mm, holotype; (b) *Neosalanx andersoni,* NRM 10287, 79 mm, holotype.

spawned eggs with detached adhesive threads of unfertilized and fertilized eggs of *Salangichthys microdon* see Okada (1960, pl. 18). Spawning ecology of this species is described by Senta (1973a). According to Wakiya and Takahasi (1937:269), after spawning "the body becomes very lean and the vertebrae become visible through the skin, whence it is generally assumed that death then ensues." I suspect that this is true in Salanginae as well as Salangichthyinae but not in *Protosalanx.*

Sexual Dimorphism

A notable feature of salangoids is their unique sexual dimorphism. In all Salangidae except *Neosalanx,* sexually mature males have the pectoral fins longer and more pointed (falcate) and the pelvic fins larger. In all adult male Salangidae the anal fin is larger than in females and has modified rays. The anterior rays of the anal fin are greatly enlarged, the middle rays thin and strongly curved, and the posterior rays short and widely separated at the base. The morphology of the anal fin is very similar in sexually mature males of all of the genera and species of Salangidae. In all Salangidae, mature males have a row of large, tightly adherent scales on the body parallel to the anal fin base (sometimes extending posteriorly a short distance beyond the anal fin base onto the caudal peduncle). The number of anal scales ranges from 14 to 28. Sexual dimorphism has not been observed in Sundasalangidae.

Although salangids differ greatly in the size of adult males, the morphology of the modified male anal fin is remarkably uniform (Fig. 1a, d). The total range of anal fin-rays is 23–32. The first two or three rays are simple, the first one or two small or minute. The last simple ray and the first four to six branched rays are greatly enlarged and somewhat thickened; near the base of each of these rays is a very large lateral projection. The next 12 or so rays are noticeably thinner and are deflected backwards near the middle of their length, so that their distal portions lie close together. In *Protosalanx* these rays are simple, but in other Salangidae they are branched. The posteriormost rays may be simple or branched, are reduced in size and not modified, except that their bases tend to be relatively wide apart (much more so than the bases of the preceding rays or of the corresponding rays in females), especially in Salanginae. The proximal pterygiophores, especially for the anterior portion of the anal fin, are also enlarged in males. In alcian-alizarin preparations the anal fin-rays and pterygiophores of sexually mature males are deeply stained with alizarin, whereas those of females tend to be less well stained with alizarin or in some instances stained only with alcian.

Near the middle of the rays in the most modified part of the male anal fin, a tough, almost tendonlike membrane arises from each ray and extends obliquely and posteroventrally across the densely webbed portion of the fin to end in a thickened, obliquely oriented non-muscular pad of tissue. The distal portion of this oblique pad is free from the surface, so it can be readily lifted, and even when not lifted forms a sort of groove for the length of the pad. This portion of the anal fin can be flexed in such a way that it forms a slight concavity. The fin may be expanded manually by pulling on the anteriormost rays; when released, it snaps back into a less expanded condition. Spawning behavior has not been reported upon, but presumably the male's anal fin remains in contact with the vent region of the female in such a way that it temporarily retains eggs and sperm in proximity while fertilization occurs externally.

In addition to the modified anal fin, sexually mature males of all Salangidae bear a row of large, cycloid scales on the side of the body above and co-extensive with the anal fin or extending a short distance beyond it onto the caudal peduncle. The scales are tightly adherent and broadly overlapping (more so anteriorly than posteriorly). In addition to the main row of anal scales, some specimens exhibit two or three smaller scales in a separate row overlying the vent. These usually have been overlooked by previous authors, and are not included in the counts of anal scales in Table 2.

Breeding tubercles and other forms of temporary sexual dimorphism have not been reported previously in salangoids. I have observed breeding tubercles in adult males and females, apparently in spawning condition, of *Protosalanx chinensis,* and in adult males of *Salangichthys microdon* and *Neosalanx jordani.* This presumably temporary tuberculation is most extensive and easily observable in an 120-mm male *Protosalanx* (CAS-SU 36025). In this specimen breeding tubercles occur on the anal, pectoral and pelvic fins, abdominal keel, and head. The strong lateral projections on the anterior face of the first nine branched anal fin-rays are entirely or almost entirely covered by a thickened, longitudinal band of thickened skin 9 mm long and 1.2 mm high. The surface of this spongy band of skin is covered with hundreds of small, overlapping, scale- or leaflike breeding tubercles, with their raised free margins projecting anteriorly. There are about 12–20 of these tubercles in a vertical series. Discrete pads of similarly thickened skin covered with similar breeding tubercles extend obliquely posteroventrally on the basal third of the first five branched anal fin-rays. There are up to eight tubercles across each ray. The skin on the middle third of the same rays appears to be only slightly thickened and bears only a few, small widely spaced, low-lying round (not scalelike) tubercles. The distal third or branched portion of the first eight branched rays is covered with thick skin densely coated with scalelike tubercles. There are up to about eight tubercles across each ray-branch. The leading edge of the third (enlarged) simple anal fin-ray bears a thick, lamellar projection of skin, 11.5 mm long and up to 2.2 mm wide, covered with widely scattered, low-lying round tubercles without free margins. The midventral abdominal keel is also notably thickened, and covered with minute, closely spaced round or granular tubercles which extend for a short distance onto the abdomen and sides of the body just anterior to the anal fin. The pelvic and pectoral fins bear round tubercles dorsally and ventrally; these are most noticeable on the enlarged outermost pectoral fin-ray. The dorsal fin is slightly tuberculate, the adipose and caudal fins non-tuberculate. The dorsal, lateral, and ventral surfaces of the head bear irregularly scattered, round, low-lying tubercles without free margins. These are largest and most numerous on its ventral surface. The skin of the oral margin of the upper and lower jaws and gular margin of the lower jaw is thickened and tuberculate. Fine granular projections, which may be minute breeding tubercles, extend in a dorsomedian longitudinal band from the dorsal fin origin anteriorly halfway to the occiput. In the two gravid females the skin is less modified, and although tuberculation is very much lighter, there are small, low-lying round tubercles on the anal, pelvic, and pectoral fins and on the head. In one of them the skin on the jaws is thickened as in the male; in the other it is not. The first female has the median abdominal fold somewhat thickened, suggestive of the more pronounced thickening of this fold seen in the male; the other female does not. Tubercles have not been observed in females of any other salangoid.

In other salangoids breeding tubercles have been observed only on the anal fin of males. An 83.1-mm male *Salangichthys microdon* (CAS 52033) has small scalelike breeding tubercles on the branched portion of the anteriormost branched anal fin-rays. These are arranged uniserially on each fin-ray branch. A 47.5-mm male *Neosalanx jordani* (AMNH 51704) has very similar scalelike tubercles on thickened skin surrounding the lateral projection at the base and on the basal half of the first four branched anal fin-rays (which are enlarged); fin-rays 6–14, which are bent, each have three to four melanophores on the basal one-fourth of their length. (Similar coloration has been observed on the anal fin in occasional males of *Salangichthys microdon.*)

Breeding tubercles apparently do not occur in Sundasalangidae, in which neither secondary sexual dimorphism nor dichromatism has been observed.

Pigmentation

The only pigmentation known to be exhibited by salangoids, apart from that of their eyes, is in melanocytes or melanophores, which tend to occur as widely separated single cells or isolated clumps of relatively few cells. In life all, or almost all, salangoids (except *Protosalanx*) are transparent or translucent, except for the prominent eyes. The most constant pigmentary feature of the salangoids is a row of melanophores at the interface of the ventral myotomic musculature and the non-segmentally muscularized ventral abdominal wall. This series of melanophores, with a single cell at about the middle of the ventral end of each myotome, from the most anterior myotome to the anal fin origin, is present in nearly all salangoid specimens examined. Usually these melanophores are longitudinally elongate, giving the appearance of a series of widely spaced thin black dashes. A second pigmentary feature found in many salangoids is a ventromedian row of widely spaced melanophores, one for each body segment. These melanophores tend to be dendritic when expanded or round when contracted, and may extend the entire length of the abdomen; sometimes they are restricted to the preanal membranous keel. These two pigmentary features of salangoids occur in many teleost larvae and in adults of other neotenic teleosts.

Some salangoids exhibit a row of melanophores along the anal fin base, one between each anal fin-ray. This row of melanophores, lying deep in the body and median rather than paired, may be the continuation of the midabdominal row of melanophores described above. This row usually extends the length of the anal fin; sometimes it continues beyond the anal fin onto the caudal peduncle near its ventral margin.

Clusters of a few melanophores occur just anterior to the bases of the pectoral and pelvic fins in most salangoids, at the tip of the snout and chin, especially in *Salangichthys,* and infrequently on the dorsal surface of the head overlying the fore- and hind-brain. In sexually mature (spawning?) males of *Salanx* and *Salangichthys* there may be a cluster of melanophores on the proximal portion of the middlemost anal fin-rays. The dorsal, anal, pectoral, and pelvic fins are otherwise usually devoid of melanophores, but the caudal fin lobes frequently are dark or dusky due to numerous fine melanophores. The anal scales of the males are always entirely devoid of melanophores.

In most salangoids the entire dorsal and most of the lateral body surfaces are devoid of melanophores. *Protosalanx chinensis* and *Neosalanx andersoni* provide notable exceptions. Young of *Protosalanx* and *Neosalanx* exhibit very few melanophores. Large and sexually ripe individuals of these two species, however, may have the dorsal and lateral surfaces of the body with numerous melanophores. Those on the dorsal body surface are fine, exceedingly numerous, and generally scattered over the entire musculature, but those on the sides are few and peculiarly restricted along the course of the myotomal septae. About a dozen melanophores lie on each myotomal septa; the melanophores of successive septae are more or less parallel to each other; the cells are obliquely elongate, conforming to the thinness and obliquity of the septae and thus forming a series of widely spaced thin black slashes. This pattern, sometimes barely evident or absent in *P. chinensis,* is very well developed in two gravid females of 129–132 mm (USNM 120746). Wakiya and Takahasi (1937) show it well developed in female *P. chinensis* (not gravid?) and *N. andersoni* (gravid); and relatively weakly developed in males of both species. It is present only on the upper part of the body in the relatively small male holotype of *N. andersoni* (NRM 10287, 79 mm). Chyung (1961) shows it well developed in a gravid *N. andersoni.* I have seen clupeomorphs but no osmeroids or other salmoniforms with similarly distributed melanophores.

Some Misconceptions

Some misconceptions about Salangidae should be noted. These concern the reported presence of scales other than anal scales, presumed absence of the swimbladder, and reputed oral brooding of eggs. The most persistent misinformation concerns the occurrence of scales on the body other than the anal scales. Günther (1866: 205) stated that the body is "naked or covered with small, exceedingly fine, deciduous scales (?)" and added in a footnote, "There is no trace of scales in specimens preserved in spirits for some time; but others, which we received lately, show scattered fragments of scales, without any regular arrangement." He was unaware of the anal scales of males. Regan (1908b:444), in diagnosing Salanginae (=Salangidae), stated simply "scales deciduous" but described the anal scales of males in a footnote. Fang (1934a:239) stated body "naked or with a few exceedingly thin, large, scattered, deciduous scales, without any regular arrangement" in addition to the anal scales of males. Nichols (1944) referred to several species with "scales small, deciduous, little evident." Nelson (1976:104) cautiously stated "body generally scaleless" without referring to the anal scales of males. As noted by Wakiya and Takahasi (1937) all salangids are totally scaleless except for the anal scales of sexually mature males; as noted above, the anal scales are large and strongly adherent. Reports of scales on other parts of the body are all attributable to dislodged scales from other fishes.

Various authors, including Günther (1866: 205), Fang (1934a:239), and Nelson (1976:104) have stated that salangids lack a swimbladder. Wakiya and Takahasi (1937:268, fig. 1) reported a physostomous swimbladder in *Protosalanx chinensis, Salanx ariakensis, S. prognathus, Neosalanx jordani, Salangichthys ishikawae,* and *S. microdon.* In *P. chinensis* and *S. ishikawae* the swimbladder is depicted as relatively large and oval, and in the others as equally long but almost uniformly slender for its entire length. The condition of the swimbladder in Sundasalangidae is unknown.

Fang (1934a:238, 252, fig. 7) suggested that Salangidae are oral brooders. In a series of 61 males and 27 females identified as *Hemisalanx* (=*Salanx*) *prognathus* collected at Chinkiang in April 1933, Fang found 6 males and 19 females with 1–21 eggs in the mouth. He also reported one *Protosalanx* (sex not mentioned) with eggs in its mouth. I have also observed a few specimens of both sexes, especially of Salanginae, with small numbers of eggs in the mouth; this is attributable to rupture of the ovaries and spillage of eggs after the fish had been caught. There is no information indicating that salangoids practice oral brooding or any other form of parental care.

This introduction to salangoids concludes with a key for their identification.

Key to Salangoidea

1a. Pelvic fin with 5 rays; adipose fin absent; pectoral fin rayless throughout life; sexually mature males without anal scales or enlarged anal fin; vertebrae 37–43; standard length to 22 mm (Sundasalangidae) 11

1b. Pelvic fin usually with 7 rays (rarely 6 or 8); adipose fin present; pectoral fin with rays except in larvae; sexually mature males with a row of large anal scales and enlarged anal fin; vertebrae 48–79; adults at least 35 mm in standard length (Salangidae) 2

2a. Teeth on palatal toothplate and lower jaw in two rows; teeth on tongue in two marginal rows or widely spread over basihyal toothplate (Protosalanginae) .... *Protosalanx chinensis*

2b. All oral teeth in single rows 3

3a. Head extremely depressed; snout very elongate and relatively pointed; cranial fontanel entirely closed in juveniles and adults; premaxillae larger than maxillae, those of opposite sides meeting broadly in front of snout; premaxillary teeth relatively large; supramaxilla absent; vertebrae 66–79 (Salanginae) 4

3b. Head moderately depressed; snout moderately elongate and broadly rounded; cranial fontanel with anterior and posterior portions open throughout life, premaxillae smaller than maxillae, more or less separated from each other in front of snout; premaxillary teeth relatively small, tiny, or absent; supramaxilla present; vertebrae 48–65 (Salangichthyinae) 7

4a. Tongue with a median row of conical teeth (subgenus *Leucosoma*) .... *Salanx reevesi*
4b. Tongue toothless 5

5a. Head strongly pointed; lower jaw not projecting beyond upper jaw; presymphyseal fleshy appendage, bone, and teeth frequently present in adults; vertebrae 72–79 (subgenus *Salanx*) 6
5b. Head less strongly pointed; lower jaw projecting slightly beyond upper jaw; no presymphyseal fleshy appendage, bone, or teeth; vertebrae 70–73 (subgenus *Hemisalanx*) .... *Salanx prognathus*

6a. Presymphyseal bone usually present in specimens over 100 mm standard length, relatively elongate and with up to 17 teeth on each side; vertebrae usually 77–78 (rarely 76 or 79) .... *Salanx cuvieri*
6b. Presymphyseal bone usually absent, or relatively short and with no more than 6 teeth on each side; vertebrae 72–75 .... *Salanx ariakensis*

7a. Palatal toothplate with minute teeth; premaxilla with numerous small or minute teeth, snout relatively elongate; vertebrae 59–65 (*Salangichthys*) 8
7b. Palatal teeth absent; premaxilla usually toothless or with 1–5 minute teeth; snout relatively short except in *Neosalanx andersoni*; vertebrae 48–65 (*Neosalanx*) 9

8a. Pectoral fin-rays 14–19 .... *Salangichthys microdon*
8b. Pectoral fin-rays 20–28 .... *Salangichthys ishikawae*

9a. Snout relatively short, standard length to 64 mm, males with 14–21 anal scales, vertebrae fewer than 60 10
9b. Snout relatively elongate, standard length to 100 mm, males with 20–28 anal scales, vertebrae 63–65 .... *Neosalanx andersoni*

10a. Vertebrae 55–59; standard length to 64 mm; total rakers on first gill arch 15–19 (mainland Asia) .... *Neosalanx brevirostris*
10b. Vertebrae usually 50–53, rarely 49 or 54; standard length usually less than 50 mm; total rakers on first gill arch 9–15 (mainland Asia) .... *Neosalanx jordani*
10c. Vertebrae 52–56, average 53.75 (after Wakiya and Takahasi 1937); standard length to 58 mm; total rakers on first gill arch 15 (known only from Ariake Bay, Kyushu, Japan) .... *Neosalanx reganius*

11a. Horizontal diameter of eye less than 4% of standard length; ceratobranchial 5 with 0–3 small conical teeth; total rakers on first gill arch 0–2; vertebrae 41–43 .... *Sundasalanx microps*
11b. Horizontal diameter of eye more than 5% of standard length; ceratobranchial 5 with about 8–10 large conical teeth; total rakers on first gill arch 10–12; vertebrae 37–41 .... *Sundasalanx praecox*

MATERIAL EXAMINED

Salangoid specimens deposited in the following institutions have been examined for this study: American Museum of Natural History, AMNH: British Museum (Natural History), BMNH; California Academy of Sciences, CAS, including specimens formerly deposited at Stanford University, CAS-SU; Museum national d'Histoire naturelle, Paris, MNHN; Naturhistoriska Riksmuseet, Stockholm, NRM: Museum of Zoology, University of Michigan, UMMZ; Smithsonian Institution, USNM; and Zoologisch Museum, Universiteit van Amsterdam, ZMA.

A detailed list of material examined (including alcian-alizarin preparations) is given under each species in the systematic account.

SKELETAL ANATOMY

Salangoid skeletal anatomy cannot be observed adequately from alizarin preparations because it is largely cartilaginous, and even ossified portions (including dermal bones) often fail to stain with alizarin. The only previous observations of salangoid skeletal anatomy are brief and relatively uninformative. The only general account, that of McDowall (1969:815), is limited to three paragraphs, one on the cranium, one on the jaws, and one on the remainder of the skeleton emphasizing the median fins. Wakiya and Takahasi (1937) figured toothed portions of the jaws, palate, and tongue of various salangids. Nelson (1970) described and figured the gill arches in *Salanx reevesi* and *Neosalanx brevirostris*

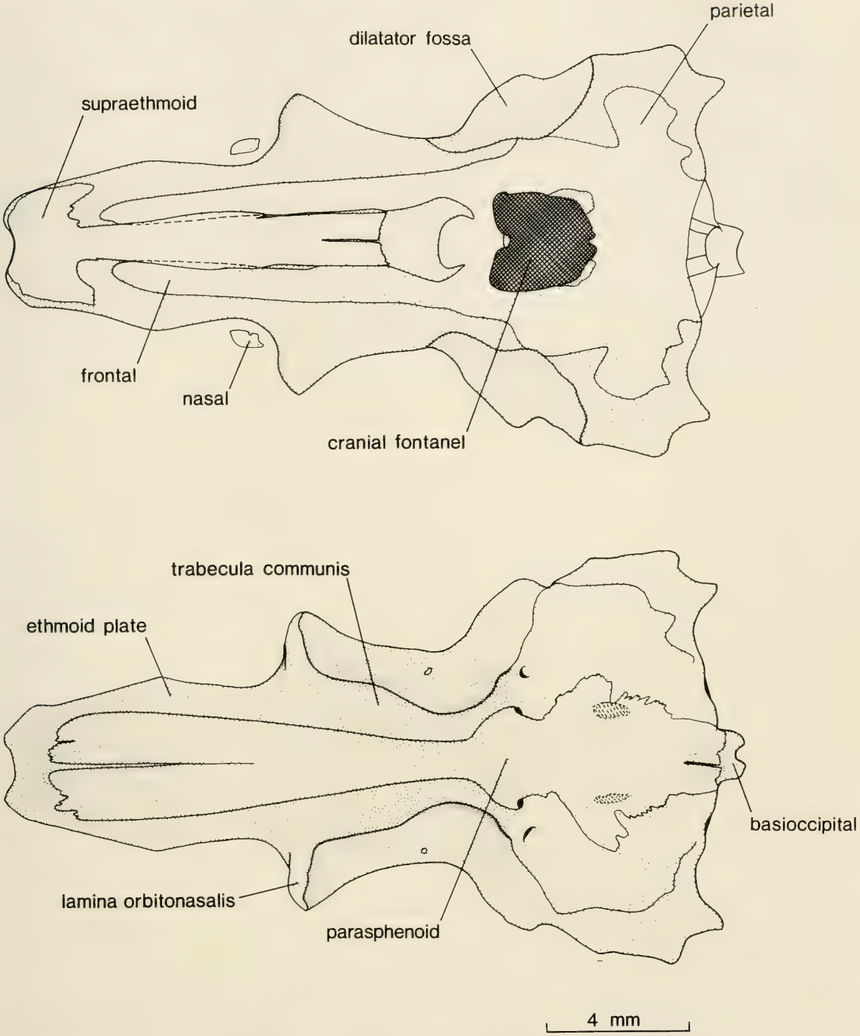


FIGURE 3. Dorsal and ventral view of cranium. *Protosalanx chinensis*, CAS-SU 6306, 158 mm.

(his *Salanx chinensis* and *Salangichthys microdon*). He particularly noted the well-developed fourth hypobranchials, "which so far as known are absent from all other adult teleostean fishes." My own observations and drawings of salangid gill arches agree closely with Nelson's. Rosen (1974; figs. 16g, 26a & b) figured and commented briefly upon the caudal skeleton and portions of the gill arches of *Neosalanx brevirostris* (his *Salangichthys microdon*).

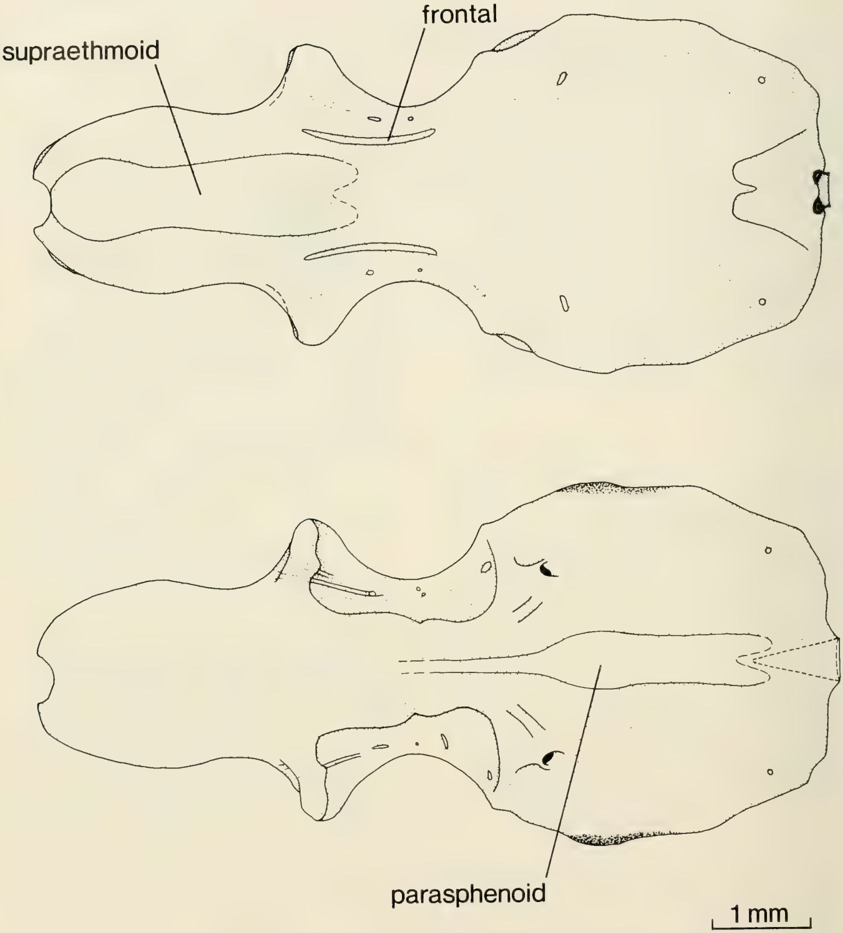


FIGURE 4. Dorsal and ventral view of cranium. *Salanx cuvieri,* CAS-SU 32454, 69.4 mm.

The advent of a technique for staining whole specimens with alcian and alizarin (Dingerkus and Uhler 1977) made the present relatively extensive observations possible but even so there have been difficulties. Some specimens stained well with alcian but not with alizarin, or vice versa, and in some specimens that otherwise stained well with both stains there are still portions of the skeleton which failed to take up noticeable amounts of either stain. Such difficulties could not always be made up for by staining additional specimens.

In general, alizarin stains only bone. Alcian stains cartilage but also stains some skeletal features which are obviously bony and have no cartilaginous precursors, such as fin-rays. Cartilaginous structures, however, often stain much more deeply with alcian than such non-cartilaginous structures. Thus the salangoid hyopalatine is almost always stained deep blue and the opercle

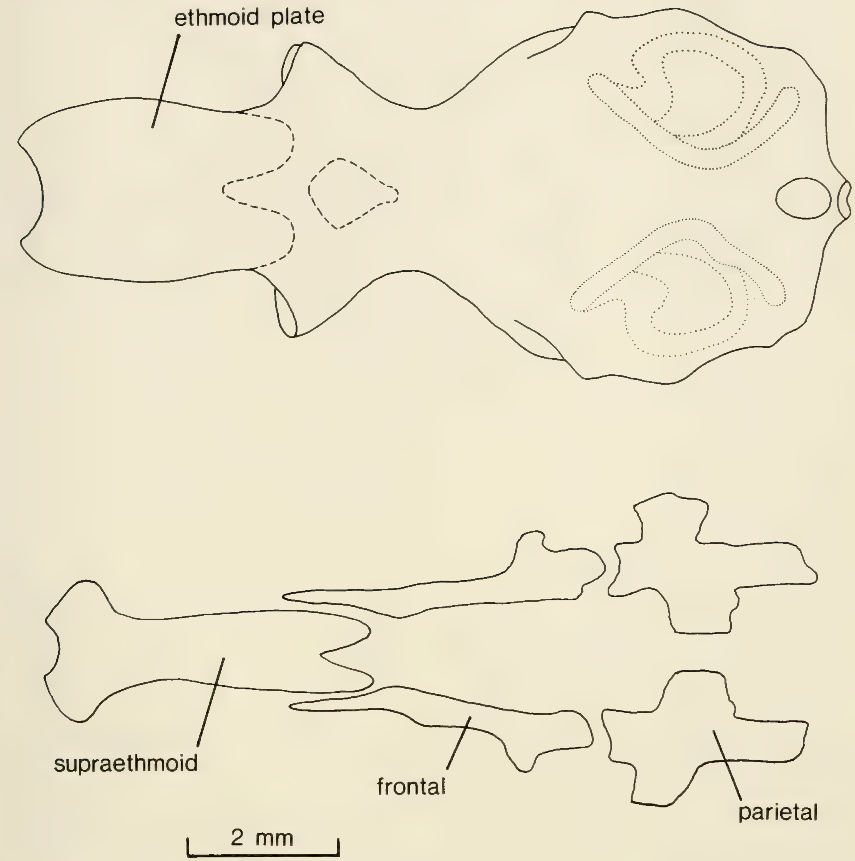


FIGURE 5. Dorsal view of cranium and membrane bones on dorsal surface of cranium. *Salanx prognathus,* CAS 51439, 110 mm.

appears variably pale blue and/or red. In a few of my figures such differences are indicated by the intensity of stippling, but in general the distribution of stain is far too complex to permit its representation in black-and-white illustrations. Some idea of the difficulty involved may be gained from Figure 20 (pelvic girdle of *Protosalanx*), in which the distribution of stain is indicated. In the cranium the distribution is far more complicated and could be conveyed only by illustrations in full color.

CRANIUM

(Figures 3–8)

The cranium of all salangoids is depressed, very strongly in Salanginae and almost as strongly in Protosalanginae, but relatively moderately in Salangichthyinae and Sundasalangidae. Some other features correlated with the cranial depression are the peculiarly underslung maxilla, ventrolateral eye position (especially in Salanginae), and perhaps the posteriorly recurved jaw teeth (especially in Salanginae and Protosalanginae).

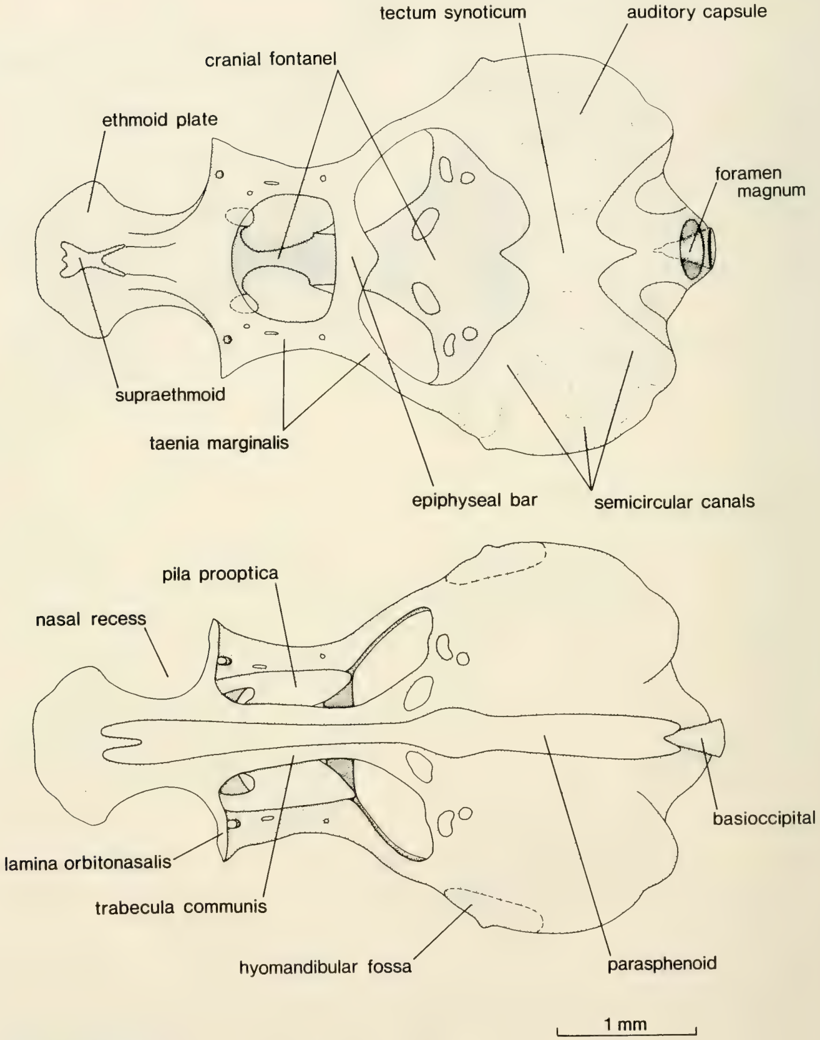


FIGURE 6. Dorsal and ventral views of cranium. *Neosalanx jordani*, CAS 52028, 38.3 mm.

The development of the cranial fontanel exhibits considerable differences. The fontanel apparently remains open anterior and posterior to the epiphyseal bar throughout life in Salangichthyinae and Sundasalangidae, although the anterior portion may be greatly reduced in larger Salangichthyinae. In Protosalanginae the anterior portion closes while the posterior portion always remains open, albeit much reduced in the largest specimens examined. In Salanginae the cranial fontanel is entirely closed in all specimens in which skeletal preparations have been examined.

Young Osmeridae in which the cranium is still

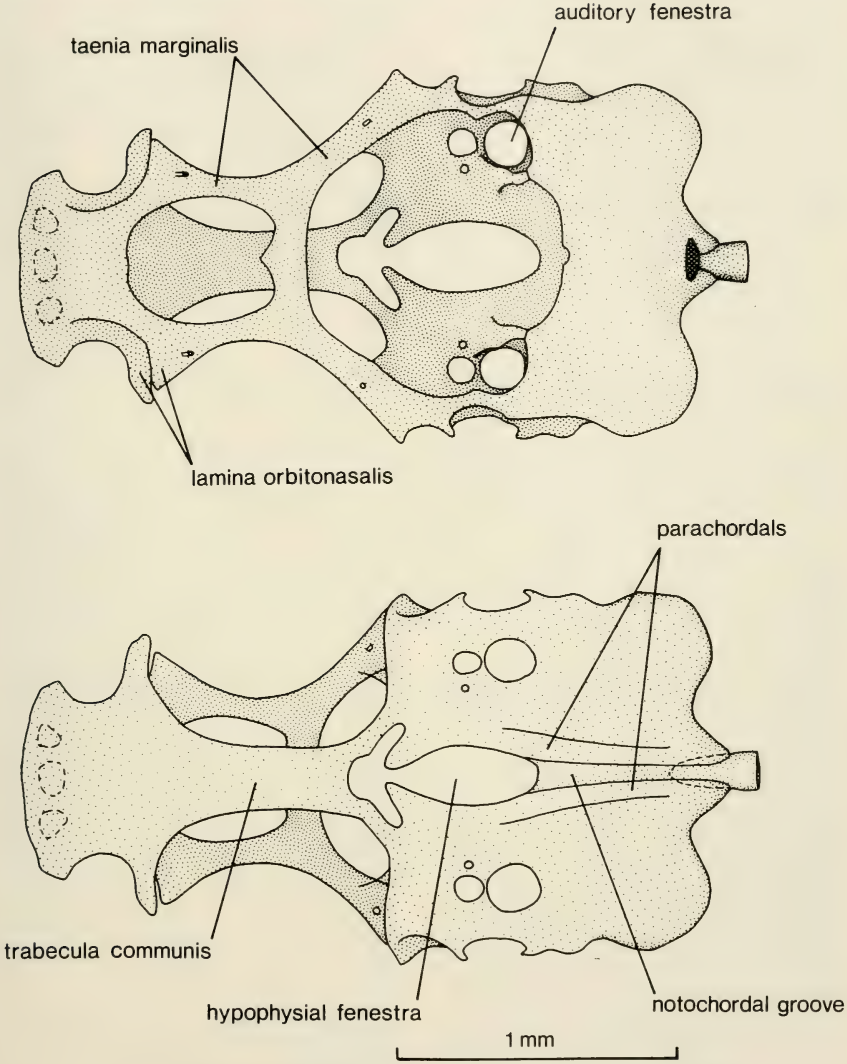


FIGURE 7. Dorsal and ventral views of cranium. *Sundasalanx microps,* CAS 44220, 17 mm.

cartilaginous have a median bar (taenia tecti medialis) separating the anterior and posterior portions of the cranial fontanel into left and right halves. Such a feature is usually but not invariably absent in salangoids. In a series of ten *Neosalanx jordani* (39.7–45.7 mm), nine have the cranial fontanel entirely undivided, but one (41.0 mm) has a median cartilaginous bar dividing both the anterior and posterior portions of the fontanel. The bar is slender posteriorly, but anteriorly it is much wider, so that the anterior portion of the fontanel is represented by two widely

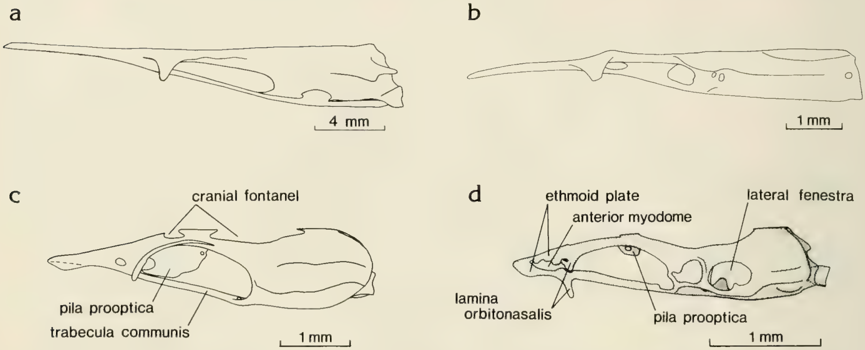


FIGURE 8. Lateral view of cranium. (a) *Protosalanx chinensis*, CAS-SU 6306, 158 mm; (b) *Salanx cuvieri*, CAS-SU 32454, 69.4 mm; (c) *Neosalanx jordani*, CAS 52028, 38.3 mm; (d) *Sundasalanx microps*, CAS 44220, 17 mm.

separated and relatively small openings. The epiphyseal bar in this specimen is also larger than usual. The condition of the cranial fontanel in this specimen closely resembles that observed in osmerid chondrocrania. In *Protosalanx* of 85–89 mm, the anterior portion of the cranial fontanel is similarly divided into greatly reduced left and right openings, which become entirely closed in specimens slightly larger.

The ethmoid plate is greatly enlarged in all salangoids. In Salangichthyinae and Sundasalangidae it is broad and moderately elongate, while in Protosalanginae and Salanginae it is broad and extremely elongate. Ossification of the chondrocranium is relatively poor in all salangoids but varies greatly. The greatest amount of cranial ossification is observed in the skulls of the largest *Protosalanx*, in which the supraethmoid, frontals, parietals, parasphenoid, and basioccipital are all stained more or less deeply with alizarin. In large *Protosalanx* the posterior portion of the parasphenoid has broad lateral wings and the basioccipital has small thin lateral wings (largely obscured by the overlying parasphenoid). Neither of these features has been observed in other salangoids. In all other salangoids the basioccipital ossification is apparently restricted to the basioccipital centrum.

In Protosalanginae the outline of the cranium is more irregular, suggesting a more primitive condition; while in Salanginae it is relatively smooth and streamlined, suggesting a more derived or specialized condition. The auditory capsules are most pronounced or laterally prominent in Salangichthyinae.

The interorbital septum is relatively open in Sundasalangidae and Salangichthyinae, almost as open in Protosalanginae, but greatly reduced in Salanginae. In Salangichthyinae the anterior-medial portion of the orbit is occupied by very large pilae proopticae arising from the ventral surface of the taenia marginalis or anterior supraorbital cartilage. In Sundasalangidae the pilae proopticae are rudimentary.

A number of cranial features that occur in Sundasalangidae have not been observed in the other (mostly juvenile and adult) salangoids examined. Thus the lamina orbitonasalis, which appears as a single apparently simple entity in other salangoids, has two components in *Sundasalanx*: a dorsoanterior contribution from the taenia marginalis and a ventroposterior contribution from the trabecular communis or posteroventral portion of the ethmoid plate. The ethmoid plate is separated by the anterior myodome into dorsal and ventral portions; the anterior myodome extends anteriorly almost to the tip of the snout. In other salangoids the anterior myodome lies much farther posterior, and the ethmoid plate is relatively thin and more or less greatly depressed (least so in Salangichthyinae).

In *Sundasalanx* the base of the cranium is largely occupied by the hypophysial fenestra, a character of all developing teleost chondrocrania usually lost at an early stage. In all other salangoids the hypophysial fenestra is closed off by cartilaginous growth and the area it once occupied may be overlaid by the parasphenoid. In Sundasalangidae the passage for the internal carotid artery is represented by an anterolateral

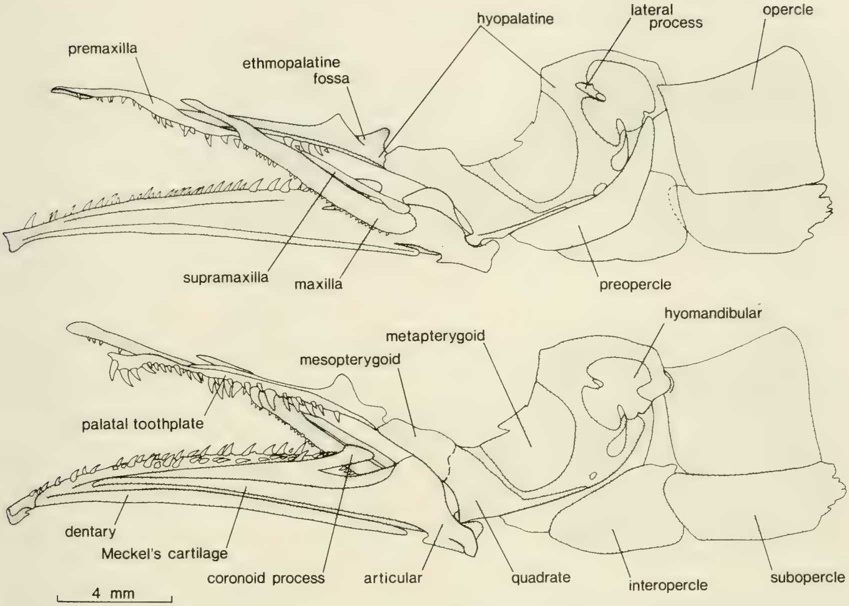


FIGURE 9. Lateral view of jaws, suspensorium, and opercular bones. *Protosalanx chinensis,* CAS-SU 6306, 158 mm.

extension of the hypophysial fenestra; in all other salangoids the passage for this pair of arteries is isolated and widely separated.

In *Sundasalanx* the base of the cranium exhibits a median groove on either side of which extends a slight ridge. This groove probably represents the pathway of the embryonic cranial notochord before its absorption (complete in all other salangoids examined) into the basioccipital centrum. The ridges on each side may be remnants of the parachordal cartilages.

JAWS

(Figures 9–13)

The jaws of salangoids are relatively generalized, in that the jaw bones, their shape, and the distribution of teeth on them are similar to those in many lower teleosts. In all salangoids the maxilla is toothed and enters broadly into the gape. All salangoids have a single supramaxilla, except Salanginae, in which this element is lacking. In some Salanginae the bony tip of the lower jaw is formed not by the dentaries, but by a median presymphyseal bone (usually tooth-bearing). Due in part to poor quality of alcian-alizarin staining of the lower jaw in salangoids, the relationships of bones that constitute it have not been adequately observed. The premaxillae and maxillae are somewhat variable (see remarks in systematic account).

SUSPENSORIUM

(Figures 9–13)

The outstanding feature of the salangoid suspensorium is the union of the hyomandibula (hyosymplectic) and pterygoquadrate, which are united into a single continuous cartilaginous element, here called the hyopalatine (=palatohyomandibuloquadrate of Roberts 1981). Only in *Sundasalanx praecox* is the hyopalatine divided into anterior and posterior portions, but the division apparently is more anterior than the primitive division between hyomandibula (or hyosymplectic) and pterygoquadrate.

In developing vertebrates the rudimentary mandibular arch divides into two cartilages where it bends around the corner of the mouth: the pterygoquadrate bar (dorsal) and the mandibular bar or Meckel's cartilage (ventral). The rudimentary hyoid arch divides into the hyomandibular (dorsal) and hyoid bar (ventral). All salangoids except *Sundasalanx praecox* show the

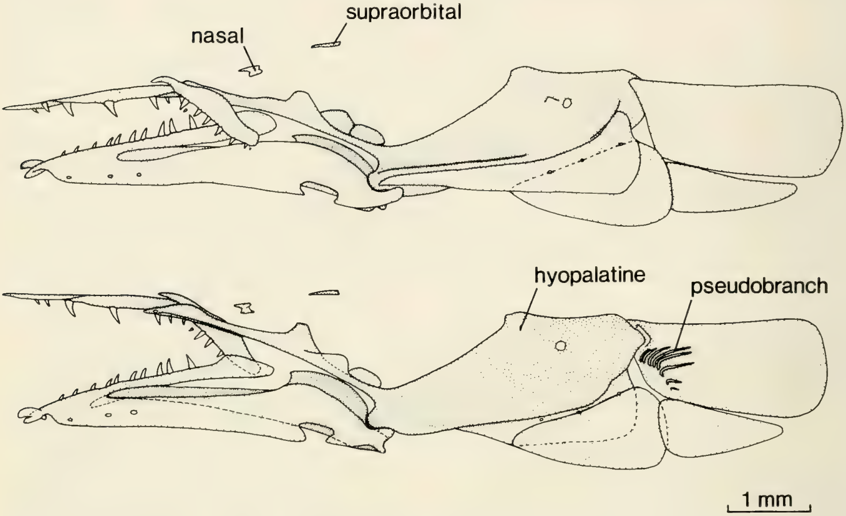


FIGURE 10. Lateral and medial views of jaws, suspensorium, and opercular bones. *Salanx cuvieri,* CAS-SU 32454, 69.4 mm.

most unusual condition of having the dorsal portions of the mandibular and hyoid arches fused into a single element. This salangoid element has readily definable features corresponding to the palatine or pterygoid, quadrate, and hyomandibula of teleosts in which these elements are separate, but it is unclear whether a portion representing the symplectic is present.

No separate symplectic has been detected in any salangoid; the symplectic may be represented by a thickening or ridge near the ventral margin of the quadrate portion of the hyopalatine.

In Sundasalangidae and some Salanginae and Salangichthyinae the suspensorium consists solely of the cartilaginous hyopalatine, but in other Salanginae and Salangichthyinae and in Protosalanginae a number of perichondral, endochondral, or dermal ossifications develop on the suspensorium. The elements most often added are the mesopterygoid and an anterior palatal toothplate (=ectopterygoid?), which may or may not bear teeth. The suspensorium exhibits more ossification in large *Protosalanx* than in any other salangoids examined: heavily toothed palatal toothplate, mesopterygoid, and partial ossification of quadrate and hyomandibula.

Whether the dorsal portions of the mandibular and hyoid arches are similarly fused in any other fishes is unknown. In the few fishes for which the development of these arches has been adequately observed it would appear they are separate, including *Salmo* (DeBeer 1937), *Elops* (pers. obs.), *Hepsetus* (Bertmar 1959). In young salmoniforms I examined (including *Salmo, Galaxias, Lepidogalaxias, Hypomesus,* and *Spirinchus*) cartilaginous pterygoquadrate and hyomandibular or hyosymplectic are always separate.

Circumorbital Bones

(Figure 12)

A supraorbital bone is seen in all Salangidae but is absent in Sundasalangidae. The dermosphenotic or sixth infraorbital appears to be absent in all salangoids. An isolated infraorbital (fourth or fifth?) is seen in some Salangichthyinae but is greatly reduced (Fig. 12).

Gill Arches

(Figures 14–17)

The upper elements of the gill arches of salangoids are relatively generalized and, except in Sundasalangidae, so are the lower elements. Except for the upper and lower pharyngeal toothplates the salangoid gill arches apparently are entirely cartilaginous. Four basibranchials are probably present in all salangoids but in none are all of them separate. In Protosalanginae, Sa-

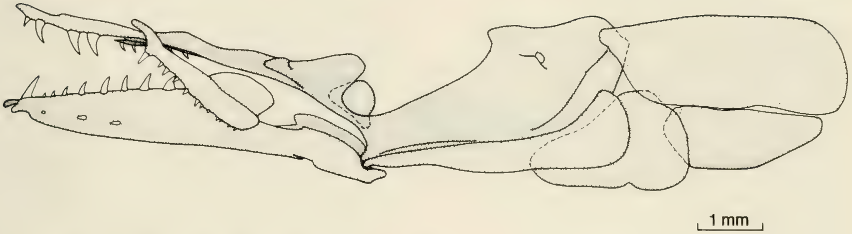


FIGURE 11. Lateral view of jaws, suspensorium, and opercular bones. *Salanx prognathus*, CAS-SU 51439, 110 mm.

langinae, and Salangichthyinae basibranchials 2 and 3 are indistinguishably fused to each other, and in some Salanginae basibranchials 1, 2, and 3 may be so fused.

All salangoids have four hypobranchials; hypobranchial 4 is always separate and relatively large.

The basibranchial series in salangoids is entirely cartilaginous. Not only do the basibranchials themselves not ossify, but basibranchial toothplates, a characteristic feature of many salmoniforms including salmonids, osmerids, and galaxiids, are absent. The basic basibranchial arrangement in Salangidae appears to be basibranchial 1 separate, basibranchials 2 and 3 fused, and basibranchial 4 separate. A basibranchial 5 is fused to basibranchial 4 in various salmoniforms, and is apparently usually present in many salmonoids, osmeroids, and galaxioids (including *Lepidogalaxias*) as a thin cartilaginous shaft projecting posteriorly between the fifth ceratobranchials. In some instances there is a clear demarcation between basibranchials 4 and 5, and they may be separate or at least not completely fused. Basibranchial 5, fused with basibranchial 4, is indicated in Salangidae by Nelson (1970), but in Salangidae I have examined there is no indication of a fusion or demarcation between the presumed basibranchial 5 and basibranchial 4. Basibranchial 5 does not project so far posteriorly nor is it slender and rodlike as in other Salmoniformes in which its presence is less doubtful. I therefore tentatively consider basibranchial 5 absent in Salangidae. That it is absent in Sundasalangidae seems highly likely.

Gill rakers are poorly ossifed (never stained with alizarin) and edentulous (frequently dentigerous in salmonoids, osmeroids, esocoids). Those on the trailing (inner) face of the arches usually are fewer and smaller than those on the leading (outer) face (Figs. 14–17). Total number of gill rakers on leading face of first gill arch is 8–19 in Salangidae and 0–10 in Sundasalangidae (Table 2).

Dentition

The most complete and presumably most primitive dentition in salangoids is observed in

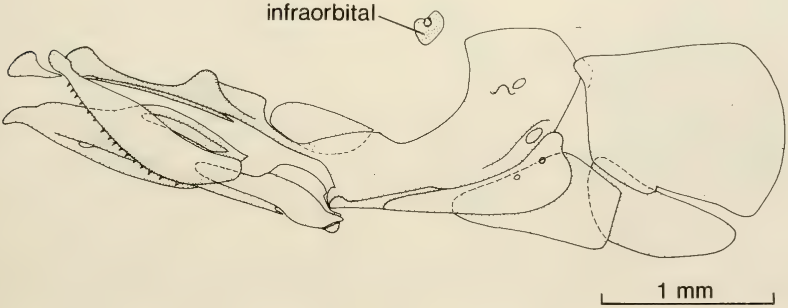


FIGURE 12. Lateral view of jaws, suspensorium, and opercular bones. *Neosalanx jordani*, CAS 52058, 35.1 mm.

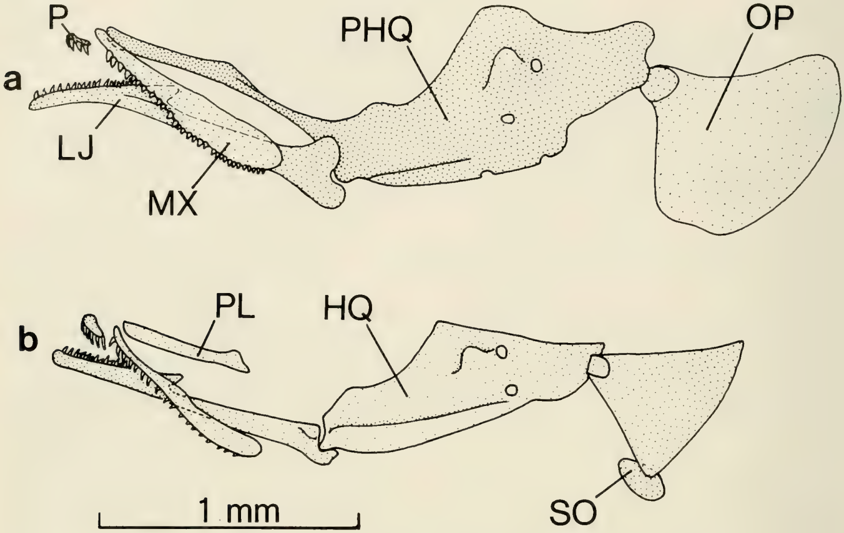


Figure 13. Lateral view of jaws, suspensorium, and opercular bones. (a) *Sundasalanx praecox*, CAS 52031, 17 mm; (b) *Sundasalanx microps*, CAS 44290, 17 mm. HQ = hyomandibula + quadrate, LJ = lower jaw or Meckel's cartilage, MX = maxilla, P = premaxilla, PHQ = hyopalatine cartilage, PL = palatine, OP = opercle, SO = subopercle.

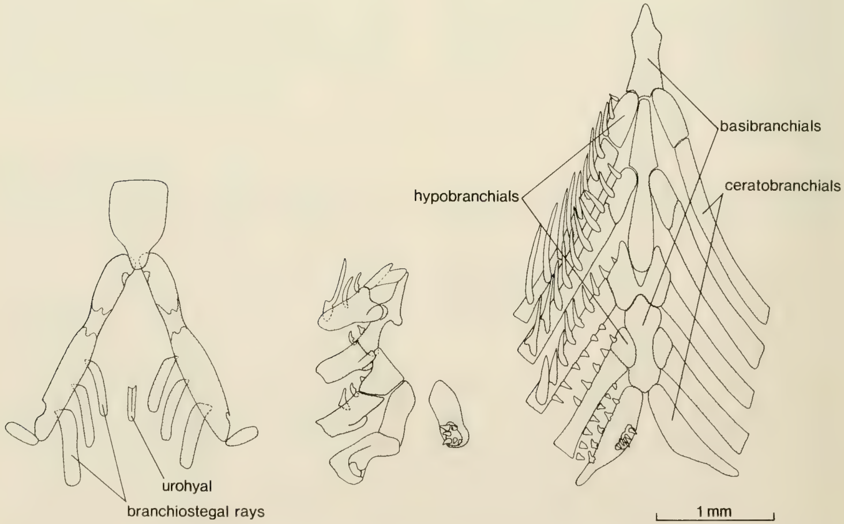


Figure 14. Dorsal and ventral views of hyoid and branchial arches. *Protosalanx chinensis*, CAS-SU 6306, 153 mm.

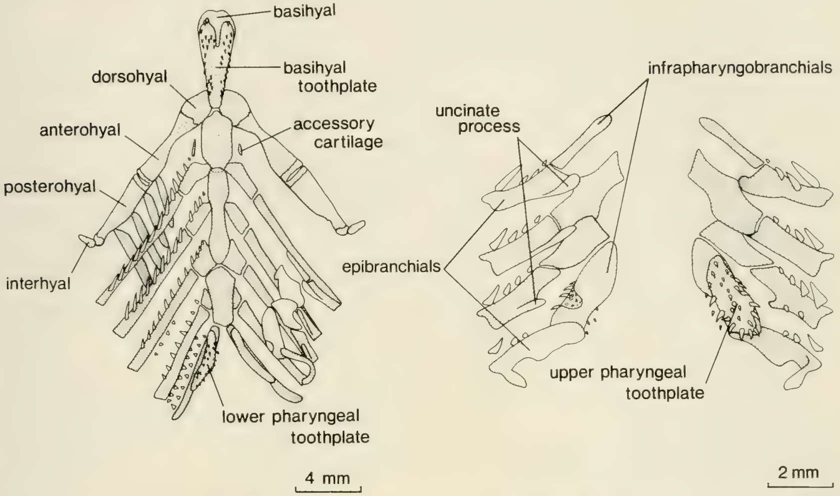


FIGURE 15. Dorsal view of hyoid and branchial arches and ventral view of upper pharyngeal elements. *Salanx cuvieri,* CAS-SU 32454, 69.4 mm.

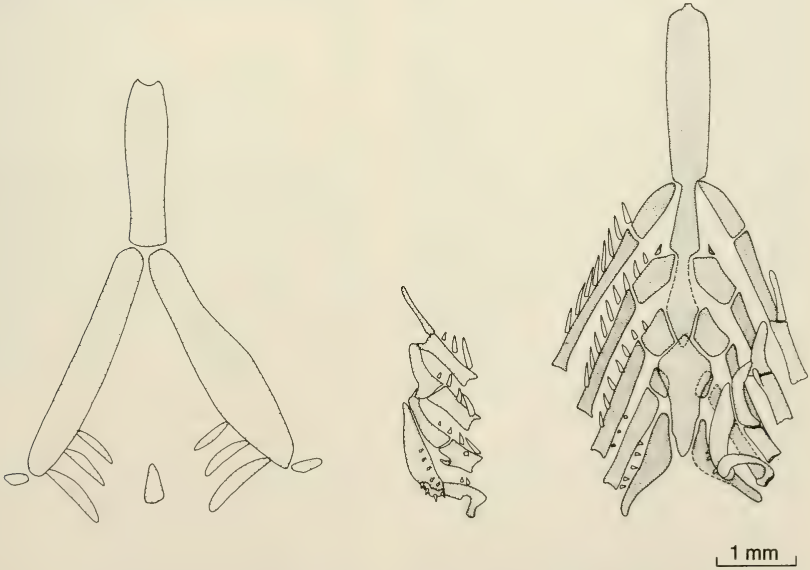


FIGURE 16. Dorsal view of hyoid and branchial arches; ventral view of infrapharyngobranchial 4 and upper pharyngeal toothplate. *Neosalanx jordani,* CAS 52058, 38.3 mm.

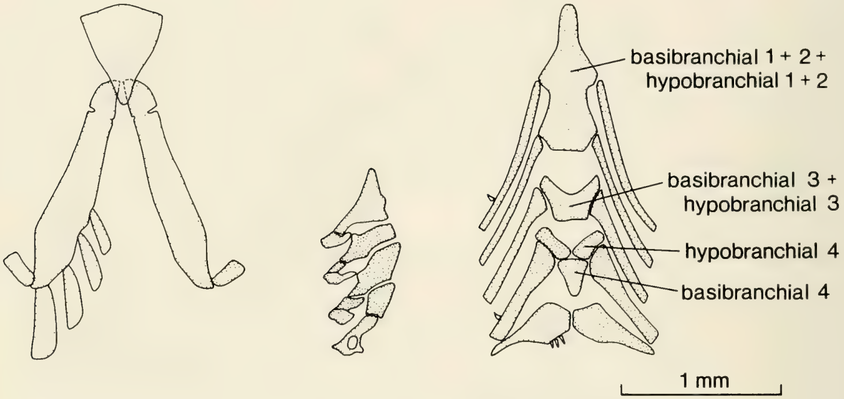


FIGURE 17. Dorsal view of hyoid and branchial arches. *Sundasalanx microps*, CAS 44220, 17 mm.

Protosalanx, with numerous large, conical teeth on the premaxilla, maxilla, palatal toothplate (=ectopterygoid?), tongue (basihyal toothplate), and upper and lower pharyngeal toothplates. As in all Salangidae, there are only two pairs of pharyngeal toothplates: the upper, on infrapharyngobranchial 4, and the lower, on ceratobranchial 5; the branchial arches are otherwise entirely toothless.

In *Protosalanx* the teeth on the palatal toothplate and lower jaw are in two rows, as in many other salmoniforms, but in all other salangoids the teeth on each tooth-bearing element except those in the pharynx are restricted to single rows. In largest specimens of *Protosalanx* the tongue teeth are more or less widely scattered over the surface of the basihyal (as in Fig. 9), but in smaller ones they are restricted to two marginal rows, as in salmoniforms generally. The only other salangoid with tongue teeth, *Salanx* (*Leucosoma*) *reevesi*, has them in a single median row on the basihyal toothplate, a unique specialization for salmoniforms. This character is diagnostic of the subgenus *Leucosoma*.

The maxilla and lower jaw are well-toothed in all salangoids; the palate is toothless in *Neosalanx* and *Sundasalanx*. In *Neosalanx* the teeth on the premaxilla, maxilla, and lower jaw are very small, and frequently the premaxilla and lower jaw are entirely toothless. In *Sundasalanx* bony pharyngeal toothplates apparently fail to form, and the pharyngeal teeth appear to be directly attached to the cartilaginous infrapharyngobranchial 4 and ceratobranchial 5. The only bony tooth-bearing elements in *Sundasalanx* appear to be the premaxilla and maxilla; the lower jaw teeth are loosely attached to Meckel's cartilage.

PECTORAL GIRDLE

(Figures 18–19)

All salangoids have a secondary pectoral girdle (connecting the primary girdle to the back of the cranium) consisting of three dermal bones: posttemporal, supracleithrum, and cleithrum. Postcleithra are absent except in Salanginae, in which there is a single postcleithrum. In Salangidae, the primary shoulder girdle consists of the entirely cartilaginous paired scapulocoracoids and one or two series of radials. The basic number of primary radials appears to be five in all Salangidae. The first primary radial, associated with the outermost (enlarged) pectoral fin-ray, is relatively simple; it is largest in males of Protosalanginae and Salanginae. The other primary radials are complex, with numerous deep divisions approximately corresponding in number to the fin-rays. These divisions are most numerous in Salangichthyinae, particularly *Neosalanx*, but are well developed in all Salangidae. Comparable divisions or fimbriae occur in the pectoral basal plate of

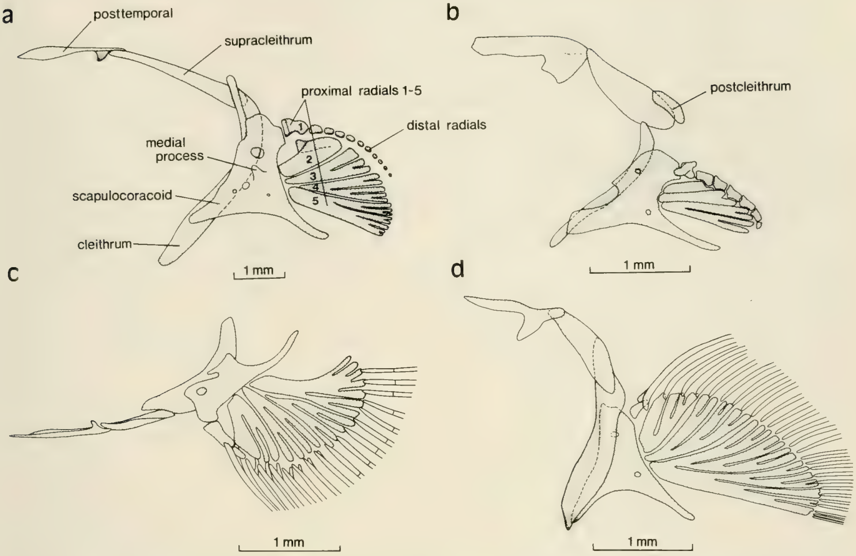


FIGURE 18. Left half of pectoral girdle. (a) *Protosalanx chinensis,* CAS-SU 6306, 158 mm (medial view); (b) *Salanx cuvieri,* CAS-SU 32454, 69.4 mm (lateral view); (c) *Neosalanx jordani,* CAS 52058, 43.1 mm (dorsal view); (d) *Salangichthys ishikawae,* CAS 6780, 74 mm (lateral view).

the salmoniform *Dallia pectoralis* but are not present in other salmoniforms I have examined and do not seem to have been reported in any other teleosts. Secondary radials, more or less corresponding in number to the pectoral fin-rays, are small and simple. The mesocoracoid is lacking in all salangoids except that *Protosalanx* has a process on the median surface of the scapulocoracoid that may represent the ventral portion of the mesocoracoid (Fig. 18a, medial process). In Sundasalangidae the primary pectoral girdle consists of a U-shaped median scapulocoracoid and a basal plate. Fin-rays are absent.

PELVIC GIRDLE

(Figure 20)

The left and right halves of the pelvic girdle develop in the ventral myotomic wall, and, as the ventral myotomic progression is arrested in Salangidae while the myotomes are still widely separated, the pelvic girdle halves remain widely apart and fail to form any sort of ligamentous or cartilaginous connection between each other. As pointed out by Klyukanov (1975), in Salmoniformes the two halves of the pelvic girdle are usually joined at least anteriorly for a short distance by strong cartilaginous or ligamentous tissues.

AXIAL SKELETON

(Figure 1)

All salangoids have a pair of small dorsal cartilages straddling the intervertebral disc between the basioccipital and first vertebral disc; such cartilages occur in many (perhaps most or all) Salmoniformes.

In all Salangidae the neural arches of vertebrae 1 and 2 are fused dorsally; this condition has not been observed in Osmeridae or any other salmoniforms I have examined. In Sundasalangidae the neural arches of vertebrae 1 and 2 are separate from each other and morphologically similar to those of the vertebrae immediately succeeding them.

In salangoids the mineralized portion of each centrum is relatively elongated and hourglass shaped, so that the intervertebral joints are narrow and the notochord greatly constricted. In

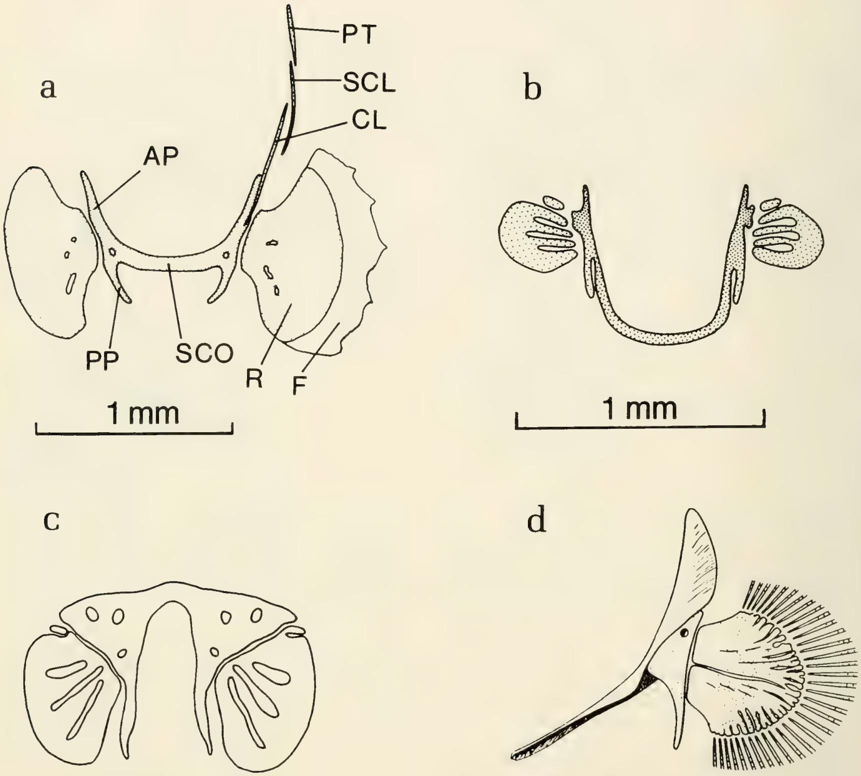


FIGURE 19. Pectoral girdle. (a) *Sundasalanx microps,* CAS 44220, 17-mm adult (posterior view); (b) *Elops hawaiiensis,* CAS 52035, 30-mm leptocephalus larva (posterior view); (c) *Sardina pilchardus,* 20–30 mm (ventral view?, after Goodrich 1922); (d) *Dallia pectoralis,* (lateral view, after Starks 1904; apparently based on CAS-SU 12615, 125 mm, Nushagak River, Alaska); AP = ascending process, CL = cleithrum, F = fin margin, PP = posterior process, PT = posttemporal, R = basal plate, SCL = supracleithrum, SCO = scapulocoracoid. In (b) and (c) the first primary radial has pinched off from the basal plate.

salmonids, osmerids, galaxiids, and other Salmoniformes, especially in the young stages, the mineralized portion of each centrum tends to be relatively short and cylindrical, so that the intervertebral space is much larger and the vertebral section of the notochord is entirely intact. A comparable condition is not present in any salangoid skeletal material I have examined.

Ribs are absent or weakly developed and stain poorly. They are small, weakly stained with alcian when present (Fig. 1b).

Gosline (1960) and others have pointed out that neural and hemal spines of most Salmoniformes, especially posteriorly, may be flattened or laminar, even to the extent of resembling a continuous keel. The neural and hemal spines of salangoids are always relatively slender, especially posteriorly.

A round, oval, or elongate and splintlike adipose fin cartilage lies at the base of the adipose fin in all Salangidae. A survey of lower teleosts for the adipose fin cartilage by Matsuoka and Iwai (1983) revealed its presence in Salangidae, Osmeridae, Plecoglossidae, Myctophidae, and Neoscopelidae; it was not observed in other lower teleosts with an adipose fin including Sal-

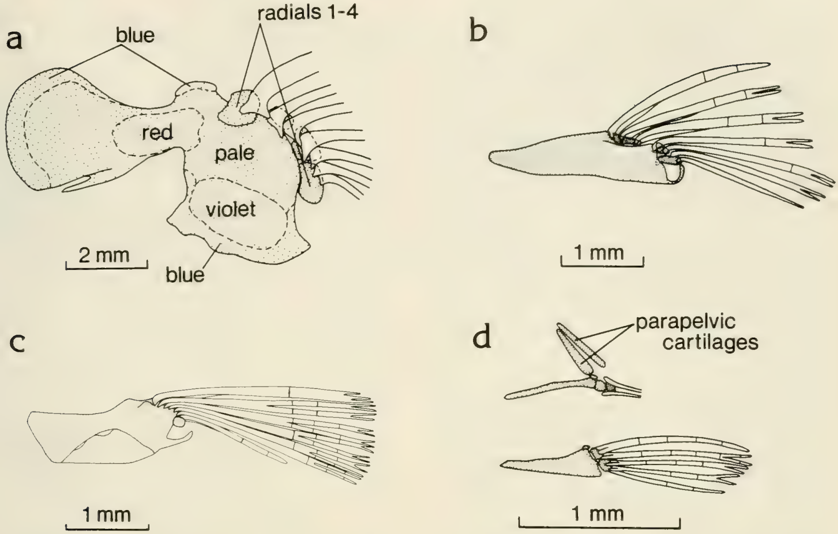


FIGURE 20. Ventral view of left half of pelvic girdle. (a) *Protosalanx chinensis,* CAS-SU 6306, 158 mm; (b) *Salanx cuvieri,* CAS-SU 32454, 69.4 mm; (c) *Neosalanx jordani,* CAS 52028, 43.1 mm; (d) *Sundasalanx microps,* CAS 44220, 17 mm (with lateral view of pelvic girdle and parapelvic cartilages above).

monidae, Retropinnidae, Prototroctidae, Aulopodidae, Synodontidae, Chlorophthalmidae, Argentinoidei, Characoidei, or Siluriformes. The similar morphology of the adipose fin cartilages in Salangidae and Osmeridae, as noted by Matsuoka and Iwai, is possibly indicative of relationship between these two families.

Caudal Fin Skeleton

(Figure 21)

The caudal fin is more or less deeply forked, and the upper and lower lobes are about equal. Principal caudal fin-rays are invariably 10+9; upper and lower procurrent caudal fin-rays are moderately numerous (to 14). The complex ural or hypural centrum apparently consists of three centra and uroneural 1 (sometimes also uroneural 2?) fused into a single unit. The three centra involved are the terminal centrum and postterminal centra 1–2, according to the nomenclature of Gosline (1960), or preural centrum 1 and ural centra 1–2, according to Rosen (1974). In none of the skeletal material examined is there any indication of separate centra posterior to the complex hypural centrum. Epurals 0–3. A separate uroneural 2 is sometimes present, but uroneural 1 is apparently always fused to complex hypural centrum. Free radial or pterygial cartilages are sometimes present, usually between ray halves at the base of the anteriormost 2–3 upper or lower procurrent rays and the lowermost upper and uppermost lower principal rays. Hypurals six. Six separate hypurals occur in *Salangichthys microdon* (Rosen 1974, Fig. 26). *Protosalanx chinensis* occurs with hypurals 1–2 and 5–6 separate, but with 3–4 fused near the base. The hypurals are more fused in *Neosalanx, Salanx,* and *Sundasalanx.* In *Salanx* parhypural and hypurals 1–2 are fused near the base; hypurals 1–2 and 3–4 are fused for their entire length except for oblong basal foramina where fusion evidently failed to complete. In *Sundasalanx* parhypural and hypurals 1–3 are evidently fused into a single element.

SYSTEMATICS

In the present account the salangoids are recognized as a salmoniform superfamily separate from osmeroids, which they superficially resemble. There are two families, Sundasalangidae, with

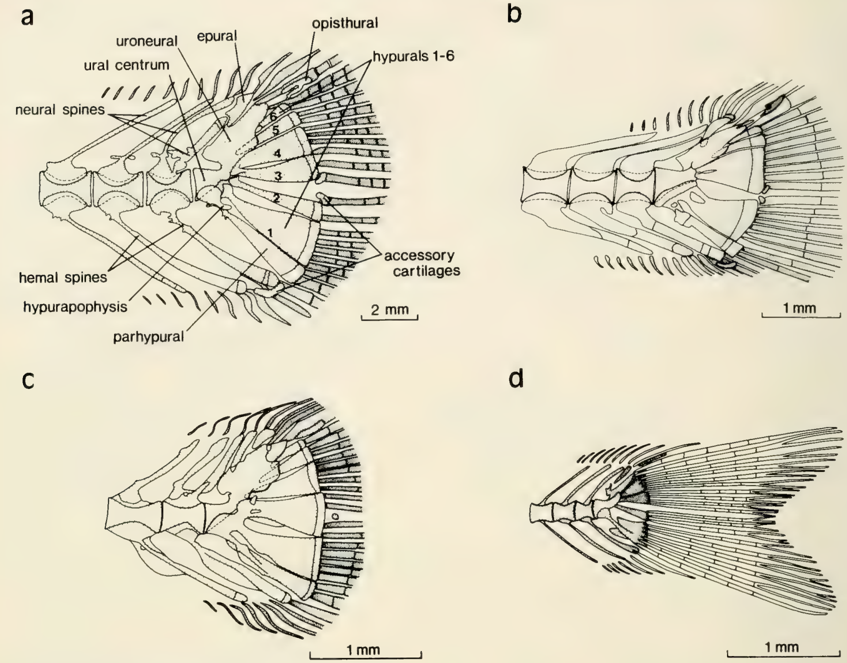


FIGURE 21. Lateral view of caudal fin skeleton. (a) *Protosalanx chinensis,* CAS-SU 6306, 158 mm; (b) *Salanx cuvieri,* CAS-SU 32454, 61.7 mm; (c) *Neosalanx jordani,* CAS 52028, 43.1 mm (note: hypurals 2 and 3, normally separate from each other in all salangoids, are fused in this specimen); (d) *Sundasalanx microps* CAS 44220, 17 mm. In a–c left half of fin rays removed to facilitate observation of median structures.

only a single genus and two species, and Salangidae. Salangidae is further divided into three subfamilies, four genera, and eleven species. The genus *Salanx* is further divided into three subgenera; this taxonomic category is not employed in the other genera of salangoids. In addition to the new superfamily Salangoidea, the new subfamily Salangichthyinae is proposed for *Neosalanx* and *Salangichthys,* leaving the subfamily Protosalanginae with only the genus *Protosalanx.* No new genera or species are proposed. Some previous workers, particularly Regan (1908b) and Fang (1934a, b) recognized far more species than I have, especially in the subgenus *Salanx* (genera *Salanx* and *Parasalanx* of Regan). This is attributable in part to their basing species on only one or a few type-specimens and utilizing characters such as cranial proportions, body depth, and relative position of dorsal and anal fins which vary considerably within the species. Neither Regan nor Fang utilized vertebral counts, which I find extremely useful in distinguishing species. My extensive data on vertebral counts of types and other material are presented in Table 2.

My counts of vertebrae, fin-rays (except pelvic) anal scales, branchiostegal rays, and gill rakers are presented in Table 2. This table includes all species of salangoids herein recognized as valid except *Neosalanx reganius,* which I have not examined. Pelvic fin-ray counts are excluded because they are invariably 5 in Sundasalangidae and almost invariably 7 in Salangidae (6 in one observed specimen of *Neosalanx jordani,* 8 in two specimens of *Salangichthys microdon*). Previous authors have presented data on most of the species but have often lumped data from various localities (and frequently of two or more species). In order to minimize this problem, my data are presented separately for each locality.

Although Table 2 includes meristic data obtained from whole specimens, radiographs, and cleared and stained specimens, the stained specimens provide the best material for accurate count of fin-rays, teeth, and gill rakers. It is difficult to observe the jaw teeth and lowermost pectoral fin-rays in *Neosalanx* except in stained material. In dorsal and anal fin-ray counts the last "two" rays ("divided to base") are counted as one ray. In vertebral counts the basioccipital centrum is not counted and the hypural complex centrum is counted as one. In salangoids, especially in females, the anteriormost anal-fin pterygiophore does not provide a ready basis for distinguishing abdominal and caudal vertebrae. In order to obtain additional meristic data from the vertebral column and at the same time obtain more precise data on the relative position of fin origin, I have taken data on the vertebrae parallel to the origins of the pelvic, dorsal, and anal fins. The number of vertebrae posterior to a vertical line through the base of the last anal fin-ray is also recorded.

Radiographs are usually satisfactory for obtaining vertebral counts of salangoids and sometimes for fin-ray counts. Sometimes the vertebrae may show up very faintly but it is almost always possible to obtain a count repeatable to within one vertebra. Fin-rays, however, frequently cannot be accurately counted on radiographs, and I have only incorporated data on fin-ray counts taken from radiographs when the radiographs seemed reliable.

Some characters utilized by other workers to distinguish species are not emphasized here because they do not seem useful. This particularly applies to pectoral fin-ray counts in *Neosalanx* and to the elongation of the head or cranium, relative position of the dorsal- and anal-fin bases, and body depth, especially in *Salanx*. In salangids the number of pectoral fin-rays generally continues to increase slightly with growth, especially so in those such as *Neosalanx*, in which the rays are exceptionally numerous. The elongation of the cranium (particularly its anterior portion) is extremely variable in *Salanx*, as noted also by Wakiya and Takahasi (1937:289). This variation is individual and is probably enhanced by growth. The position of the dorsal and anal fins relative to each other is also highly variable in salangids, subject to individual variation as well as sexual dimorphism. In defining species of *Salanx* too much reliance has been placed on slight differences in fin positions based on only one or two specimens. *Salanx*, *Salangichthys*, and other salangids vary enormously in body depth due to sex-related body changes and nonsexual factors of condition and preservation.

In discussing salmonoid classification, Gosline (1971:119) stated:

> The suborder Salmonoidei as here recognized (Families Salmonidae, Osmeridae, Plecoglossidae, Salangidae, Retropinnidae, Aplochitonidae, and Galaxiidae) is a group of highly diverse inshore and freshwater salmoniform fishes. Though the included families no doubt should be divided into superfamily groupings, inadequate knowledge of the Salangidae and the Southern Hemisphere forms would seem to make any formal superfamily classification premature at the present time. Informally, the members may be divided between Northern and Southern Hemisphere forms. The diverse forms from the Southern Hemisphere seem to be most closely related to the northern osmerids. . . . The Northern osmeroids are represented by four quite distinct lines: Salangidae, Plecoglossidae, Osmeridae, and Salmonidae.

Rosen (1974) divided the suborder Salmonoidei into two superfamilies, Salmonoidea—including the Southern Hemisphere families (except Retropinnidae) and Salmonidae—and Osmeroidea (with four families listed as incertae sedis: Osmeridae, Plecoglossidae, Retropinnidae, and Salangidae). I have not investigated Retropinnidae or the highly aberrant Plecoglossidae but suspect that Retropinnidae (particularly *Prototroctes*) and *Plecoglossus* may indeed be closely related to each other and perhaps to Osmeridae. But I have not been able to find any good evidence (in the form of shared specializations or derived characters) between Salangidae and any one or combination of these families. I have therefore designated the new superfamily Salangoidea, which is coequal with the superfamilies Osmeroidea and Salmonoidea (and Galaxioidea, if this is also to be recognized).

SALANGOIDEA, NEW SUPERFAMILY

This superfamily apparently differs from all other Pisces in having a suspensorium in which the cartilaginous palatine and pterygoid (of the mandibular arch) and quadrate and hyomandibular (of the hyomandibular arch) are fused into a single element, the hyopalatine. Gill arches with well-developed fourth hypobranchials—so far as known absent from all other adult teleosts (Nelson 1970). Pharyngobranchials 4. Anterior pharyngobranchial modified as an elongate "suspensory pharyngeal"; only fourth pharyngobranchial bears teeth (teeth absent in *Sundasalanx*). Fifth ceratobranchial with well-developed teeth (absent in osmeroids; McAllister 1963:4). Branchiostegal rays 2–5 (7–19 in salmonoids, 5–10 in osmeroids, 3–9 in galaxioids). Cranium moderately to excessively flattened (more so than in any other salmoniforms). Maxillary bone, bearing teeth for its entire length, with its posterior half abruptly curved medially beneath head (so that teeth on posterior half of maxillary are directed anteriorly rather than ventrally). Scales entirely absent except for a row of strongly adherent anal scales in adult male Salangidae.

Dermosphenotic and circumorbital bones absent, except for a single small troughlike bony element observed in *Neosalanx*, which may represent a fifth or sixth circumorbital (not dermosphenotic). Supraocciptal bone absent (present in most other salmoniforms).

Pectoral fins pedunculate throughout life (with pectoral radials in a fleshy pedestal separate from body). Pelvic fin-rays usually 5 or 7 (rarely 6 or 8; 8 in osmeroids). Principal caudal fin-rays invariably 10+9 (as in most lower teleosts including salmoniforms with generalized caudal fins; galaxioids have fewer).

Salangoids apparently have no laterosensory canals on the body. The cephalic laterosensory canals, although well developed, are superficial (i.e., not enclosed in bony tubules) and often difficult to observe in their entirety. Those of *Salanx chinensis*, illustrated by Nelson (1970, Fig. 15), do not exhibit any particularly unusual features for lower teleosts. There are preopercular, mandibular, supraorbital, infraorbital, and extrascapular canals. The mandibular is not continuous with the preopercular. The supraorbital and infraorbital extend anteriorly only a short distance in front of the nostrils, i.e., not significantly onto the greatly depressed and enlarged snout. The infraorbital has 8 pores, the preopercular 6, and the mandibular 5.

Alimentary canal a relatively simple, straight tube. Pyloric caecae absent. Gonads paired.

Salangidae Jordan and Snyder, 1902

Pelvic fin almost invariably with 7 rays (8 observed in one specimen of *Salangichthys ishikawae* and two *S. microdon*, 6 in one *Neosalanx jordani*). Pelvic girdle without parapelvic cartilages. Pectoral fin-rays 8–34. Pectoral girdle with five proximal radials; distal ends of one or more proximal radials with more or less numerous branches; adult males with a series of anal scales and enlarged, modified anal fins; total vertebrae 49–79.

The family Salangidae comprises three subfamilies: Protosalanginae, Salangichthyinae, and Salanginae.

Protosalanginae Wakiya and Takahasi, 1937

This subfamily, here restricted to the monotypic genus *Protosalanx*, differs from all other salangoids in having the premaxilla, palatal toothplate (=ectopterygoid?), and dentary with two rows of teeth instead of at most a single row; the basihyal toothplate of the tongue also has the teeth in two marginal rows (a primitive condition for salmoniforms) or irregularly scattered over its entire surface; the only other salangoid with basihyal teeth has them in a single median row. Pelvic fins relatively larger and more anterior than in any other salangoids (see Fig. 1, Table 2).

Cranium strongly depressed (almost as much as in Salanginae); adults with anterior portion of cranial fontanel closed, posterior portion of cranial fontanel greatly reduced but remaining open throughout life (both portions closed in adult Salanginae, open throughout life in Salangichthyinae and Sundasalangidae). Lower jaw weakly projecting beyond upper jaw; premaxillae projecting anteriorly beyond snout tip as in Salanginae but failing to form a membrane-covered space through which symphyseal teeth of lower jaw project. Lower jaw without enlarged symphyseal teeth (present in Salanginae), sometimes with a weakly developed fleshy presymphyseal process but without presymphyseal teeth or bony process. Adults attaining slightly greater standard length (Table 1) and heavier-bodied than any other salangoids. Dorsal fin-rays 16–18 and anal fin-rays 30–32 (vs. 10–15 and 14–32 in all other salangoids); vertebrae 66–70 (Table 2).

Protosalanx Regan, 1908

Eperlanus Basilewsky, 1855:242.

Salanx Abbott, 1901:490.

Protosalanx Regan, 1908b:444 (type-species, by monotypy, *Salanx hyalocranius* Abbott, 1901 = *Eperlanus chinensis* Basilewsky, 1855).

Paraprotosalanx Fang, 1934a:246 (type-species, by monotypy, *Protosalanx andersoni* Fang, 1934a (non Rendahl, 1923) = *Protosalanx chinensis* Basilewsky, 1855).

Protosalanx chinensis (Basilewsky, 1855)

Eperlanus chinensis Basilewsky, 1855:242 (type-locality "in sinu Tschiliensis habitat" [not "Pekin" as usually cited]).
Salanx hyalocranius Abbott, 1901:3490 (type-locality Pei-ho at Tien-tsin).
Protosalanx hyalocranius Regan, 1908b:445.
Paraprotosalanx andersoni Fang, 1934a:246 (Figs. 4–6, text in part [non *Paraprotosalanx andersoni* Rendahl, 1923]).
Protosalanx chinensis Chyung, 1961:163.

Material Examined.—BMNH 1929.2.5.2.–3, 61–65 mm, Kiangyin; CAS 52026, 60:48.2–70.7 mm, no locality (purchased in San Francisco); CAS-SU 6306, 25:80.5–163 mm, Pei-ho at Tien-tsin, paratypes of *Salanx hyalocranius* (7:85.5–158 mm alcian-alizarin); CAS-SU 23639, 1:137 mm, Seoul; CAS-SU 36025, 3:120–136 mm, no locality; UMMZ 180096, 2:127–129 mm, Korea; USNM 120746, 2:129–132 mm, Korea.

Protosalanx appears to be the most primitive salangoid. There is no indication that it comprises more than a single species. Although Abbott's account begins "*Salanx hyalocranius* new species," it concludes "this species is probably identical with *Eperlanus chinensis* Basilewsky, from Pekin, but the name chinensis is already used for the 'whitebait of Makao'" (Abbott 1901: 490–491). In Abbott's time Salangidae were so poorly known it was reasonable for him to assume that his material might represent an undescribed species, but even so it is clear from this statement that Abbott was really proposing a replacement name. Now that Salangidae are better known it seems Basilewsky's account could only refer to this species, as explicitly recognized by Wakiya and Takahasi (1937), although they retained the name *P. hyalocranius.* The holotype of *P. chinensis* cannot be found (Barsukov, pers. comm. 1983). Since the "whitebait of Makao" has been referred to as *Leucosoma* or *Salanx chinensis* but never as *Eperlanus* or *Protosalanx chinensis,* the epithet *chinensis* is available for a species of *Protosalanx.* As this is also the earliest name proposed it must replace *hyalocranius,* and the species should be known as *Protosalanx chinensis.* The only publication to come to my attention in which this name is correctly applied is by Chyung (1961).

Wakiya and Takahasi (1937) correctly identified *Paraprotosalanx andersoni* Fang, 1934a with this species. Fang's figures agree in every respect with *P. chinensis.* The fleshy presymphyseal appendage, presumed by Fang to differentiate his *Paraprotosalanx* from *Protosalanx,* is also present in some of Abbott's type-specimens of *S. hyalocranius.* Fang's figures presumably are based upon the single large male, "S. 4374," 153 mm (total length according to Table 4, but standard length according to p. 247) from Nanking. All or almost all of the other specimens referred to *Paraprotosalanx andersoni* by Fang are probably *Neosalanx.*

It should be noted that small specimens in museum collections identified as *Protosalanx* are usually *Neosalanx* and that all or almost all published reports of smaller *Protosalanx* up to the present time are based on *Neosalanx.* For example, I find that all of the small specimens in Abbott's type-series of *S. hyalocranius* are *Neosalanx.* Young *P. chinensis* are relatively rare in collections. Those I examined (smallest 48.2 mm) closely resemble the largest adults in every way except they lack the sexually dimorphic characters of adult males. The strongly pointed snout and large teeth arranged in two rows on the palate, tongue, and lower jaw are easily observable. *Neosalanx* have no teeth on the tongue or palate, and the jaw teeth except on the maxillary are absent or minute and difficult to observe, while the males are sexually mature and provided with greatly enlarged anal fins and anal scales at relatively small size. The smallest male *Protosalanx* with anal scales is probably considerably larger than any *Neosalanx.*

Protosalanx chinensis appears heavier-bodied at all sizes and to attain a greater size than any other salangoid. The 163-mm specimen is the largest that has been reported.

Salanginae Regan, 1908b

Cranium and especially ethmoid plate very strongly depressed and elongate, more so than in any other salmoniforms. Adults with cranial fontanel entirely closed (posterior and sometimes also anterior portion of cranial fontanel open throughout life in all other salangoids). Upper and lower jaws with strongly pointed or projecting tips. Teeth relatively large and few in number. Premaxillae projecting beyond concave anterior margin of ethmoid plate to form a membrane-covered space penetrated by enlarged symphyseal teeth of lower jaw. Lower jaw often with a fleshy or bony presymphyseal process and presymphyseal teeth (Wakiya and Takahasi 1937, pl. 20, figs. 31–34). Supramaxilla absent (present in all other salangoids). Pectoral fin-rays 7–11 (20–32 in all other Salangidae). Pectoral girdle with a single postcleithrum (absent in all other salangoids). Body extremely elongate, more so than in any other salmoniforms. Basal portion of neural and hemal arches expanded, frequently covering centrum laterally and fusing with each other. Distal portion of neural arches with anterior and posterior projections, those of successive vertebrae articulating with each other. Vertebrae 68–79 (37–70 in all other salangoids).

The enlarged symphyseal teeth of the dentary and the membrane in the roof of the mouth through which they project presumably form a puncturing device to kill prey. Similar devices, with foramina in the roof of the mouth through which fanglike lower jaw teeth pass, occur in other piscivorous or predatory teleosts, including the characoids *Hepsetus, Hoplias,* and *Acestrorhynchus* (Roberts 1969).

In many respects Salanginae appear to be the most highly specialized members of the family. Even the low pectoral fin-ray count, which might be considered primitive, may be secondarily evolved, since primary pectoral radials 2–4 of Salanginae exhibit the distally fimbriate or digitate condition that is probably associated with the retention of pedunculate pectoral fins (probably a neotenic character) and evolution of large numbers of pectoral fin-rays (a specialization shared by all other Salangidae).

Salanx Oken, 1817

"Les Salanx" Cuvier, 1817:185 (French vernacular; not available for zoological nomenclature).

Salanx Oken, 1817:1183 (Latinization of Cuvier's "Les Salanx," and the earliest name available for zoological nomenclature; see ICZN Declaration 87, paragraph 12. Type-species, by monotypy, *Salanx cuvieri* Valenciennes, 1849).

Leucosoma Gray, 1831:4 (type-species, by monotypy, *Leucosoma reevesi* Gray, 1831).

Hemisalanx Regan, 1908b:444 (type-species, by monotypy, *Hemisalanx prognathus* Regan, 1908b).

Parasalanx Regan, 1908b:444 (type-species, by subsequent designation of Fang, 1934a:259, *Parasalanx gracillimus* Regan, 1908b = ?*Salanx cuvieri* Valenciennes, 1849).

Reganisalanx Fang, 1934b:509 (type-species, by monotypy, *Reganisalanx normani* Fang, 1934b = *Salanx ariakensis* Kishinouye, 1901).

Metasalanx Wakiya and Takahasi, 1937:293 (type-species, by monotypy, *Metasalanx coreanus* Wakiya and Takahasi, 1937, a nomen nudum).

The four species herein recognized as constituting the genus *Salanx* have been placed by other authors in three genera, *Salanx, Hemisalanx,* and *Leucosoma.* Wakiya and Takahasi (1937) even placed *Hemisalanx* in a subfamily of its own, Hemisalanginae, regarded by them as intermediate between Protosalanginae and Salanginae. Because these four species differ strikingly from all other salangids in several features of skeletal anatomy but agree closely with each other in conformation of the cranium and jaws, distribution and size of jaw teeth, number of pectoral fin-rays, and the peculiar modification of their neural and hemal arches and high vertebral counts, I prefer to recognize them as belonging to three subgenera in the sole genus of the subfamily Salanginae.

Salanx (*Salanx*) **ariakensis**
(Kishinouye, 1901)

Salanx ariakensis Kishinouye, 1901:359 (type-locality Ariake Bay, Kiushiu).

Salanx acuticeps Regan, 1908a:360 (type-locality Lake Candidius, Formosa).

Parasalanx acuticeps Regan, 1908b:446.

Parasalanx longianalis Regan, 1908b:446 (type-locality Liao-ho, northern China).

Parasalanx annitae van Dam, 1926:342 (type-locality Peitaiho, China).

Reganisalanx normani Fang, 1934b:509 (type-locality Ichang, as herein restricted).

Material Examined.—AMNH 10327, 7:125–147 mm, Hunan; BMNH 1888.5.15.11–12, 2:141–143 mm, Ichang (lectotype and paralectotype of *R. normani*); BMNH 1898.2.8.20–23, 4:114–123 mm, Liao-ho, northern China (syntypes of *P. longianalis*); BMNH 1904.4.2835–36, 2:116–118 mm, Lake Candidius, Formosa (syntypes of *S. acuticeps*); BMNH 1927.3.26.3, 125 mm, Nanking; BMNH 1928.6.22.6, 115 mm, Wenchow; CAS-SU 8574, 2:99.1–104 mm, Ariake Sea (identified by Kishinouye); CAS-SU 23103, 107 mm, Maruyama, Taihoku, Formosa; ZMA 112.587, 128 mm, Peitaiho, China (holotype of *P. annitae*).

In vertebral counts and in all other respects so far as known the four syntypes of *P. longianalis* agree well with other material herein referred to as *Salanx ariakensis,* except for their consistently high anal fin-ray counts of 30–32 (reported by Regan 1908b:446). Most samples of *S. ariakensis* examined have only 26–29 anal fin-rays, but two specimens from Ariake Bay have 27 and 31.

Reganisalanx normani is based primarily on the description by Regan (1908b) and supplementary notes by Fang (1934b:509) of two specimens from Ichang (BMNH 1888.5.15, 11–12), identified by Regan (ibid.) as *Salanx cuvieri.* Fang declared that the specimens represented a distinct genus but did not provide a proper generic diagnosis or description; apparently he distinguished it from *Salanx* based on the lack of a presymphyseal bone. In my opinion the character cannot be used to split the genus *Salanx*.

I have reidentified these specimens as *S. ariakensis,* a species in which the presymphyseal bone may be present or absent. I have not seen the third specimen referred to *R. normani* by Fang (ibid.). It is clear from Fang's account that he did not compare this specimen directly with the two specimens from Ichang, and it might not be conspecific. In order to fix the identity of this nominal taxon, the 141-mm undamaged specimen from Ichang (BMNH 1888.5.15.11) is hereby designated the lectotype. The 143-mm specimen, with the body damaged just behind the head and at mid-abdomen, is a conspecific paralectotype (BMNH 1888.5.15.12).

Fang (1934a) reported 11 specimens (as *Parasalanx longianalis*) with the following anal finray counts: 28(5), 29(2), 30(3), 32(1). The vertebral counts are unknown for these specimens but it seems likely from Fang's account that they are all *S. cuvieri.*

The holotype of *P. annitae* has the head relatively short and broad (for the subgenus *Salanx*) and in this respect is more like *S. ariakensis* than *S. cuvieri.* A presymphyseal bone is present, but it is short considering the large size of the specimen, and has only 2 teeth on each side. The premaxilla has 7 teeth, maxilla 12, and dentary about 10.

Salanx (*Salanx*) **cuvieri** Valenciennes, 1849

Salanx cuvieri Valenciennes *in* Cuvier and Valenciennes, 1849:360 (type-locality unknown).

?*Parasalanx gracillimus* Regan, 1908b:446 (type-locality Shanghai).

Parasalanx angusticeps Regan, 1908b:446 (type-locality China).

Parasalanx cantonensis Herre, 1932:425 (type-locality Canton).

Material Examined.—AMNH 51689, 3:88.6–106 mm, Canton; BMNH 1855.9.19.1539, 144 mm (holotype of *P. angusticeps*); BMNH 1891.1.31.20, 111 mm, Shanghai (holotype of *P. gracillimus*); BMNH 1936.10.7.13, 119 mm, Sharp Peak, Fukien; CAS 52057, 4:76.5–98.0 mm, Hong Kong (1 alizarin); CAS-SU 225732, 112 mm, Canton (holotype of *P. cantonensis*); CAS-SU 32454, 18:56–66 mm, Chuan Is. (4:61.7–69.4 mm alcian-alizarin); CAS-SU 32943, 117 mm, near Pakhoi, SW Kwangtung; MNHN 9900, 112 mm, no locality (holotype).

So far as I have been able to determine, variation in the presymphyseal bone within each species, including its presence or absence and its length or amount of dentition, is correlated chiefly with size and is not sexually dimorphic.

Notes on Holotype.—The holotype (Fig. 2a) is dried but complete and in fair condition. The body immediately posterior to the head is badly damaged and fin-rays brittle, so it must be handled with care. Cranial width (at anterior margin of eyes) 3.5 in cranial length. Presymphyseal bone, 2.1 mm long, with 1–2 moderately large teeth basally and at least 2 minute teeth distally. Premaxilla considerably elongated anteriorly, with 7–8 teeth. Maxilla with about 7 teeth. Dentary with about 13 teeth of variable size. Palatal teeth 7, very small and in a single row. The following proportional measurements are expressed as times in standard length. Length of cranium about 7; length of head (to end of gill cover) 4.7; length from anterior midline of ethmoid plate (concave) to anterior rim of orbit 16; length from tip of upper jaw (premaxilla) to anterior rim of orbit 10; diameter of eye (slightly shrunken) approximately 28.

Notes on Synonymy.—*P. angusticeps* is distinguished by Regan primarily on the basis of its exceptionally elongate head: "head nearly 4 times as long as broad; snout a little longer than postorbital length of head" versus head 3 times or a little more than 3 times as long as broad, and snout only as long as or a little shorter than postorbital length of head in all other *Parasalanx* and *Salanx* (Regan 1908b:445–446). The dentition of the holotype of *P. angusticeps,* a gravid female of 144 mm, is complete and undamaged. Presymphyseal bone elongate with 5–6 teeth on each side; premaxilla with 7 teeth; maxillary teeth 10 or 11; dentary with a small tooth anteriorly (just behind symphysis), then an enormous canine tooth, followed by 7 small teeth and 6 moderately large teeth; palatine with 8 small teeth in a single straight row.

The holotype of *P. gracillimus* is in poor condition, dried, twisted, and slightly shrunken. Its body depth, reported as 18 times its length, is attributable to the poor condition (emaciation) of the specimen. Its dentition is as follows: presymphyseal bone with 3 teeth on each side, premaxillary 5, maxillary 8, dentary with 1 moderately large, 6 small, and 5 moderately large, and palatal 7 moderately large. The vertebral column is broken anteriorly, making all of the counts based on vertebrae doubtful. Wakiya and Takahasi (1937:288) tentatively placed *P. gra-*

TABLE 2. MERISTIC CHARACTERS OF SALANGOIDS BASED ON MATERIAL EXAMINED.

	Total vertebrae	Vert. to pelvic o.	Vert. to dorsal o.	Vert. to anal o.	Caudal vert.	Dorsal rays	Anal rays	Pect. rays	Anal scales	Branch. rays	Gill rakers	Remarks
Protosalanx chinensis												
CAS-SU 6306, Tien Tsin	68–70	21–25	38–39	47–48	6–8	16–18	30–32	22–27	26–30	4(6)4(1)	16(2)	Paratypes *hyalocranius*
CAS-SU 23639, Seoul	67	23	39	45	8	16	33	25	26	—	15	
CAS-SU 36025, no. loc.	66(3)	22–23	36–37	44–48	6–8	16	31–33	20–30	22	—	13–15	
UMMZ 180096, Korea	—	—	—	—	—	16–17	31–33	23–24	23	—	12–16	
Salanx ariakensis												
AMNH 10327, Hunan	74(5)75(1)76(1)	30–31	51–52	54–55	10–11	13–14	26–28	9	22–25	—	8–12	
BMNH 1888.5.15.11–12, Ichang	74–75	31	52–53	55	10?	—	—	—	—	—	—	Syntypes *normani*
BMNH 1898.2.8.20–23, Liao-ho	73(2)75(2)	29–31	51–53	54–55	10–11	—	—	—	—	—	—	Syntypes *longianalis*
BMNH 1909.4.28–35–36, Formosa	72–73	30–31	51–52	52	10	—	27?	10?	20–21	—	—	Syntypes *acuticeps*
BMNH 1927.3.26.3, Nanking	75	30	52?	54?	—	—	—	—	—	—	—	
BMNH 1928.6.22.6, Wenchow	72	31	52	54	10	—	—	—	—	—	—	
CAS-SU 8574, Ariake Bay	74(2)	29–30	52–53	54–55	9–10	12–14	27–31	10	—	—	14	
CAS-SU 23103, Formosa	74	30	53	53	10	13	28	10	21	—	8	
ZMA 112.587, Peitaiho	75	28	51	53	—	13	27?	9	—	—	11	Holotype *annitae*
Salanx cuvieri												
AMNH 51689, Canton	77(1)78(1)79(1)	31–32	54–56	56–57	—	13–14	29	9–10	—	—	9–10	
BMNH 1855.9.19.1539, China	77	31	56	57	11?	—	29?	9	—	—	—	Holotype *angusticeps*
BMNH 1891.1.31.20, Shanghai	76?	31?	54?	57?	—	—	—	—	—	—	—	Holotype *gracillimus*
BMNH 1936.10.7.13, Fukien	77	31	—	—	—	—	—	—	—	—	—	
CAS 52027, Hong Kong	77(1)78(1)79(1)	30–32	54–56	55–58	—	12–14	27–30?	9–10	—	—	8–9	
CAS-SU 25732, Canton	77	31	55	57	10	13	28	9–10	—	—	11?	Holotype *cantonensis*
CAS–SU 32454, Chuan Is.	76(2)77(5)78(4)	31–32	53–55	55–57	12	13	27	—	—	3	11	
CAS-SU 32943, Kwantung	78	32	55	56	11	14?	27?	9	—	—	11	
MNHN 9900, no loc.	77	31–32	55	56	10	12	29	9	—	—	—	Holotype *cuvieri*
Salanx prognathus												
BMNH 1873.7.30.69, Shanghai	71	30?	52	53	9	12?	25	—	—	—	—	Holotype *prognathus*
CAS 51439, Kiangsu	71(5)	30–31	51–52	51–53	10	12–14	25–28	7–8	16–20	3	10–11	
CAS-SU 33990, Hong Kong	70–73	30–31	51–52	52–53	10–11	13–14	26–29	7–9	18–21	—	9–11	
Salanx reevesi												
AMNH 10336, Fukien	68	28	47	53	6	11	27	10	—	3	—	
AMNH 11161, Fukien	68	27	46	52	7	10	28	10	—	3	16	
CAS-SU 1511, Swatow	70–73	28–30?	48–49	53–55	7–9	10–11	30(1)	11	19	3	13	
CAS-SU 25738, Canton	71	29	48	55	6	11	28	10	—	—	13?	
CAS-SU 61189, Hong Kong	70	27	47	54	7	12	28	11	—	3	15	

TABLE 2. CONTINUED.

	Total vertebrae	Vert. to pelvic o.	Vert. to dorsal o.	Vert. to anal o.	Caudal vert.	Dorsal rays	Anal rays	Pect. rays	Anal scales	Branch. rays	Gill rakers	Remarks
Neosalanx andersoni												
NRM 10287, Chihli	63	24	37	43	9	15	30	34	20–21?	—	15	Holotype *andersoni*
Neosalanx brevirostris												
AMNH 10337, Hunan	55(9)56(11)57(2)	20–22	31–34	39–42	6–8	12–14	25–28	—	—	3	15(3)	
AMNH 10480, Tung Ting	55	20	32–33	40	6	13	26	—	—	—	14	
AMNH 11155, Fukien	57	21	33–34	41	7	14	25	—	—	—	17	
AMNH 37044, Foochow	56(1)57(1)	20	33–34	41–42	6–7	14–15	25(2)	—	—	—	17	
AMNH 51690, Canton	57(6)58(14)59(3)	20–22	32–35	42–44	7	14	26–30?	—	—	—	17(2)	
CAS 52032, Hong Kong	58	21	32	41	—	14	28	—	—	—	—	
CAS-SU 1540, Swatow	58(2)59(1)	21	33	42	5	13–14	28(3)	26–30	—	3	19	
CAS-SU 68888, Seoul	55(1)56(1)57(1)	20–21	31–33	40–42	—	15	24(1)	28	15?	—	15–16	
MNHN 1922.184–189, Tonkin	57(3)58(2)59(1)	19–21	34–35	41–44	6–7	14–15	25–26	24–27	—	—	—	Syntypes *brevirostris*
Neosalanx jordani												
AMNH 51705, Canton	51(1)52(6)54(1)											
AMNH 51704, Foochow	53	21	32	40	8	13	23	—	—	—	14 or 15	
CAS 52028, Kiangsu	50(7)51(3)52(1)	18–20	30–32	35–37	5–8	11–13	23–25	20–26	13–16	2–3	9–10	
CAS 52029, Hong Kong	48	20	32	41–42	—	14	29	—	—	—	17?	
CAS-SU 68625, Tien Tsin	50(3)51(5)52(9)53(1)	19–20	30–32	36–38	5–7	12–14	23–25	21–22	—	3–4	12–14	
Salangichthys ishikawae												
CAS-SU 6780, Same	59(2)60(1)	25–26	37–39	42–43	8–9	14–15	25–26	25–28	—	3–4	16–17	
CAS-SU 68889, Ariake Bay	61	26	38	43	9	15	24?	26	—	—	19	
Salangichthys microdon												
CAS 52033, Kawasaki	61(2)62(3)63(1)	26–27	40	43–44	9	12–13	25–28	14–18	17	—	18	
CAS 53034, Kituara	59(2)60(1)61(4)62(1)	23–26	36–39	42–45	8–9	10–13	22–25				14–16	
CAS-SU 134, Tokyo	61(2)62(3)	25–26	39–40	43–45	8–9	12–13	24–27	14–16	—	3–4	16	
Sundasalanx microps												
CAS 44220, Kapuas	41(2)42(4)43(1)	15–16	25–27	29–31	3–4	12–14	17–21	0	0	3	0–2	Paratypes *microps*
Sundasalanx praecox												
CAS 52031, Tale Sap	37(2)38(7)	13–14	23–24	26–28	3–4	12–13	16–19	0	0	3	10	Paratypes *praecox*
CAS 52036, Mekong	39(1)40(3)	14–15	24–25	29	3–4	12–15	16–21	0	0	3	10–12	
CAS 52037, Muar	37(1)40(4)41(7)	14–15	25–26	30–31	3–4	12–14	14–16	0	0	3	10?	

cillimus as a synonym of *P. ariakensis,* and perhaps they were correct. This matter is of some nomenclatural significance, since *P. gracillimus* is type-species of Regan's *Parasalanx.*

The holotype of *P. cantonensis* has a very elongate presymphyseal bone with 10 teeth; premaxillary teeth 8, maxillary teeth 10, dentary teeth 13; palatal teeth 11.

Length of the head (and cranium) is exceptionally variable in all genera of Salangidae, even including the relatively short-snouted genus *Neosalanx,* and is particularly variable in the long-snouted subfamily Salanginae. Variable elongation of the head and particularly the snout with its flattened ethmoid plate is evident in the large series of *Protosalanx chinensis* and *Neosalanx jordani* I examined, even though these are relatively small specimens. *P. angusticeps* is based on a single specimen, the holotype, which happens to be the largest referred to *S. cuvieri* that I have examined. In vertebral counts and other characters it apparently agrees well with other material of *S. cuvieri.*

Salanx (*Hemisalanx*) **prognathus** (Regan, 1908b) new combination

Hemisalanx prognathus Regan, 1908b:445 (type-locality Shanghai).
?*Salanx brachyrostralis* Fang, 1934a:257 (type-locality Nanking).
?*Reganisalanx brachyrostralis* Fang, 1934b:509.
Metasalanx coreanus Wakiya and Takahasi, 1937 (otherwise unpublished manuscript name placed in synonymy of *H. prognathus* by Wakiya and Takahasi 1937:293).

Material Examined.—BMNH 1873.7.30.69, 111 mm, Shanghai (holotype); CAS 51439, 34:97.5–120 mm, Kiangsu Prov. (12:97.5–112 mm alcian-alizarin); CAS-SU 33990, 8: 94–114 mm, Tai Po, New Territory, Hong Kong.

This species has been recognized as representing a monotypic genus since its original description, and Wakiya and Takahasi (1937) even placed it in a monotypic subfamily (Hemisalanginae). Apart from its somewhat shorter, blunter snout, and slight differences in dentition, however, it is very similar to specimens of the subgenus *Salanx* lacking a presymphyseal bone. The magnitude of the differences between *Hemisalanx* and *Salanx* (sensu stricto) is comparable to that between the latter and *Leucosoma,* which I also regard as only subgenerically distinct.

Regarding *S. brachyrostralis,* Wakiya and Takahasi (1937) placed it in the synonymy of *S. prognathus* with a question mark, as is done here. Neither Wakiya and Takahasi nor I have examined the holotype ("S. 4227, 144 mm total length").

Wakiya and Takahasi (1937:293) placed *Reganisalanx normani* in the synonymy of *H. prognathus* with a question mark, but I have examined the type-specimens and have reidentified them as *S. ariakensis.*

Salanx (*Leucosoma*) **reevesii** (Gray, 1831)

?*Albula chinensis* Osbeck, 1757 (type-locality West River at Canton?; original not consulted).
Leucosoma reevesi Gray, 1831:4 (type-locality China).
Leucosoma chinensis Richardson, 1846:303.
Salanx reevesii Valenciennes *in* Cuvier and Valenciennes, 1849:363, Pl. 646.
Salanx chinensis Günther, 1866:205.

Material Examined.—AMNH 10336, 130 mm, Fukien; AMNH 11161, 74.5 mm, Fukien; CAS-SU 1511, 4:87.8–140 mm, Swatow (2:87.8–102 mm alcian-alizarin); CAS-SU 25738, 127 mm, Canton; CAS-SU 61189, 153 mm, Castle Peak Bay?, Hong Kong.

Salanx reevesi is second only to *Protosalanx chinensis* as the largest and heaviest-bodied salangoid. It is the only species of Salangidae in which males with anal scales have not been reported previously. A 130-mm specimen from Swatow (CAS-SU 1511) is a mature male with its anal fin greatly enlarged and 17 anal scales. It is the only member of the subgenus *Leucosoma,* distinguished by a median row of 6–8 teeth on the tongue or basihyal bone.

Albula chinensis Osbeck, 1765, has been identified with this species by various ichthyologists following Richardson (1846) but, as pointed out by Wakiya and Takahasi (1937:291–292), its identity cannot be verified. While *Albula chinensis* evidently is a member of the Salanginae, there apparently are no type-specimen(s) extant (Kullander, pers. commun., 1983) and it is impossible to tell from Osbeck's description which species he had. The presence of teeth on the tongue, which would positively identify it as *S. chinensis,* is not mentioned.

In addition to having teeth on the tongue, *Leucosoma* has jaw teeth that are somewhat larger than those in the subgenera *Hemisalanx* and *Salanx.* In all other features of skeletal anatomy, however, *Leucosoma* falls in the genus *Salanx.* It has nearly the same vertebral counts as the subgenus *Hemisalanx,* and its cranial shape appears to be identical with that in the subgenus *Salanx.*

Salangichthyinae, new subfamily

Cranium only moderately depressed (as in Sundasalangidae). Cranial fontanel with posterior and apparently anterior portions open throughout life. Head rounded anteriorly, premaxillae failing to meet at midline, not projecting significantly beyond snout. Teeth greatly reduced in size, small or minute, those on maxilla very numerous (about 15–40). Maxilla expanded, much larger than premaxilla. Body moderately elongate. Vertebrae 48–65 (66–79 in all other Salangidae).

This subfamily contains two genera, *Neosalanx* and *Salangichthys,* formerly placed in Protosalanginae (Wakiya and Takahasi 1937).

Neosalanx Wakiya and Takahasi, 1937

Neosalanx Wakiya and Takahasi, 1937:282 (type-species, by original designation, *Neosalanx jordani* Wakiya and Takahasi, 1937).

The species of this genus are poorly known. In museum collections and older literature they are usually misidentified as *Protosalanx* or *Salanx.* Wakiya and Takahasi (1937) recognized four species, three of which they described as new. Although they recognized that *Protosalanx andersoni* Rendahl belonged to *Neosalanx,* they overlooked three previously described taxa, which also apparently belong to it: *Protosalanx brevirostris* Pellegrin, 1923; *Protosalanx tangkahkeii* Wu, 1931; and *Salanx argentea* Lin, 1932. All three of these were mistakenly placed by Fang (1934a:240) in the synonymy of *Protosalanx hyalocranius.* I briefly examined the type-specimens of Pellegrin's *P. brevirostris* in Paris, and have since studied radiographs of them, but have not seen the types of the taxa described by Wu and Lin.

Wakiya and Takahasi (1937) distinguished four species of *Neosalanx,* mainly on the basis of differences in counts of vertebrae and fin-rays. Without knowing more about interpopulational meristic and other variation in *Neosalanx,* it is difficult to evaluate the species. Specimens I examined tend to fall into groups, based on vertebral counts, identical to those recognized as species by Wakiya and Takahasi, and I have identified my material accordingly.

Wakiya and Takahasi (1937) described *Neosalanx* as a new genus despite the fact that one of its included species, *Protosalanx andersoni* Rendahl, 1923, was proposed by Fang (1934a) as type-species for his genus *Paraprotosalanx.* It is obvious from Fang's account that he mistook specimens of *Protosalanx chinensis* and probably either *Neosalanx brevirostris* or *N. jordani* as *Protosalanx andersoni* and that his generic diagnosis is based mainly on *P. chinensis.* At this point the nomenclaturally parsimonious solution would have been for Wakiya and Takahasi to recognize *Paraprotosalanx* as a valid genus with *Protosalanx andersoni* Rendahl, 1923 (not of Fang 1934a), as its type-species. They chose, however, to coin a new name and designated as type-species the new species *N. jordani.* Given that they did so, and that no publication has appeared subsequently in which *Paraprotosalanx* is treated except as a synonym of *Neosalanx,* I provisionally recognize *Neosalanx* as valid. It should be noted, however, that judging from Article 70 of the International Code of Zoological Nomenclature (1964 ed.) this case should be referred to the International Commission.

Neosalanx andersoni (Rendahl, 1923)

Protosalanx andersoni Rendahl, 1923:92 (type-locality Chihli, Shan-Hai-Kuan).
Neosalanx andersoni Wakiya and Takahasi, 1937:285.

Material Examined.—NRM 10287, 79 mm, Chihli, Shan-Hai-Kuan (holotype).

This species differs from all other *Neosalanx* by its relatively large size, to 100 mm (vs. only to 64 mm) and more numerous total vertebrae, 63–65 (vs. 59 or less). Wakiya and Takahasi reported anal scale counts of 25–28 in *N. andersoni* and only 14–21 in other *Neosalanx,* but I find only 21 or 22 anal scales on the male holotype. *N. andersoni* is known only from rivers in Korea and China flowing into the Yellow Sea.

The jaws of the holotype of *Neosalanx andersoni* appear to be almost entirely toothless. I detected a single small conical tooth on the right premaxilla, none on the left. The dentaries appear to be entirely toothless. The maxillae, although having irregularities in the margin where teeth may have been affixed, are toothless or almost toothless except for a very few minute teeth. There seem to be no palatal or glossal teeth.

The anterior and posterior portions of the cranial fontanel are widely separated and reduced in size (especially the anterior portion). There is no indication of a tectum medialis.

A small patch of minute, scaly breeding tubercles occurs near the base of the 9th and 10th anal fin-rays, and more extensive areas of tubercles have evidently been sloughed off. Pelvics enlarged but without tubercles; lower jaw very strongly projecting. Snout elongate, as in *Salangichthys* (snout-tip to anterior margin of orbit =4.2 mm).

Anal scale row continues onto ventral margin of caudal peduncle a considerable distance (4 scales).

Tip of snout dorsally and tip of lower jaw, dorsal surface of cranium over brain, dorsal surface of body with irregularly distributed small melanophores. No melanophores on anal fin, and none or almost none on caudal fin, ventral body surface, including pelvic and pectoral fin bases.

Neosalanx brevirostris (Pellegrin, 1923) new combination

Protosalanx brevirostris Pellegrin, 1923:351 (type-locality Tonkin).

?*Protosalanx tangkahkeii* Wu, 1931:219 (type-locality Amoy).

?*Salanx argentea* Lin, 1932 (type-localities Sangchang stream; Henngchow Bay; Canton).

Protosalanx brevirostralis Fang, 1934a:232, 236, 240 (misspelled; referred to synonymy of *Protosalanx hyalocranius*).

Neosalanx hubbsi Wakiya and Takahasi, 1937:284 (type-locality Tien-tsin).

Neosalanx tangkahkeii taihuensis Chen, 1954? (reference not seen).

Material Examined.—AMNH 10337, 22:43.8–60.7 mm, Hunan (2:58.4–60.7 mm alizarin); AMNH 10480, 53.5 mm, Tung Ting Lake, Hunan; AMNH 11155, 60.5 mm, Fukien; AMNH 37044, 2:49.6–60.8 mm, Foochow, Fukien; AMNH 51690, 26:48–65 mm, Canton; CAS 52032, 2:46.1–48.3 mm, Hong Kong (48.3 mm alizarin); CAS-SU 1540, 3:56.8–57.9 mm, Swatow; CAS-SU 68888, 3:56.0–58.2 mm, Seoul; MNHN 1922.184–189, 6:65–70 mm, Tonkin (syntypes of *P. brevirostris*); USNM 219923, 2: 51.0–57.4 mm, Liang tsi Lake, Hupeh (formerly identified as *N. tangkahkeii taihuensis*).

Protosalanx brevirostris has not been recognized as a valid species or even referred to since Fang (1934a), without examining the types, erroneously placed it as a junior synonym of *Protosalanx hyalocranius.* I briefly examined the types, which are in rather poor condition, during a visit to Paris in November, 1982, but did not have specimens of other *Neosalanx* on hand for comparison. I have since examined radiographs of the types. Since their vertebral counts—57(2), 58(2), 59(1)—correspond only to those reported by Wakiya and Takahasi for *Neosalanx hubbsi,* I conclude that they are conspecific.

Neosalanx brevirostris is known from the mainland coast of Asia, from the Yellow Sea coast of Korea south to Tonkin.

In most specimens of *Neosalanx* the premaxillaries are toothless or have relatively few teeth (1–6 reported by Wakiya and Takahasi (1937), presumably based on examination of numerous specimens, and 0–2 in a large number of specimens I examined). Wakiya and Takahasi (1937) reported only 1–2 premaxillary teeth in *N. hubbsi.* Thus it is noteworthy that the 48.3-mm specimen from Hong Kong (CAS 52032) here referred to this species has about 20 minute teeth on each premaxilla. Tooth counts have not been made on the type-specimens of *N. brevirostris.*

Despite considerable effort to trace its original description, the taxon *Neosalanx tangkahkeii taihuensis* is known to me only from an article by Wang et al. (1980), an abstract of which appeared in *Aquatic Sciences and Fisheries Abstracts.* The article reports on its artificial fertilization and larval development (see Addendum).

Neosalanx jordani Wakiya and Takahasi, 1937

Neosalanx jordani Wakiya and Takahasi, 1937:282 (type-locality "River Rakuto, Corea").

Material Examined.—AMNH 51705, 8:29–33 mm, Canton; AMNH 51704, 47.5 mm, Foochow, Fukien; CAS 52028, 177:33.0–45.5 mm, Kiangsu, Chekiang Prov. (14:35.1–44.8 mm alcian-alizarin); CAS 52029, 1:36.8 mm, Hong Kong; CAS 52030, 311:22–58 mm, purchased in San Francisco; CAS-SU 68625, 160:35.3–47.1 mm, and UMMZ 55601, 20:35.5–41.3 mm, Pei-ho at Tien-Tsin (paratypes of *Salanx hyalocranius* Abbott, 1901) (10:39.7–45.7 mm alcian-alizarin).

Wakiya and Takahasi (1937) characterize this species as having 49–54 vertebrae (average 50.95). The range of material I examined is 48–54. The species is known from rivers along mainland coast of Asia, from the Yellow Sea coast of Korea south to Hong Kong.

Neosalanx reganius Wakiya and Takahasi, 1937

Neosalanx reganius Wakiya and Takahasi, 1937:283 (type-locality "Ariake Bay, Kyushu, Japan," possibly erroneous).

Neosalanx regani Matsubara, 1955:214 (unjustified spelling).

Wakiya and Takahasi (1937:283) reported 52–56 (average 53.75) vertebrae for this species. It is known only from the type-specimens, supposedly collected in Ariake Bay. I have not examined any *Neosalanx* from Japan.

Salangichthys Bleeker, 1860

Salangichthys Bleeker, 1860:101 (type-species, by monotypy, *Salangichthys microdon* Bleeker, 1860).

Salangichthys microdon Bleeker, 1860:101

Salangichthys microdon Bleeker, 1860:101 (type-locality Yeddo-Tokyo).
Salangichthys kishinouyei Wakiya and Takahasi, 1913:552 (type-locality Seishin, Korea and Shimane-ken, Japan).

Material Examined.—AMNH 13149, 28:50–64 mm, Daomori-ken, Japan; CAS 52033, 6:74.8–86.7 mm, Kawasaki; CAS 52034, 9:31.6–36.1 mm, Lake Kituara (alcian-alizarin); CAS-SU 134, 10:78–92 mm, Tokyo (5:81–86 mm alcian-alizarin); CAS-SU 22637, 61:32–67 mm, Sendai, Matsushima Bay, Japan.

Salangichthys kishinouyei originally was distinguished from *S. microdon* by Wakiya and Takahasi (1913) on the basis of its having 1) mandibular, maxillary, and palatal teeth more widely spaced; 2) snout shorter; 3) anal fin origin in females more anterior; and 4) threads of external egg membrane thicker, their ends club-shaped and ending freely without fusing to each other to form a ring. They later concluded that these differences represent intraspecific variation in populations of *S. microdon* on the Japan Sea coast of Sakhalin, Korea, Honshu, and Kyushu and placed *S. kishinouyei* as a synonym of *S. microdon* (Wakiya and Takahasi 1937:279–280).

Matsuoka and Iwai (1983, Fig. 2) illustrated an alcian-alizarin preparation of *S. microdon* (locality not indicated) with 65 total vertebrae. The highest number of vertebrae otherwise known in *Salangichthys* is 63 (Table 2).

Salangichthys ishikawae Wakiya and Takahasi, 1913

Salangichthys ishikawae Wakiya and Takahasi, 1913: 552 (type-locality Miyagi-ken, Japan).

Material Examined.—CAS-SU 6780, 9:67.6–74.3 mm, Same, Rikuoku (3:70.3–74.2 mm alcian-alizarin); CAS-SU 68878, 20:48–63 mm, Pacific coast of Aomori-ken, northern Honshu; CAS-SU 68889, 70.7 mm, Ariake Bay, Kyushu (locality possibly erroneous).

Salangichthys ishikawae is distinguished from *S. microdon* mainly by having 20–27 pectoral fin-rays instead of only 14–19 (see Senta 1973c). Differences in counts of vertebrae and anal scales, based on few specimens, are of doubtful significance (see Table 2).

According to Wakiya and Takahasi (1937:281), *S. ishikawae* "lives in water of rather higher salinity than *S. microdon* . . . and seems to be a northern species," known only on the Pacific coast of Honshu. The specimen herein reported from Ariake Bay, Kyushu, represents a southerly range extension of about 500 km if its locality data are correct. It was found with two specimens of *Salanx ariakensis* collected by Kishinouye in Ariake Bay (CAS-SU 8574).

Sundasalangidae Roberts, 1981

Primary pectoral girdle consisting of single median element (identical to the condition in various larval teleosts, but unknown in adults of any other teleost). Pectoral fin rayless, supported by a single undivided basal radial. Pelvic fin with 5 rays. Each half of pelvic girdle with two parapelvic cartilages (unknown in any other teleosts). Adipose fin absent. Adult males without anal scales or sexually dimorphic anal fins. Neural spines much more elongate than in Salangidae. Hemal arches of last 12 or so abdominal vertebrae with elongate hemal spines (abdominal vertebrae without hemal spines in all other salangoids). Vertebrae 37–43. Caudal fin skeleton with parhypural fused to hypurals 1 and 2 (parhypural separate in all other salangoids).

If specialized is defined as deviation from the morphology of any known group of salmoniforms that could possibly serve as the ancestral stock of Salangoidea, then *Sundasalanx* is by far the most specialized of all salangoids.

The samples of *Sundasalanx* available at the time of their original description differed so much (in regard to eye size, non-overlapping vertebral counts, etc.) that it seemed to me that they could not be the same species. Samples examined subsequently, from Muar and the Mekong, tend to be intermediate between the two described species. I have tentatively identified the new samples with *Sundasalanx praecox,* but the question of the number of species in the genus should be reconsidered when more material becomes available. The genus has not been found yet in Sumatra but is to be expected there.

Sundasalanx Roberts, 1981

Sundasalanx Roberts, 1981:297 (type-species, by original designation, *Sundasalanx praecox* Roberts, 1981).

Sundasalanx microps Roberts, 1981

Sundasalanx microps Roberts, 1981:300 (type-locality Kapuas River at Kampong Nibung, about 100 km NE of Sintang and 7 km NE of Selimbau).

Material Examined.—CAS 44220, paratypes, 34:14.6–19.9, Kapuas River at Kampong Nibung (paratypes) (7:13.5–18.0 mm alcian-alizarin).

Sundasalanx praecox Roberts, 1981

Sundasalanx praecox Roberts, 1981:299 (type-locality Khlong Falamee, Tale Sap, about 2 km W of Pak Payoon, Kra Isthmus, Southern Thailand).

Material Examined.—CAS 52031, 6:16.4–17.7 mm Khlong Falamee, Tale Sap, near Songkhla, Thailand (paratypes; alcian-alizarin); UMMZ uncat. and CAS 52036, 65:15.7–22.5 mm, Mekong River and tributaries in Thailand from Ban Dan to Nakon Phanom (4:18.2–20.3 mm alcian-alizarin; USNM 229304 and CAS 52037, 121:12.3–18.0 mm, Muar River 7–18 miles inland from Bandar Maharani (formerly Muar City) (12:16.5–17.8 mm alcian-alizarin).

When more material becomes available and the species of *Sundasalanx* are re-examined, the pigmentation of the Muar specimens (CAS 52037, USNM 229304) should be taken into consideration. In the *Sundasalanx* examined, each sample tends to have a more or less distinctive pigmentation or pattern of melanophore distribution shared by all of the specimens. Thus the type-series of *S. microps* is characterized by having a series of large midventral melanophores, one per myotome, extending from the pectoral fin to the anal fin. Midventral melanophores are absent in the type-series of *S. praecox*. In the Muar specimens here identified as *S. praecox*, however, a series of midventral melanophores extends from about pelvic-fin origin to the anal fin, thus resembling the pigmentation of *S. microps*. On the other hand, each of the Muar specimens has a series of large melanohores along the base of the anal fin, one melanophore between the base of each branched fin-ray. Other samples of *Sundasalanx* examined do not exhibit this feature.

In the original description of *S. praecox* (Roberts 1981:299) it is stated that the type-series has maxillary teeth about 15–19 vs. about 30 in *S. microps*; the reverse is true.

Discussion

Anyone who has looked into recent accounts of salmoniform classification realizes that it is in disarray. In this group current classifications are based largely on skeletal anatomy, and as long as the skeletal anatomy of major groups such as salangoids remain uninvestigated and others only partially investigated, no stable classification can be expected. McDowall (1969) briefly examined the skeletal anatomy of "*Salangichthys microdon*" (actually *Neosalanx*?) stained with alizarin and concluded that Salangidae "is not part of the galaxioid radiation." He also stated "a more complete study (of salangid skeletal anatomy) may be desirable, should a full range of material be available, especially if it should reveal some species with more complete ossification to enable more precise determination of affinities." A species with somewhat more complete ossification actually does exist—*Protosalanx chinensis*—but even in this species truly adequate observations of skeletal anatomy cannot be based on specimens stained solely with alizarin. The question is no longer relevant, however, since adequate skeletal preparations of salangoids usually can be obtained using the alcian-alizarin technique.

All modern accounts of salangid classification agree in placing them in the order Salmoniformes. My information on salangoid skeletal anatomy, however, has not provided me with obvious answers about their relationships to other salmoniforms, but has only emphasized their distinctness. The presence of two (marginal or submarginal) rows of teeth on the basihyal toothplate of *Protosalanx* confirms the integrity of the order Salmoniformes and the placement of Salangoidea within this order but nothing more. The presence of a taenia medialis in the cranium of young *Protosalanx* and a single specimen of *Neosalanx* suggests a shared derived character (synapomorphy) with osmeroids, but this character may well prove primitive for salmoniforms, perhaps to be found in many of them.

Higher classification of Salmoniformes has been the subject of considerable interest in the last two decades or so, with contributions by Gosline (1960), Greenwood et al. (1966), Weitzman (1967), McDowall (1969), Rosen (1974), Klyukanov (1975), and Fink and Weitzman (1982). A major issue is whether esocoids (pikes, northern mud-minnows, and relatives) are Salmoniformes, and should include the southern *Lepidogalaxias*, as advocated by Rosen. This view is contested by Fink and Weitzman, who exclude esocoids from Salmoniformes and relate *Lepidogalaxias* to Galaxiidae and osmeroids. Another major issue is whether relations of the southern "salmonoids" (Galaxiidae, etc.) lie with the northern salmonoids (Salmonidae, etc.) or with osmeroids. The hypothesis that stomiatoids are Salmoniformes (Weitzman 1967) has been rejected by Rosen (1974), Klyukanov (1975), and Fink and Weitzman (1982). Fink and Weitzman also point out that no satisfactory evidence has yet been advanced to support the hypotheses of relationships among osmeroids, salmonids, and galaxioids. Here I shall comment briefly on relationships of the salangoids to other Salmoniformes, particularly osmeroids and galaxioids, and present some evidence bearing on relationships of *Lepidogalaxias.*

Gosline (1960) suggested a close relationship of Osmeridae, Salangidae, and Plecoglossidae, distinguishing them from the Southern Hemisphere Retropinnidae, Aplochitonidae, and Galaxiidae. Greenwood et al. (1966) placed Salangidae in a suborder Galaxioidei including Retropinnidae, Galaxiidae, and Aplochitonidae without explanation. McDowall (1969) concluded that Salangidae are a very specialized offshoot of the salmonoids and not part of the galaxioid radiation.

In observing the skeletal anatomy of salangoids I have been watchful for specialized characters indicative of phyletic relationship to other Salmoniformes. While my study has revealed highly specialized characters (such as the hyopalatine) indicating monophyly of salangoids, it has not provided (or at least I have not noticed) characters that would link salangoids in a monophyletic taxon with Osmeridae or any other group. Rosen (1974) pointed to specializations of the anal fin and associated scales in males of *Lepidogalaxias* and *Mallotus,* but concluded (p. 304) that these do not indicate relationship to Salangidae, and I agree. The anal scales and anal fin modifications of male salangoids appear to be a unique specialization, as does the hyopalatine. Salangoids lack some skeletal features found in Osmeridae, notably in the ethmoid region. Whether this absence is due to loss or reflects a primitive condition is unclear. Development of a tectum taenia medialis in the cranial fontanel, characteristic of the osmeroid chondrocranium, occurs in some salangoids and may be indicative of relationship, but further observation may reveal that the character is widespread in Salmoniformes. The peculiar morphology of the salangoid egg case (Wakiya and Takahasi 1937, Okada 1960) may be similar to that in osmeroids (compare photographs of *Hypomesus olidus* and *Salangichthys microdon* eggs in Chyung 1961, figs. 242–243). Similar specializations possibly also occur in *Plecoglossus* but have not been reported in any of the northern salmonoids or in galaxioids.

According to McAllister (1963:6) "the neotenic Salangidae strongly resemble larval Osmeridae but may be distinguished by their reduced pointed head and elongated anterior portion of the body, as well as osteological characters." Skeletal preparations of larval Osmeridae examined by me differ from salangoids in many respects. There are certain similarities in appearance of the largely transparent and lightly pigmented larvae of osmeroids and salangoids but these are mainly such as are to be found in larvae of non-related teleosts, and their value in assessing relationships is dubious. Skeletal anatomy of larval osmeroids I have examined differs from that of salangoids almost as much as does skeletal anatomy of adult osmeroids. I have not examined skeletal anatomy of Plecoglossidae, but this family appears to be very specialized and there is no evidence that it is particularly closely related to Salangidae. Gosline (1960:346) and others have mentioned certain similarities between the salangids and the extraordinarily specialized galaxoid *Lovettia* but I believe such resemblance is due to independently acquired neotenic characters.

Considerable interest has centered on the phylogenetic significance of the little salmoniform *Lepidogalaxias salamandroides* recently discovered in western Australia (Mees 1961). Among many peculiar features, it has in sexually mature males an extraordinarily modified anal fin partially covered by a sheath of anal scales suggestive of the anal scales of male Salangidae. The extremely complex modifications of the anal finrays go far beyond that seen in the anal fin of the salangids or any other salmoniform, and I doubt that in the relatively simple modifications of the anal fin in male salangids any uniquely shared specializations (or synapomorphies) with *Lepidogalaxias* can be recognized. The presence of a sheath of enlarged anal scales, on the other hand, demands closer comparison with those of salangids, which are otherwise unique among salmoniforms (and perhaps all other teleosts). The anal scales in *Lepidogalaxias* are greatly enlarged and disposed in two main rows, rather than a single row, as in salangids. Two 31–34-mm specimens I examined have seven to eight scales in the upper row and three in the lower. There also appear to be some scales or scalelike structures associated with the vent itself. Unlike that of salangids, however, the anal sheath covers the

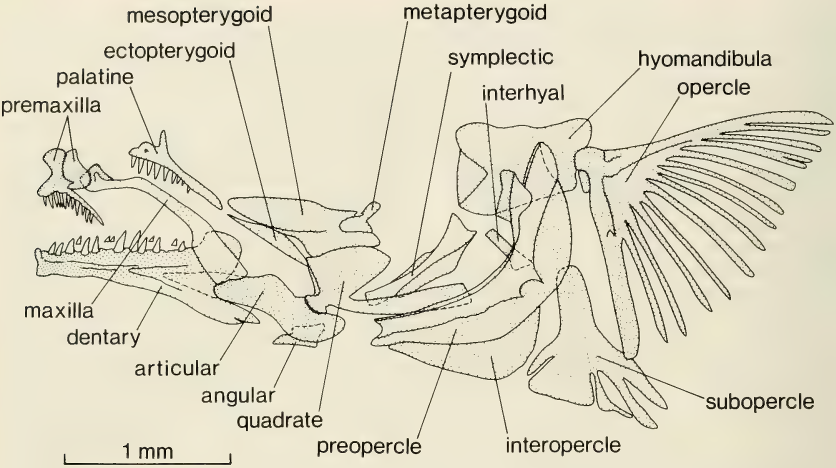


FIGURE 22. *Lepidogalaxias salamandroides* (uncat., 23.5 mm). Jaws, facial ones, and suspensorium (lateral view).

anal fin, especially the modified portions. In salangids the anal scales are on the body above the anal fin, and the rays themselves are entirely exposed. Whatever the phyletic significance, it would certainly be of interest to know more about the functional significance of the anal scales and modified anal fins in *Lepidogalaxias* and in Salangidae.

Fink and Weitzman (1982) suggested that a single row of mesopterygoid teeth is a synapomorphy indicating monophyly for the osmeroids (including Salangidae) and galaxioids (including *Lepidogalaxias*). Although Gosline (1960) stated that the mesopterygoid is absent in Salangidae, it is actually present in most of them. But while most Salangidae have palatal teeth, the salangoid mesopterygoid is invariably toothless, even in *Protosalanx* and *Salanx chinensis* which have well-developed basihyal teeth. Thus the concept of a "tongue-bite" character, based on basihyal and mesopterygoid teeth, and uniting galaxioids and osmeroids, does not hold for salangoids.

While my observations of salangoid skeletal anatomy have not provided me with the key to their higher relationships, I earnestly hope that they may do so for future workers who are able to make more extensive comparisons. In examining *Lepidogalaxias* I find no characters indicative of close relationship to Osmeridae or Salangidae, but the structure of the jaws and gill cover reveals specialized characters linking this strange western Australian fish to the southern galaxioid radiation.

Based largely on the assumption that *Lepidogalaxias* possesses uniserial mesopterygoid teeth, and without having examined skeletal material, Fink and Weitzman (1982) suggested its relationships lie with osmeroids and galaxioids. I have examined skeletal anatomy of several larval and juvenile or subadult *Lepidogalaxias*; the largest of these has a well-developed median patch of teeth on the prevomer and a pair of well-developed tooth patches on the anterior palatine area (ectopterygoid? = endopterygoid of Mees 1960) but the large, well-developed mesopterygoid is toothless. On the other hand, specialization of bones in the jaws and gill cover (Fig. 22) indicates relationship with galaxioids. The extraordinary fimbriate condition of the bony opercle, also of the subopercle, appears to be a highly specialized character shared only (i.e., synapomorphic) with galaxioids (see McDowall 1969, Fig. 3b–e, and Rosen 1974, Fig. 13). The short and laterally directed premaxilla and toothless maxilla with its strongly concave margin may represent another synapomorphy with galaxioids. My observations suggest that *Lepidogalaxias* is indeed related to Galaxiidae, as suggested by Nelson (1970), but I doubt that it represents the "primitive sister group of galaxiids or galaxioids"; it is more likely to be a highly specialized galaxiid or galaxioid derivative. As pointed out by Scott (1966), its osteology should be examined carefully and thoroughly; this has yet to be done. For the present I would like to point out a difference between the branchial arches of *Lepidogalaxias* and Umbridae which merits further investigation. In *Lepidogalaxias* and Umbridae the basibranchial plate has five basibranchials, and the fifth is cartilaginous. In *Lepidogalaxias* the basibranchial plate is apparently immobile; that is, the basibranchials apparently do not move backward and forward in relation to each other. In Umbridae, however, as exemplified by *Novumbra hubbsi,* basibranchial 5 is movably articulated to basibranchial 4 in such a fashion that it can be rocked back and forth beneath it; and thus the pair of toothplate-bearing fifth ceratobranchials, firmly attached to basibranchial 5, are also moved back and forth. Whether such basibranchial mobility occurs in other Umbridae or in esocoids generally is unknown; it has not been observed in galaxioids, osmeroids, or salangoids (the latter apparently lack basibranchial 5).

In assessing phylogenetic relationships one should not be overly impressed by the presence of primitive characters, even in groups in which such characters supposedly have been lost for a long time.

Atavism, the expression of ancient characters "buried in the genome," occurs far more often than generally recognized. This, rather than a Lamarckian interpretation, is doubtless the correct explanation for the appearance of breeding tubercles on the palms of the midwife toads (*Alytes obstetricans*) painstakingly studied by Kammerer (see Koestler 1973). Characters such as eyes, teeth, scales, bone, or the pelvic girdle may be repeatedly suppressed, and may not be physically expressed in any members of quite large groups, without ever having been lost from the genome. For purposes of phylogenetic analysis, I suggest it is parsimonious to assume that primitive characters are never lost from the genome, and that this is really why it is futile to rely on them. Thus the fully scaled condition of *Lepidogalaxias* does not suggest to me that it represents the primitive sister group of the otherwise scaleless galaxioids.

I believe that utilization of the caudal skeleton as a guide to phyletic relationships among teleosts, especially those with the primitive teleost complement of six separate hypurals and 10+9 principal caudal fin-rays, has inevitably resulted in confusion of primitive with advanced characteristics in the caudal fin skeleton. While teleosts as a whole exhibit great diversity in their caudal skeleton (Monod 1968), the main features of the caudal skeleton are remarkably similar in many teleosts with forked caudal fins and the primitive complement of principal caudal fin-rays. Thus the caudal fin skeleton of salangoids is strikingly similar in many respects to that of *Elops,* many clupeoids, characoids, and cyprinoids as well as of osmeroids and other salmoniforms. There are two possible explanations (or hypotheses) for such similarities, both predicated upon the assumption that the caudal fin structure of *Elops* and the others is primitive for teleosts. The first, and traditional, explanation is that all descended from ancestors that never deviated from morphologically primitive caudal fins. The second is that teleosts with secondarily generalized caudal fins have repeatedly reverted to a primitive type of caudal fin skeletal morphology.

Salangoids often have been referred to as neotenic. According to Jordan and Snyder (1902: 592), "the straight alimentary canal, distinct muscle segmentation, very thin ventral wall of the abdominal cavity, and other characters of salangoids suggest a larval stage of development." Among other characters, they were certainly thinking of the near perfectly transparent state of the fish in life. Thus when the fish die, the flesh turns perfectly white, and, in the absence of scales, the myotomes stand out very clearly, as in many larval fish. Berg (1947), Gosline (1960), Weitzman (1967), and McDowall (1969), remarked that Salangidae seem to be neotenic but did not elaborate. If the term *neotenic* means simply attaining sexual maturity while retaining some larval characteristics, salangoids are surely neotenic, probably more so than any other salmoniform fishes. The following characteristic features of salangoids are among those which may be neotenic:

1) Body almost entirely transparent in life.

2) Pectoral fin pedunculate, with a broad, fleshy, pedestallike base more or less free from the lateral musculature of the body, and placed high on

the side of the body, just like the pedunculate pectoral fin of many lower teleost larvae.

3) Skeleton in large measure cartilaginous; many bones found in adults of other salmoniforms absent.

4) Body scaleless throughout life except for anal scales in sexually mature male salangids.

5) Ventral body musculature incomplete, evidently due to an arrested ventral myotomic progression, so that the ventral abdominal wall is thin and non-muscular.

6) Left and right halves of pelvic girdle more or less widely separated from each other, failing to form a cartilaginous union by means of posteromedian processes as in most other salmoniforms.

7) Abdomen posterior to pelvic fin with a membranous median keel.

8) Fourth gill arch with well-developed hypobranchials.

9) Primary pectoral girdle consisting of a median scapulocoracoid in Sundasalangidae (a condition also present in larvae of *Elops* and other lower teleosts).

10) Dorsal and anal fins placed relatively far posteriorly (least so in *Protosalanx*).

On the other hand, salangoids exhibit considerable diversification and a number of peculiar modifications or specializations which are obviously not neotenic, including:

1) Marked sexual dimorphism in Salangidae, involving enlarged pectoral and anal fins, modified anal fin-rays, and development of the anal scales in sexually mature male salangids.

2) Strongly depressed cranium and skull; marked ventromedian curvature of maxilla.

3) Voracious feeding habits and canine dentition, especially in Salanginae.

4) Vertebral counts of 37–79, the highest counts found in Salanginae with excessively elongate body form.

5) Proximal radials of pectoral fin highly modified in all Salangidae; pectoral fin-rays very numerous in all Salangidae except Salanginae.

6) Fusion of cartilaginous hyomandibular and mandibular arches to form a hyopalatine.

7) Fusion of basibranchials and hypobranchials in gill arches of Sundasalangidae.

Thus salangoids resemble larval fish in many ways. But the problem arises of distinguishing between characters that are truly neotenic and characters that represent convergence of adults with larvae. Upon first observing the beautifully simple condition of the primary pectoral girdle in *Sundasalanx,* and taking into consideration the fused condition of ventral elements in the branchial arches of *Sundasalanx* and of the pterygoquadrate and hyomandibula in all salangoids, I was inclined to regard it as due to secondarily evolved simplification and/or reduction and fusion of the primitively separate left and right halves. But a morphologically identical "median" pectoral girdle and "fused" radial plate was reported in larval clupeoids by Goodrich (1922) and I have found it in larval *Elops hawaiiensis* (Fig. 19b) and anchovies. In all of these larvae, as in *Sundasalanx,* the scapulocoracoid has three clearly divided portions (a transverse median bar, an ascending process, and a posterior projection) and the basal radial or plate is perforated by three foramina. In further development, the three foramina of the pectoral plate presumably enlarge until the basal plate in all of these forms except *Sundasalanx* divides into proximal radials 2–5. (The primitive number of proximal radials for all teleosts appears to be 5, observed even in many teleosts having highly modified pectoral fins.) *Sundasalanx* is the only known fish which retains a median scapulocoracoid at sexual maturity. The other salangoids presumably have such a median pectoral girdle as larvae, but although the scapulocoracoid is apparently cartilaginous in all Salangidae examined, it is clearly divided into two halves in all specimens examined, including *Salangichthys microdon* of only 39 mm SL. Goodrich (1922:508) tentatively concluded that the fusion of the endoskeletal pectoral girdle he found in young clupeids represents a specialization peculiar to larval Clupeidae. The present finding that morphologically identical girdles occur in at least some Elopomorpha and Salmoniformes as well suggests that it is indeed a primitive characteristic of teleosts. The duration of the median condition apparently corresponds more or less closely with a period when the pedunculate pectoral fins are being used most actively, the primary pectoral girdle is still largely or entirely cartilaginous, and the mesocoracoid arch has not developed.

ADDENDUM

The galley proofs of this paper were already set when Prof. Xin-Luo Chu of the Kunming Institute of Zoology of Academia Sinica visited the California Academy of Sciences (January

1984) bringing specimens of *Neosalanx tangahkeii taihuensis* for me to examine. These specimens, CAS 54330, 4: 69.7–76.8 mm, were caught in Kunming Lake where the species was introduced in 1981 from artificially reared stock originating in Lake Taihu. The specimens have total vertebrae 56(1), 57(2), 59(1) and gill rakers 15(2), 16(1), 18(1). I therefore conclude that *N. tangahkeii taihuensis* is a junior subjective synonym of *N. brevirostris*. *N. brevirostris* is a valuable commercial fish and much of the production (especially of Lake Taihu) is marketed abroad. In the near future it may be widely introduced in lakes in China which lie outside the natural range of *Neosalanx*.

It may be worthwhile for Chinese workers to investigate the aquacultural potential of the other two species of *Neosalanx* occurring in China. *N. andersoni,* which may grow slightly larger than *N. brevirostris,* has a relatively restricted northerly distribution, indicating that it is adapted to colder waters. *N. jordani,* the smallest species, has a wide range largely overlapping that of *N. brevirostris,* but my observations indicate that the two species usually do not occur together in nature. *N. jordani* has fewer gill rakers and this together with its smaller size indicates a probable difference in feeding habits. It could be of practical as well as scientific value to compare the ecology and fisheries biology of these three species.

ACKNOWLEDGMENTS

For providing specimens, information, advice, or assistance I wish to thank the following persons: Tokiharu Abe, Janine Abel, Gerald R. Allen, Vladimir Barsukov, Marie-Louise Bauchot, W. H. Butler, Xin-Luo Chu, Alexandra Creighton, Oliver Crimmen, Robert Drewes, Norma Feinberg, Bo Fernholm, W. I. Follett, Michael Hearne, Susan Jewett, Sven Kullander, Robert McDowall, Gareth Nelson, Han Nijssen, Nicolai Parin, Ingrid Radkey, Walter Rainboth, Donn E. Rosen, Lars Wallin, Stanley H. Weitzman, and Alwyne Wheeler.

This study was carried out mainly in the Department of Ichthyology of the California Academy of Sciences, National Marine Fisheries Laboratory at Tiburon, and the Tiburon Center for Environmental Studies (of San Francisco State University), and was supported in part by grant DEB77-24574 in the Systematic Biology Program of the National Science Foundation.

LITERATURE CITED

ABBOTT, J. F. 1901. List of fishes collected in the River Pei-Ho, at Tien-Tsin, China, by Noah Fields Drake, with descriptions of seven new species. Proc. U.S. Natl. Mus. 23: 483–491, 7 figs.

BASILEWSKY, S. 1855. Ichthyographia Chinae Borealis. Nouv. Mem. Soc. Nat. Moscou, 10:215–263, 9 pls.

BERG, L. S. 1947. Classification of fishes, both recent and fossil. J. W. Edwards, Ann Arbour, Michigan.

———. 1962. Freshwater fishes of the USSR and adjacent countries. 4th ed., 1:6 + 504 pp. (English transl., Jerusalem).

CUVIER, G. 1817. Le regne animal. Paris. 2. Poissons, pp. 104–351.

———, AND A. VALENCIENNES. 1849. Histoire naturelle des poissons. Paris-Strasbourg, 22:xx + 532 pp., pls. 634–650.

DE BEER, G. R. 1937. The development of the vertebrate skull. Oxford Univ. Press, London and New York.

DINGERKUS, G., AND L. D. UHLER. 1977. Enzyme clearing of alcian blue stained whole small vertebrates for demonstration of cartilage. Stain Tech. 52(4):229–232, 3 figs.

FANG, P. W. 1934a. Study on the fishes referring to Salangidae of China. Sinensia, Nanking 4(9):231–268, 9 figs., 8 tables.

———. 1934b. Supplementary notes on the fishes referring to Salangidae of China. Sinensia, Nanking 5(5–6):505–511.

FINK, W. L., AND S. H. WEITZMAN. 1982. Relationships of the stomiiform fishes (Teleostei), with a description of *Diplophos*. Bull. Mus. Comp. Zool. 150(2):31–93, 23 figs.

GOODRICH, E. S. 1922. On a new type of teleostean cartilaginous pectoral girdle found in young clupeids. J. Linn. Soc. London 34:505–509, 6 figs.

GOSLINE, W. A. 1960. Contributions toward a classification of modern isospondylous fishes. Bull. Brit. Mus. Nat. Hist. (Zool.) 6:325–365.

———. 1971. Functional morphology and classification of teleostean fishes. The University Press of Hawaii, Honolulu. x + 208 pp., 29 figs.

GRAY, J. S. 1831. Descriptions of three new species of fishes, including two undescribed genera (*Leucosoma* and *Samaris*) discovered by John Reeves, Esq., in China. Zool. Miscell., pp. 4–5.

GREENWOOD, P. H., D. E. ROSEN, S. H. WEITZMAN, AND G. S. MYERS. 1966. Phyletic studies of teleostean fishes, with a provisional classification of living forms. Bull. Amer. Mus. Nat. Hist. 131(4):339–456, pls. 21–23, 9 figs.

GÜNTHER, A. 1866. Catalogue of the fishes in the British Museum. 6. London, xv + 368 pp.

HERRE, A. W. 1932. Fishes from Kwantung Province and Hainan Island, China. Lingnan Sci. J., Canton, 11(3):423–443, 1 fig.

JORDAN, D. S., AND J. O. SNYDER. 1902. A review of the salmonoid fishes of Japan. Proc. U.S. Natl. Mus. 24:567–593, 5 figs.

KISHINOUYE, K. 1901. New species of *Salanx* found in Ariake Bay (in Japanese). Zool. Mag. Tokyo, 13(157):359–360.

KLYUKANOV, V. A. 1975. The systematic position of the Osmeridae in the order Salmoniformes. J. Ichthyol. 15(1): 1–17, 13 figs.

KOESTLER, A. 1973. The case of the midwife toad. Random House, Inc., New York. 192 pp.

LIN, S. Y. 1932. On fresh-water fishes of Heungchow. Lingnan Sci. J., Canton, 11(1):63–68.

MATSUBARA, K. 1955. Fish morphology and hierarchy. Ishizaki-Schoten, Tokyo, 1, 789 pp., 289 figs.

Matsuoka, M., and T. Iwai. 1983. Adipose fin cartilage found in some teleostean fishes. Japan. J. Ichthyol. 30(1): 37–46, 4 figs., 1 table.

McAllister, D. E. 1963. A revision of the smelt family, Osmeridae. Natl. Mus. Canada Bull. 91:1–53, 14 figs.

McDowall, R. M. 1969. Relationships of galaxioid fishes with a further discussion of salmoniform classification. Copeia 1969(4):796–824, 10 figs., 2 tables.

Mees, G. 1961. Description of a new fish of the family Galaxiidae from Western Australia. J. Roy. Soc. Western Australia 44(2):33–38, 1 fig., 2 pls.

Monod, T. 1968. Le complexe urophore des poissons téléostéens. Mem. Inst. Fond. Afrique Noire 81.

Nelson, G. J. 1970. Gill arches of some teleostean fishes of the families Salangidae and Argentinidae. Jap. J. Ichthy. 17: 61–66, 2 figs.

Nelson, J. S. 1976. Fishes of the world. New York, John Wiley and Sons, 416 pp.

Nichols, J. T. 1944. The fresh-water fishes of China. Amer. Mus. Nat. Hist., New York, xxxvi + 322 pp., 143 figs., 10 pls., 1 map.

Okada, Y. 1955. Fishes of Japan. Maruzen Co., Ltd., Tokyo. 434 + 28 pp., 391 figs.

———. 1960. Studies on the freshwater fishes of Japan. Pref. Univ. Mie, Tsu, Mie Pref., Japan, 12 + 860 + 2 pp., 133 figs., 61 pls., 135 tables.

Oken, L. 1817. V Kl. Fische. Isis oder Encylopadische Zeitung 8(148):1181–1183.

Osbeck, P. 1757. Dagbok öfver en Ostindisk Resa åren 1750–52, med anmärkningar uti Naturkunnigheiten, främmende språk, etc. Stockholm, vi + 376 pp., 12 pls. (not consulted; this work is better known from the German edition published in 1765).

Pellegrin, J. 1923. Description d'un poisson nouveau du Tonkin appartenant au genre *Protosalanx* Regan. Bull. Mus. Natl. Hist. Nat. Paris 29(5):351–352.

Regan, C. T. 1908a. Descriptions of new fishes from Lake Candidius, Formosa, collected by Dr. Al Moltrecht. Ann. Mag. Nat. Hist. ser. 8, 2:358–360.

———. 1908b. A synopsis of the fishes of the subfamily Salanginae. Ann. Mag. Nat. Hist. ser. 8, 2:444–446.

Rendahl, H. 1923. Eine Neue Art der Familie Salangidae aus China. Zool. Anz. 56:92.

Richardson, J. 1846. Report on the ichthyology of the seas of China and Japan. Rep. 15th meeting Brit. Assoc. Adv. Sci., Cambridge, 1845, 187–320.

Roberts, T. R. 1969. Osteology and relationships of characoid fishes, particularly the genera *Hepsetus, Salminus, Hoplias, Ctenolucius,* and *Acestrorhynchus.* Proc. California Acad. Sci. 36(15):391–500, 60 figs.

———. 1981. Sundasalangidae, a new family of minute freshwater salmoniform fishes from Southeast Asia. Proc. California Acad. Sci. 42(9):295–302, 6 figs.

Rosen, D. E. 1974. Phylogeny and zoogeography of salmoniform fishes and relationships of *Lepidogalaxias salamandroides.* Bull. Amer. Mus. Nat. Hist. 153(2):265–326, 45 figs., 2 tables.

Scott, E. O. G. 1966. The genera of the Galaxiidae. Australian Zool. 13(3):244–258.

Senta, T. 1973a. Spawning ground of the salmonoid fish, *Salangichthys microdon,* in Takahashi River, Okayama Prefecture (in Japanese with abstract in English). Japan. J. Ichthyol. 20(1):25–28.

———. 1973b. On the salmonoid fish, *Salangichthys microdon,* in spawning season, in Takahashi River, Okayama Prefecture (in Japanese with abstract in English). Japan. J. Ichthyol. 20(1):29–35.

———. 1973c. On the number of anal fin rays of the salmonoid fish, *Salangichthys microdon* (in Japanese with abstract in English). Japan. J. Ichthyol. 20(3):179–181, 3 tables.

Starks, E. C. 1904. The osteology of *Dallia pectoralis.* Zool. Jahrb. (Abt. Syst. Geog. Biol.) 21(3):249–262, 2 figs.

van Dam, A. J. 1926. Two new fishes from China. Ann. Mag. Nat. Hist. ser. 9, 18:342.

Wakiya, Y., and N. Takahasi. 1913. Nihon san shirauo [Salangidae of Japan]. Zool. Mag. Tokyo 25:551–555.

———, and ———. 1937. Study on fishes of the family Salangidae. J. Coll. Agric. Tokyo Univ. 14(4):265–295, 3 figs., pls. 16–21, 2 tables.

Wang, W., C. Zhu, X. Zhong, S. Chen, and Y. Chang. 1980. A study on artificial fertilization and early development of *Neosalanx tangkahkeii taihuensis* in autumn. J. Fish. China 4(3):303–307 (not seen).

Weitzman, S. H. 1967. The origin of the stomiatoid fishes with comments on the classification of salmoniform fishes. Copeia 1967(3):507–540.

Wu, H. W. 1931. Description de deux poissons nouveaux provenant de la Chine. Bull. Mus. Natl. Hist. Nat. Paris, ser. 2, 3(2):219–220.

PROCEEDINGS
OF THE
CALIFORNIA ACADEMY OF SCIENCES

Vol. 43, No. 14, pp. 221-238, 17 figs., 1 table

July 12, 1984

PREDATORY BEHAVIOR OF THE WHITE SHARK (*CARCHARODON CARCHARIAS*), WITH NOTES ON ITS BIOLOGY

By

Timothy C. Tricas

Department of Zoology, University of Hawaii at Manoa,
Honolulu, Hawaii 96822

and

John E. McCosker

Steinhart Aquarium, California Academy of Sciences,
Golden Gate Park, San Francisco, California 94118

Abstract: The feeding behavior of the white shark (*Carcharodon carcharias*) was studied at Dangerous Reef, South Australia. Cinematographic analyses of shark feeding patterns show that a single bite action is comprised of a uniform sequence of jaw and head movements. The components are: 1) snout lift, 2) lower-jaw depression, 3) palatoquadrate protrusion, 4) lower-jaw elevation, and 5) a bout-ending snout drop. Durations for a complete bite action ranged from 0.750 to 1.708 s ($\bar{x} = 0.985$ s) for a 3.5 m (TL) subject. Various approach behaviors to baits were also documented.

The stomach contents of nine white sharks captured in northern and central California waters consisted entirely of fish prey associated with inshore and pelagic habitats. Records of the stomach contents of 24 additional sharks were combined and analyzed, and indicated fish to be the most frequent prey items, while marine mammals were also common. Analysis of prey type in relation to shark size shows small sharks (<3 m) feed primarily on fish prey, while larger sharks feed on marine mammals, especially pinnipeds.

Cursory field experiments and observations indicate sharks detect and are attracted to electric fields. Telemetric studies of white shark thermal biology show that they are warm-bodied, approximately 4-5°C above ambient water temperature.

Length-weight records for 127 sharks were analyzed and found to have the relationship: $W = 3.8 \times 10^{-6} L^{3.15}$, where W is weight in kg and L is length in cm. The largest reliable record for a white shark is that of a 6.4-m, 3324-kg specimen captured near Cojimar, Cuba, in 1945.

A hypothesis is proposed to explain the "bite and spit" paradox related to attacks on pinnipeds and humans. Comments concerning the risk associated with contemporary surfboard design are included.

Introduction

The white shark (*Carcharodon carcharias*) (Fig. 1) is the largest piscivorous marine fish in the world and is well known for its aggressive behavior and potential threat to humans (Fast 1955; Collier 1964; Follet 1974; Ellis 1975; McCosker 1981). It is circumglobal in distribution, but most commonly inhabits the coastal temperate waters of North America, South Africa, and South Australia.

FIGURE 1. Tagged male white shark swimming near the surface at Dangerous Reef, South Australia. Photo by Al Giddings.

In spite of its size and fearsome reputation, surprisingly little is known about the natural history and behavior of this large fish. Almost all published information on the general biology of white sharks comes from anecdotal observations and notes obtained from commercial fishing or whaling operations (Squire 1967), regional species lists and range extensions (Bigelow and Schroeder 1948; Day and Fisher 1954; Royce 1963), and newspaper articles on captures by fishermen or accounts of attacks on humans.

The predatory behavior and feeding mechanics involved in prey capture by white sharks has remained, until the recent application of scuba and high speed photography, essentially unknown. Previous studies on the feeding morphology of other species of sharks were based largely on anatomical data where muscle and supportive tissue functions were inferred from examination of preserved specimens (Luther 1909; Haller 1926). This approach provided functional insight, based largely on articulations and spatial arrangements of skeletal tissues and head musculature. In some cases, however, the inflexibility of preserved materials has led to misinterpretations of the true mechanics of jaw protrusion and feeding in sharks (see Compagno 1977). Whereas examination of fresh pliant specimens may be more appropriate for functional analyses, they still provide only speculative data on sequential and temporal relationships of structures involved in feeding activity. Moss (1972) provided a qualitative analysis of feeding mechanisms in living carcharhinid sharks using observational, photographic, and electrical muscle stimulation techniques. Studies on the temporal and sequential mechanics of feeding behavior in sharks are still lacking, however, when compared to the more thorough cinematographic studies on teleostean fishes (Osse 1969; Liem 1978; Lauder 1980).

Because white sharks are rarely captured, documentation of their food habits is scattered throughout the literature. Most records come from notes on the stomach contents of dead fish (Schroeder 1938; Bonham 1942; LeMier 1951; Scattergood 1962) or from fortuitous observations of feeding in the field (Day and Fisher 1954; Pratt et al. 1982). More complete accounts are provided on the relationships of white sharks to pinnipeds (Ainley et al. 1981; and Le Boeuf et al. 1982) and sea otters (Ames and Morejohn 1980). There still remains, however, the need for a comprehensive collation of the prey items taken by this predator so that a more complete assessment of predator-prey relationships can be made.

This paper presents new data obtained during a recent expedition to South Australia that relate to white shark predatory behavior and general biology. We analyze the feeding mechanics of white sharks in the field by use of cinematographic techniques and provide information on their sensory biology and thermal physiology. In addition, we have synthesized previously published and unpublished data on the length-weight relationships, predator-prey interactions, and general behavior of this shark. Based upon what is known about the predatory behavior of white sharks, we present a new interpretation of the curious pattern of non-feeding attacks upon marine mammals and humans.

STUDY AREA AND METHODS

White sharks were studied in the field during a ten-day period in January 1980, in waters near Dangerous Reef, South Australia. The reef consists of two small, low islands approximately 16 km east of Port Lincoln (Fig. 2). Sharks were attracted to the 20-m vessel, *Nenad,* using tuna and meat byproducts as bait. Sharks feeding on baits both at and below the surface were photographed using Actionmaster 500 cameras and 7247 Kodak color reversal film exposed at shutter speeds of 24 and 200 frames per second. Frame-by-frame analyses were performed on a Movieola 16-mm film editor.

Stomach content and morphological data from nine sharks on record at the California Academy of Sciences were analyzed. These data were then combined with other published records and further examined. To prevent multiple entries of a record into the analyses, only well-documented reports that included information on capture locality, number of sharks sampled, measured lengths and weights (no estimations), and specific prey types were used.

Two types of ultrasonic telemetry packages, constructed by the senior author, were used in this study to monitor shark body and ambient water temperatures. All transmitter circuits consisted of a crystal-controlled oscillator (carrier frequencies = 31.700 or 32.768 kHz) gaited by a thermistor-controlled pulse circuit sensitive from 10°C to 33°C. The first tag consisted of a single transmitter with a thermistor probe (embedded on the surface of the transmitter housing) that monitored ambient water temperature around the animal. Its dimensions were 4.6 × 3.2 × 2.0 cm, and it weighed approximately 60 g in air. The second unit consisted of a cylindrical package with two transmitters of different carrier frequencies. One transmitted temperature data from a thermistor in contact with the surrounding water, the other from a thermistor embedded under the barb of a dart at the end of a 31 cm-long wire leader. Total package dimensions were length 17 cm × diam. 3.2 cm, with a weight of approximately 100 g in air.

FIGURE 2. The study area, Dangerous Reef, South Australia.

The water temperature sensing package was applied from underwater using scuba (and a cage). A stainless steel dart was attached to an applicator tip on the end of a speargun shaft, and shot 3 cm deep into the shark's mid-lateral musculature. The dual-temperature sensor package was applied externally to another shark from the swimstep of the research vessel via barb and applicator pole. Signals were tracked with a tuneable ultrasonic receiver and a staff-mounted directional hydrophone. Absolute maximum range of the transmitter-hydrophone system under ide-

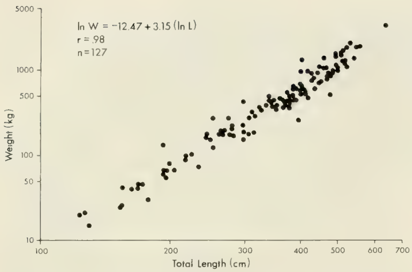


FIGURE 3. Length-weight relationship for the white shark. Data taken from complete records for 127 sharks. Functional (geometric mean) regression equation given on figure (see Ricker 1973 for discussion). Non-transformed power equation for relationship is $W = 3.8 \times 10^{-6} L^{3.15}$, where W = weight in kg and L = total length in cm.

al conditions was approximately 1500 m. However, practical working distances were much less due to transmission loss in the shallow waters around the reef (20–30 m deep). Ranges were estimated by relative audible strength calibrated prior to tracking sessions.

A set of cursory experiments were performed to test the sensitivity of sharks to weak electric fields. Sharks attracted to the boat by chum were presented two pieces of bait, approximately one meter apart, suspended on the surface from lines attached to the end of 7-m bamboo poles. Two saltwater electrodes, similar to those used by Kalmijn (1978), were attached to one bait (the experimental). Electrodes consisted of one-meter lengths of 6.3 mm inside diameter tygon plastic tubing filled with a 3% seawater-agar gel. One end of each tube was open to the water, while at the other end a 32-mm stainless steel pin with wire lead was inserted. Lead wires (+ and −) were connected to a Grass S-6 stimulator. The two saltwater electrodes were attached behind the experimental bait and spaced 10 cm apart. The control consisted of bait only. The experimental bait was presented in two different experiments that used 1) pulsed (2.2 volts at source, 5 Hz, 1.9 ms duration) current, and 2) constant (0.5 and 2.2 volts at source, DC) current electrical fields. Each test sequence began when a shark visually oriented to and approached the baits. Once the shark was within 2 m of the baits, the stimulator was turned on and choice of bait fed upon recorded. Relative positions of the control and experimental baits were randomly determined to control for extrinsic cues.

RESULTS AND DISCUSSION

SIZE.—The length-weight relationships of 127 white sharks, based on records at the California Academy of Sciences and those of published and contributed sources, are shown in Fig. 3. The largest shark record we found was that of a 6.4-m-long (21 ft), 3324-kg (7302-lb) individual captured off Cojimar, Cuba, in 1945 (Guitart and Milera 1974). The maximum size previously reported for a white shark originated from an incorrect record of an 11.1-m individual from Port Fairy, Australia, reported by Günther (1870). Randall (1973) re-examined the jaws of this specimen and concluded that the correct total length was approximately 5 m, well within the size distribution of sharks currently on record. The purported capture of a 9-m (29.5-ft) white shark said to be from Vila Franca, Azores, is probably erroneous (see Ellis 1983). The smallest published record was a 125-cm (49-in), 20-kg (44-lb) specimen reported by Smith (1951). Robert Johnson (pers. comm.) has advised us of three juveniles captured off Baja California that ranged from 130 to 135 cm (51 to 53 in) total length and weighed less than 18.2 kg (40 lb).

Remarkably, we found no well-documented records of female white sharks with fetuses or pups. Bigelow and Schroeder (1948) reported embryos ranging in length from 20 to 61.6 cm, but gave no further source information. One female taken near Alexandria, Egypt, was reported to have nine embryos, each 0.61 m (2 ft) long and weighing 49 kg (108 lb). This erroneous weight probably represents a total for all nine embryos, and translates to a more reasonable mean of 5.4 kg (12 lb) for each fish. We can only speculate about this lack of pregnant females in the capture record. Females may pup in less frequently sampled areas, such as remote geographic regions, oceanic waters, or deeper pelagic habitats. Although it is possible that females fast while pregnant, this would not completely account for the phenomenon, because many of the largest females on record were taken by harpoon rather than with bait and hook. Perhaps pregnant females undergo spontaneous parturition when hooked or harpooned and therefore eliminate key embryonic evidence before they are landed. More critical examination of the reproductive tract of

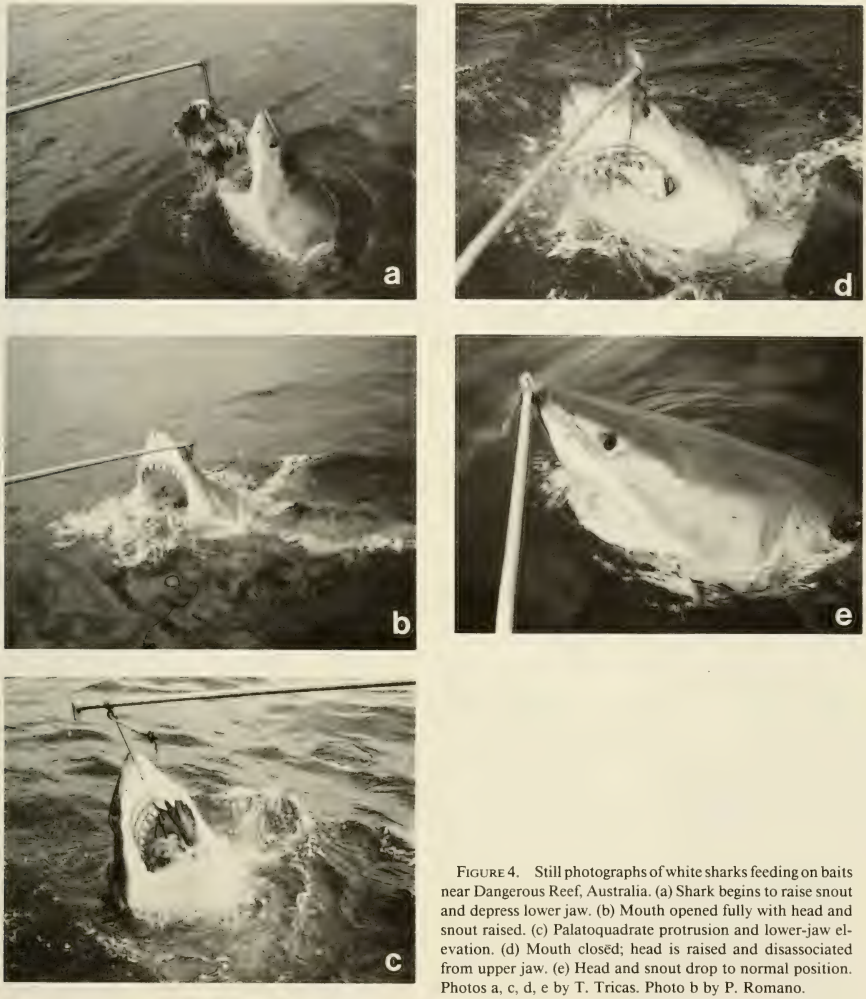


FIGURE 4. Still photographs of white sharks feeding on baits near Dangerous Reef, Australia. (a) Shark begins to raise snout and depress lower jaw. (b) Mouth opened fully with head and snout raised. (c) Palatoquadrate protrusion and lower-jaw elevation. (d) Mouth closed; head is raised and disassociated from upper jaw. (e) Head and snout drop to normal position. Photos a, c, d, e by T. Tricas. Photo b by P. Romano.

freshly landed specimens might provide useful insight to this enigma.

FEEDING ETHOLOGY.—The following section is based on our observations and the analyses of films taken of white sharks feeding on bait at Dangerous Reef, Australia. Although baited situations can only simulate natural conditions, the feeding behaviors observed in these sessions represented natural patterns because white sharks normally take prey at the surface (Ainley et al. 1981; personal observations).

The following descriptions of the structures and mechanics involved in biting actions of white sharks employ terminology similar to that used by Moss (1972, 1977). Cinemaphotographic analysis of 36 feeding bouts revealed five basic components that constitute a single feeding action.

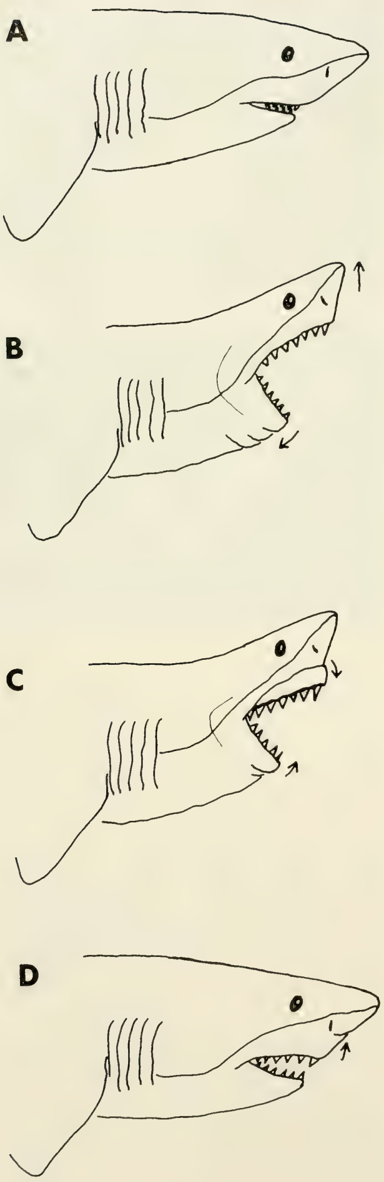
1) Snout Lift: This movement involves an upward lifting of the snout and head, and initiates the feeding action (Figs. 4a and b, 5b). The degree of snout lift ranged from a slight upward movement to a pronounced elevation that produced an acute angle behind the head (30–40° above the longitudinal body axis). The intensity of snout lift varied in relation to size of bait, angle of approach to the bait, and possibly to level of motivation (e.g., hunger).

2) Lower-Jaw Depression: Like the snout lift, lower-jaw depression occurs at the start of a feeding action. It is characterized by a ventro-posterior movement of the tip of the lower jaw (Figs. 4a and b, 5b). This motion, along with the snout lift, fully extends the gape.

3) Palatoquadrate Protrusion: Closure of the mouth is marked by disassociation of the upper jaw from its original juxtaposition ventral to the cranium, and subsequent protrusion out of the oral cavity. The upper jaw rotates in an antero-ventral direction, while the snout remains at its elevated position (Figs. 4c, 5c). During palatoquadrate protrusion the teeth become fully exposed and are directed downward. Eversion of the upper jaw was readily visible by exposure of the reddish connective tissue on the surface of the jaw cartilage.

4) Lower-Jaw Elevation: Concurrent with the initiation of palatoquadrate protrusion, the lower jaw begins an antero-dorsal (upward) motion (Figs. 4c, 5c). These movements collectively produce the closing action of the jaws.

5) Snout Drop: After single-bite feeding bouts the snout returns to its normal pre-feeding position. This results from a drop of the head and snout, and a retraction of the palatoquadrate cartilage to its position immediately ventral to the cranium (Figs. 4e, 5d). During multiple-bite bouts,



←

FIGURE 5. Components of a feeding action pattern. (A) Shark just prior to initiation of feeding action. Snout and lower jaw are at normal resting position. (B) Snout lift and lower-jaw depression result in maximum gape. (C) Palatoquadrate protrusion rotates upper jaw forward and downward exposing upper teeth. Lower jaw moves forward and upward. These two components comprise the actual bite. (D) Snout drop entails retraction of palatoquadrate cartilage to its normal juxtaposition beneath cranium. Snout drop occurs at the end of a feeding bout and is not an essential component of the biting action. Arrows indicate direction of jaw movements.

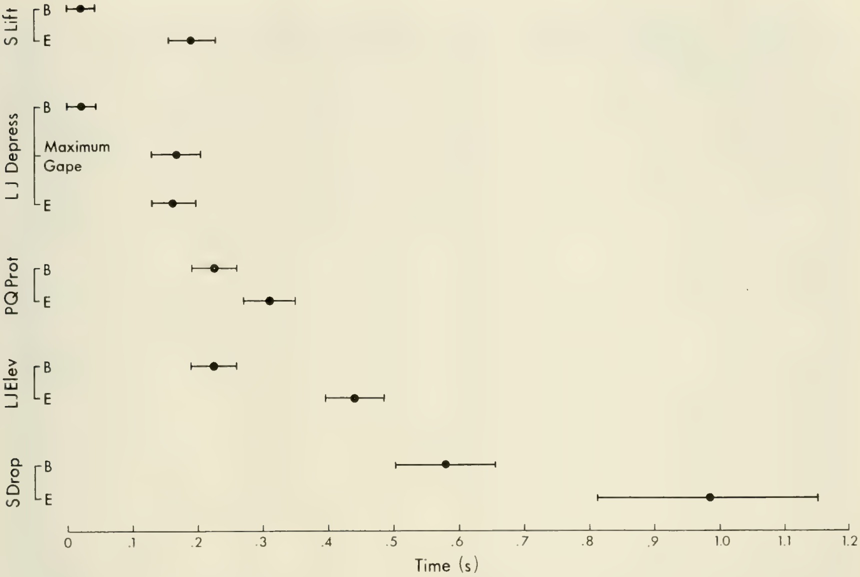


FIGURE 6. Timing of feeding actions for eleven consecutive bites made by a 3.5 m (TL) white shark. Mean times indicated by dots. Horizontal lines show 95% confidence limits. Key: B = begin, D = depression, E = end, Elev = elevation, LJ = lower jaw, PQ Prot = palatoquadrate (upper jaw) protrusion, S = snout.

the snout remains partially elevated prior to the next biting action (Fig. 4d). The retention of an elevated snout in these cases results in shorter time intervals between bites.

Mean durations for components of eleven complete successive feeding events recorded for one shark are shown in Figs. 6 and 7. Depression of the lower jaw was the fastest component ($\bar{x}$ = 0.140 s), and the snout drop duration the longest ($\bar{x}$ = 0.405 s). Total time for a complete biting action, including the snout drop, ranged from 0.750 s to 1.708 s ($\bar{x}$ = 0.985 s). Temporal analyses of film footage showed that the sequence of each feeding component fell in a fixed order with a non-overlapping range of time limits for each individual head and jaw movement. While each action showed a range in timing, minimal overlap was detected between events. The four components occurred within a mean time of 0.443 s, and never was a shark observed to partially complete a bite once the snout lift and lower-jaw depression actions were initiated. The snout drop, however, was not always an integral part of a feeding action, except at the termination of a feeding bout (as discussed above), and may be subject to sensory feedback or motivational changes.

Our observations on the mechanics of jaw protrusion in the white shark are similar to those of

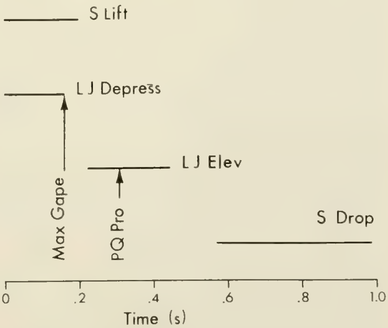


FIGURE 7. Range of durations for feeding events. Data from same shark as in Fig. 6.

Alexander (1967) on *Squalus.* He too found a head lift component to precede jaw eversion. This action is initiated by contraction of the muscles at the posterior region of the head and may lead to a pronounced snout lifting prior to feeding in other sharks (Backus et al. 1956; Moss 1972). Actual jaw protrusion in the white shark begins after maximum gape is achieved and the mouth begins to close (Figs. 4, 5). In fact, full protrusion of the palatoquadrate cartilage is not achieved until about midway through the jaw closing action. Once the mouth begins to close, palatoquadrate extension is very fast ($\bar{x} = 0.083$ s, $n = 11$) and represents the actual downward movement of the fully exposed teeth during a bite.

The mechanics and function of the protrusible jaw in large sharks has played a major role in the evolution of their feeding habits (see Moss 1977 for review). Special hydrodynamic problems exist for non-demersal sharks because of their lack of a gas-filled swim bladder (but see Bone and Roberts 1969) and maneuverable paired fins (Alexander 1967). The general streamlined body form is considered an evolutionary response to this problem (Alexander 1967; Budker 1971; Thomson and Simanek 1977). The development of a protractile jaw has allowed large lamnid and carcharhinid sharks to retain a hydrodynamically efficient fusiform body and the capacity to take clean bites with a subterminal mouth. The rounded pattern of bites taken from prey too large to swallow whole comes primarily from the upward and forward rotation of the lower jaw that secures the mouth to the prey, and the downward and forward cutting rotation of the upper jaw. The detached hyostylic association of the upper jaw and chondrocranium also permits the upper jaw to close downward much faster than it could if it had to pull the head with it as it closed. This rapid downward movement of the massive unattached upper jaw produces a strong resultant force that facilitates the cutting action of the serrated teeth.

PREDATORY BEHAVIOR.—Sharks used various capture modes to take baits depending on the bait's size and its position relative to the surface. In situations where large pieces of meat were suspended or floating at the surface, two common approaches were observed.

1) Underwater Approach: In this behavior, sharks swam parallel to and approximately 0.5 m below the surface until less than 1 m away from the bait. In situations where bait was freely floating on the surface, sharks swam at normal swimming speeds as the prey was engulfed. In cases where the bait was suspended by pole and line, sharks would typically bite the bait and attempt to pull it under by depressing their heads. Sharks that did not sever the line would often hang vertically and repeatedly bite at the bait, displaying all components of the bite behavior. Sharks were persistent in attempts to take the bait after an attack was made.

2) Surface Charge: The second, less common feeding behavior on bait at or near the surface was a rapid accelerated rush. Here a shark would approach and engulf the bait as it swam by at a relatively fast rate. This behavior was most commonly observed on newly arrived sharks in an excited state. Unlike the underwater approach, a charge was made at the surface. This behavior created considerable disturbance well before the bait was taken. Charging behavior of a similar nature was described for the blue shark (*Prionace glauca*) feeding on dense surface schools of squid (Tricas 1979).

White sharks were also observed feeding underwater, and exhibited different predatory behaviors than when taking prey from the surface. Two additional modes are presented.

3) Normal Underwater Pass: This feeding behavior was observed when a shark approached a relatively small submerged bait. Sharks approached with the mouth opened wider than during normal swimming and raised the snout slightly when approximately 1 m from the bait. When the bait contacted the underside of the snout, the lower jaw depressed slightly and the bait was taken. In this behavior the snout lift and lower jaw movements were present, but not as pronounced as in surface feeding modes, and there was no protrusion of the upper jaw. The underwater pass appeared to be first mediated by vision prior to contact, and second by tactile sensory input when the snout touched the prey just prior to initiating a feeding action. Additional sensory systems (e.g., gustatory or electroreceptive) may also be involved in normal feeding situations at close ranges.

4) Side-Roll: A similar approach to a normal underwater pass occurred where a shark rolled onto its side just prior to engulfing the submerged prey. Here the shark maintained its horizontal approach until approximately 1–2 m away from the bait. It then rolled aproximately 60° from normal, took the prey, and returned to an upright swimming attitude.

These latter two approaches involved no detectable change in swimming speed and employed the characteristic movement sequence of head and mouthparts.

Numerous observations on the variability in feeding patterns of sharks in relation to prey type and feeding conditions exist. Budker (1971) reported that in normal feeding situations sharks exhibit no body contortions when they consume small fish prey which are swimming at their own level or slightly below. This appears to be the case for white sharks taking small pieces of bait in normal underwater passes. He further states that there are only two situations that might require a different type of approach to a bait. These are either when a bait is attached to a hook and the shark must turn on its side to avoid the line with its snout, or when bait is floating and the shark must thrust its snout out of the water to get its mouth around the bait. We agree with his conclusion in regards to floating baits, with the addition that this includes natural feeding situations as well. This behavior has been observed for white sharks feeding on pinnipeds at the surface (Ainley et al. 1981; personal observations), and for tiger sharks (*Galeocerdo cuvier*) feeding on both surface baits and normal prey (see Moss 1972; Gilbert 1963 for pictures). In addition, it is clear that side-roll behaviors may also occur in natural feeding situations, and are not necessarily responses to obstructions during feeding. Tricas (1979) found that blue sharks approached small, moving anchovy baits from behind and took them in a normal swimming posture, while larger whole mackerel baits were taken from behind by sharks that partially rolled onto their sides. This variation was attributed to the size of the prey and its position relative to the mouth just prior to capture.

Observations of white shark feeding behavior are limited to artificial situations in which sharks were attracted to feed on tethered fish or horsemeat (this study) and the few instances when white sharks were observed feeding on dead cetaceans (e.g., Pratt et al. 1982). Some information has been gained from interviews with shark attack victims, although most of these did not see the shark before or during the attack (cf. Miller and Collier 1981) and may have made biased observations. White sharks have been kept alive for short periods in large aquariums, but none have attempted to feed (McCosker 1981).

On the basis of information discerned from white shark attacks on pinnipeds and humans, and our observations of their feeding on bait, we can best summarize the predatory attack strategy as follows. An adult white shark is not agile enough to capture a fleeing, darting pinniped; hence, it generally attacks its prey by surprise. Bite scars on northern elephant seals (*Mirounga angustirostris*), California sea lions (*Zalophus californianus*), Australian fur seals (*Arctocephalus doriferus*) (Fig. 8), and sea otters (*Enhydra lutris*) (Fig. 9, also see Ames and Morejohn 1980) are usually located on the ventral region of the body (e.g., haunches and flippers). This indicates that attacks were made from behind and beneath the prey. A typical attack scenario might entail a shark swimming a few meters beneath the surface, searching for the silhouette of a pinniped or sea otter at the surface. Once a prey is sighted, the shark ascends and at close range (approximately 1 m) begins a feeding action as described above. After attacking large prey such as an elephant seal, the shark probably routinely retreats a short distance from the injured (and at least partially immobilized) prey and swims cautiously within the area, apparently waiting for the pinniped to bleed to death or lapse into shock. During the attack, white sharks often roll their eyes posteriorly, which reduces the risk of injury to the eye by the teeth or nails of a struggling prey. The retreat behavior is also adaptive since it eliminates the chance of injury via contact after the initial attack is made. This "bite and spit" strategy might explain why seals that have escaped after attack usually have a single massive bite. This might also provide insight into the paradox of why humans are rarely consumed after being attacked. Since humans rarely dive or swim alone, the victim is usually quickly rescued or removed from the attack area by others, precluding a second attack. The white shark-related human fatalities that have occurred in California and Oregon waters since 1926 (5 of 40 attack victims) have all resulted from traumatic blood loss and did not involve massive consumption by the shark. This alternative theory might be more reasonable than the suggestion that humans are "distasteful" to white sharks.

FIGURE 8. Wounds inflicted upon pinnipeds by white sharks. It is possible to hypothesize the posture of prey and the attack behavior of the shark from bite scars. Elephant seals (*Mirounga angustirostris*): (A) Subadult survivor at Año Nuevo Island, California. Note lower jaw puncture wounds and tearing caused by upper jaw teeth. Photo by R. Bandar. (B) Adult female survivor at Southeast Farallon Island, California. Again note lower and upper teeth wounds. Photo by S. H. Morrell. California sea lions (*Zalophus californianus*): (C) Adult survivor at Año Nuevo Island. Photo by R. Bandar. (D) Subadult male carcass (left) and Richard Ellis (right) at Año Nuevo Island. Photo by Pam Wing. (E) Subadult male carcass along the central California coast. Photo by R. Bandar. Southern fur seal (*Arctocephalus doriferus*): (F) Large adult male survivor at South Neptune Island, South Australia. Photo by J. McCosker.

particularly when one considers the euryphagic diet of the fish.

PREDATOR-PREY RELATIONSHIPS.—The stomach contents of nine white sharks (193–511 cm total length) captured in northern and central California waters are presented in Fig. 10. Seventy-eight percent of the sharks had recognizable food items in their stomachs. The most frequent prey was the California bat ray (*Myliobatis californica*), found in four stomachs; other fish prey were less frequent in the diet. Fifty-six percent of the sharks examined contained elasmo-

FIGURE 9. Sea otters (*Enhydra lutris*) from the central California coast. Above, adult in normal feeding or basking posture along the edge of a kelp bed in Monterey Bay. Photo by J. McCosker. Below, lacerated carcass from which several white shark tooth fragments were removed, suggesting that the animal was bitten at the surface while in a belly up, prone position. Pismo Beach. Photo by J. Ames.

branchs, and 44 percent contained teleost prey species. No evidence of predation on marine mammals was found in the nine sharks.

Although the white sharks took prey that normally occur in both pelagic and inshore habitats, the two most frequent prey are generally associated with demersal inshore communities. The California bat ray (*M. californica*) is common in bays and inshore sandy habitats 2–50 m deep, where it feeds on benthic sand-dwelling invertebrates. The spiny dogfish (*Squalus acanthias*) is also demersal, being found in both shallows and deeper offshore waters. Other prey species that live on the bottom in inshore areas are the lingcod (*Ophiodon elongatus*) and the cabezon (*Scorpaenichthys marmoratus*). These latter two species are relatively sedentary, have small home ranges, and show cryptic coloration. Limbaugh

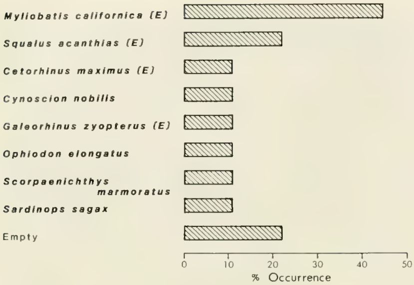


FIGURE 10. Stomach contents of nine sharks captured in northern California waters on record at California Academy of Sciences. % occurrence = percentage of the nine shark stomachs that contained that prey item. E = elasmobranch, all others are teleosts.

(1963) reported cabezon from the stomachs of three immature sharks captured at La Jolla, California, and described a number of incidents that indicate *S. marmoratus* is an important prey for young white sharks. Earlier researchers questioned how sharks could detect and capture such inconspicuous and apparently inaccessible prey; our studies suggest that weak electric fields might be involved in prey detection (see Sensory Biology section below).

The white sea bass (*Atractoscion* (=*Cynoscion*) *nobilis*) also occurs in shallow rocky inshore habitats, and is often found among canopies of giant kelp (*Macrocystis pyrifera*). Unlike the majority of the other inshore prey species, however, it occasionally swims in the water column as well as on the bottom.

White sharks have been reported to feed on the carcasses of captured basking sharks (Fast 1955), although we know of no published accounts of predation under natural circumstances. However, potential vulnerability of basking sharks to large predators was suggested by Limbaugh (1963) in an account of a dead basking shark with a large wound probably inflicted by killer whales. Basking sharks, which reach lengths of more than 11 m, are found seasonally in offshore waters of central and northern California. From aerial surveys made over a 2.5-yr period near Monterey, California, Squire (1967) found that basking sharks were most common from September through May, when water temperatures were generally below 14°C. White shark sightings, however, were most common in the warmer-water months of May through August, when water temperatures neared or exceeded 14°C. The cause of the seasonal disappearance of basking sharks from the coastal waters of California remains unknown. Other prey that inhabit pelagic waters include the soupfin shark (*Galeorhinus zyopterus*), the Pacific sardine (*Sardinops sagax*), and occasionally bat rays (*Myliobatis californica*) (Roedel and Ripley 1950; Feder et al. 1974).

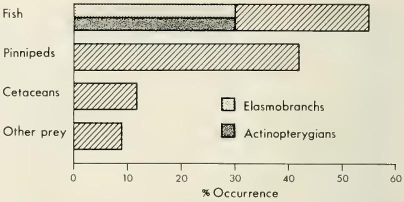


FIGURE 11. Stomach contents of 33 white sharks. Data combined from this study and other published records. % occurrence = percentage of the 33 sharks that contained the prey category. Fish prey subdivided into elasmobranchs and rayed-fin fishes (teleosts and sturgeons). Other prey include birds, crustaceans, and sea turtles.

Combined data on the food habits of 33 white sharks from this study and other published records are shown in Fig. 11. Here again, fish were the most frequent prey items, occurring in over half of white sharks in the analysis. Elasmobranchs and rayed-fin fishes (teleosts and sturgeons) comprised equal proportions (each occurred in 30 percent of sharks analyzed) of the piscine prey. Pinnipeds were also a major component in the diet of sharks, while cetaceans and other prey groups were less common. Bass et al. (1975) provided the only other gut content data from white sharks useful for comparison. They too found both elasmobranchs (40 percent of sharks examined) and teleost fishes (25 percent) as the most common prey items, although little information was given on specific identification.

Figure 12 shows the distribution of fish and mammal prey in relation to shark size. Fish prey predominated in the diet of sharks approximately 3 m or less (TL), while pinnipeds and cetaceans predominated in those of larger sharks. This shift in diet may occur for a number of reasons. For example, larger sharks are less agile and would be less successful in chasing and cap-

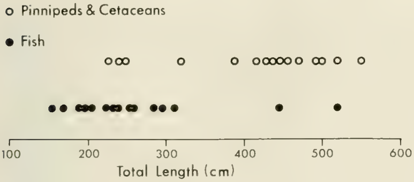


FIGURE 12. The relationship between white shark length and prey type. Data taken from stomach contents of the 33 specimens in Fig. 11.

turing smaller fish prey that dart about when pursued. Larger sharks may thus switch to different prey types and associated new hunting modes. In addition, the energetic requirements of large, warm-bodied sharks may be better met by prey high in fat content (i.e., high-energy–density prey). Carey et al. (1982) estimated the metabolic rate for a 4.6-m white shark, and concluded that the animal could survive for approximately 1.5 months on 30 kg of whale blubber (a conservative meal size). They suggest this to be adaptive during long intervals between encounters with prey. Although little is known of the movements of white sharks, they do show seasonal peaks in abundance in California waters (Squire 1967; Ainley et al. 1981), which might indicate some sort of regional or long-distance movement.

Morphological differences between large and small sharks may also account for different predatory tactics. Fig. 13 shows the relationship between tooth shape and shark total length. Smaller sharks have a relatively long, narrow tooth shape that is better adapted for grasping prey like small fishes. This feature is so well developed in small white sharks that they are often incorrectly identified as mako sharks (*Isurus* spp.) (Smith 1951, 1957). At about 3 m TL, the teeth broaden at the base and take on the diagnostic triangular serrated form. Unlike the long narrow teeth, this shape is well-suited for gouging and cutting pieces from prey too large to swallow whole. Le Boeuf et al. (1982) found evidence that marine mammals were the only prey of large white sharks they examined from California. Of seven specimens examined, all but one were approximately 4 m or longer and had evidence of marine mammals in their stomachs. The only exception was the smallest shark (2.4 m TL), which had only a 10-cm patch of pinniped pelage in its stomach.

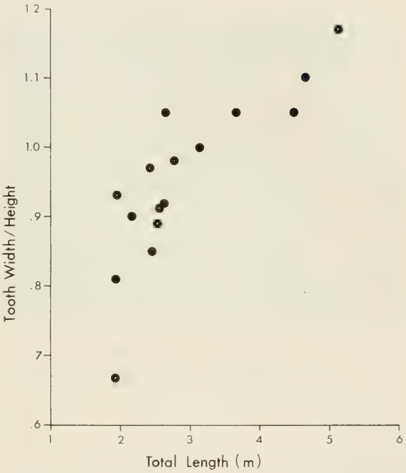


FIGURE 13. The relationship between shark total length and tooth shape. Tooth shape expressed as the ratio of width of enamel base to medial height of enamel for the first tooth, right side, upper jaw of 16 sharks. Low ratio indicates a long narrow tooth shape; higher ratio indicates relatively broad triangular shape.

Perhaps this shark's teeth were too narrow to excise a portion of flesh.

In California waters, elephant seal populations at offshore rookeries peak in both the spring and winter months (Le Boeuf et al. 1974), but almost no predation occurs during the spring peak. Hypothetical explanations advanced to explain this seasonal discrepancy in predation include either: 1) sharks fasting while breeding; 2) water too cold for sharks to feed; or 3) emigrations of sharks from the area. Even though sharks occur in California waters during the spring (Miller and Collier 1981), the decrease in shark attacks is probably due to emigrations of large sharks from coastal areas (see Squire 1967). Adult male seals are more susceptible to shark predation because they spend more time in the water near the rookery during the breeding season than do females (Le Boeuf et al. 1982). It is possible that the loss of peripheral males to sharks may not adversely affect the population because of the polygynous mating system of the elephant seal, where relatively few dominant males do the majority of the breeding.

Although it is clear that white sharks do nor-

FIGURE 14. Underwater photo of a male white shark (approximately 3.5 m TL) in a "tail stand" posture with snout directly over zinc anode on rudder of study vessel. Photo by T. Tricas.

mally prey upon elephant seals, the significance of the interaction is not evident. Ainley et al. (1981) reported an increase in the number of attacks on elephant seals at the Farallon Islands between 1970 and 1979, but their data indicate a density-dependent relationship between number of attacks and numbers of elephant seals. More data are needed on the mortality rates of attacked seals and on numbers in the shark population before any effects of shark predation on elephant seal populations can be quantitatively assessed.

SENSORY BIOLOGY.—Our cursory field experiments and observations qualitatively indicate white sharks are sensitive to electric fields. In the pulsed electric field tests, sharks took the experimental bait 8 times (73 percent) and the control 3 times (27 percent). In the constant current (DC) tests the experimental was taken 4 times (44 percent) and the control 5 times (56 percent). Although our sample size was too small to show any statistically significant preference for baits with either type of electric field, sharks did take baits with the pulsed electric field almost three times more often than the control. The sharks also appeared to be more responsive to pulsed fields than to continuous fields. Kalmijn (1971, 1974) reported that sharks were most responsive to weak electrical fields at frequencies from 0 (DC) to 8 Hz.

We also observed the behavior of sharks to metallic objects attached to the bottom of the boat. On three occasions one of us (TCT) watched from underwater a 3.5-m shark approach zinc plates attached to the boat's rudder and assume a near vertical "tail stand" posture (Fig. 14). The shark remained upright for approximately 10–20 s as it waved its snout approximately 5–10 cm above the zinc. Sharks were also observed several times to swim back and forth with their snouts very near a 10-m-long copper grounding strip on the bottom of the boat's hull.

We interpret these observations as a response by sharks to the galvanic currents produced by the electrochemical interaction between the metallic plates and seawater. White sharks have a well-developed system of ampullae of Lorenzini (Fig. 15), and although the role of electric detection of prey by sharks is well demonstrated (see Kalmijn 1978, 1982), the degree of importance for such a sensory modality in white sharks remains unknown. It is noteworthy, however, that electric fields produced by large mammals (e.g., humans and presumably pinnipeds) in seawater are well within the sensory range of elasmobranchs (Kalmijn 1971). Perhaps young white sharks are able to detect electrically sedentary camouflaged fish prey like the cabezon (*Scorpaenichthys marmoratus*). It also seems reasonable that the ampullae would be particularly useful to detect: 1) the location of a marine mammal at the moment just prior to attack; 2) any change in position or escape attempts by the prey; and 3) any change in the prey's condition, such as bleeding, which might alter the strength or signature of the electric field.

TELEMETRY.—Two sharks were tagged with temperature-sensing transmitters during this study. The first shark (a 4.5-m male) carried a unit that monitored ambient water temperature only. After tagging, the shark remained around the boat even after all baits were removed from the water. The boat was then moved away from the area and the shark began to move westward; parallel to the north shore of Dangerous Reef. Once past the island the shark moved offshore in a northwesterly direction. Contact was lost with the animal approximately 4 h after initial tagging, due to its rapid speed and bad seas that created poor tracking conditions. During this time the shark swam in waters 20–21°C as indicated by the temperature sensor on the transmitter.

The second shark was tagged on 22 January 1980. The body temperature probe was placed 31 cm deep into the lateral musculature, ap-

Figure 15. Distribution of the ampullae of Lorenzini on the head of a young female white shark (CAS 37917). Figure by C. J. Slager.

proximately 25 cm below the first dorsal fin. This shark was monitored continuously near the boat for approximately 2 hr, until it swam out of range. It returned to the anchored boat near midnight, and then again departed. Results of the thermal data are presented in Table 1 and Fig. 16. The shark swam in water ranging from 20.9° to 21.5°C. Mean difference between ambient and body temperature was 3.7°C, and ranged from 3.2° to 4.3°C. Largest and smallest differences were recorded when the shark entered water of a different temperature, before internal temperatures could conform. This time lag to thermal equilibrium and variation in muscle temperature indicate that the shark did not thermoregulate. Carey et al. (1982) found that a 4.6-m white shark had a body temperature 3–5°C higher than the surrounding water. Their shark swam over deeper waters, and for the most part remained in the thermocline. Temperatures were lower in their study, ranging approximately from 5° to 19°C ambient, and 18°

Table 1. Epaxial Muscle Temperatures of a 3.5 m (TL) Male White Shark Monitored at Dangerous Reef, South Australia on 22 January 1980. Mean (ΔT) = 3.7°C. SD = 0.37.

Measurement	Temp (°C) Water	Body	Difference (ΔT)
1	21.2	25.2	4.0
2	21.5	24.7	3.2
3	21.2	24.7	3.5
4	21.2	25.2	4.0
5	21.2	25.2	4.0
6	21.2	25.2	4.0
7	21.2	24.7	3.5
8	20.9	25.2	4.3
9	20.9	24.7	3.8
10	20.9	24.2	3.3
11	20.9	24.2	3.3
12	20.9	24.2	3.3

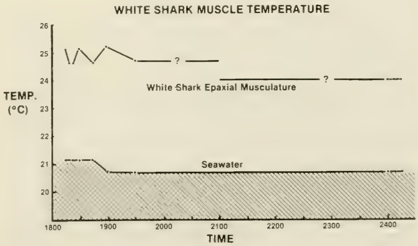


Figure 16. Temperature difference between ambient seawater and epaxial musculature of a 3.5 m TL white shark, monitored on 22 January 1980 at Dangerous Reef, South Australia. Question marks (?) indicate time interval when shark swam away from anchored study vessel and out of telemetry range. Figure by K. O'Farrell.

FIGURE 17. (Right) Silhouette of a surfer on a contemporary surfboard. (Left) Silhouette of an adult female (TL = 1.7 m) harbor seal (*Phoca vitulina*). Photo by Al Giddings.

to 23°C muscle temperature. Our study took place in relatively shallow waters around Dangerous Reef (<30 m), and we found no sign of a marked thermocline. The water and shark-muscle temperatures we recorded were generally higher (20.9°–21.2° and 24.2°–25.2° C, respectively), but they are consistent with the values for body temperature elevation over ambient recorded by Carey et al.

One of the primary advantages of being warm-bodied is thought to be related to the changes in muscle physiology as temperature increases. It is known that a 10°C increase in temperature may result in a three-fold increase in the contraction-relaxation rate of frog muscle (Hartree and Hill 1921). For fish, this may be translated to an increase in potential tail-beat frequency and a related increase in sustained swimming speed. Higher speeds may be selectively advantageous when chasing prey or fleeing from predators. In addition, conservation of heat theoretically allows for more total energy conversion to work, thus enabling an animal to swim longer distances on a given meal. Being warm-bodied might also allow for temporary excursions into colder or deeper waters. This thermal inertia (see Neill et al. 1976) would not only expand the range of environments which the animal could exploit, but would also permit increased swimming efficiency for predation at otherwise limiting environmental temperatures.

ON WHITE SHARKS AND SURFBOARDS.—In conclusion, we comment on the increasing attacks by white sharks upon humans who surf in the north Pacific. Since 1972, there have been 11 recorded white shark attacks upon surfers in California and Oregon (Miller and Collier 1981) and one such attack in Hawaii in 1959 (Balazs and Kam 1981). The similarity in appearance of the silhouette of a prone human on a surfboard or "belly board" to a large surface-basking pinniped is clear (Fig. 17), and observations of attacks by sharks upon surfers fit well with our assessment of the feeding strategy of white sharks. Attacks have occurred in the vicinity of pinniped rookeries, such as the much-publicized death of Lewis Boren on 19 December 1981 at Spanish Bay, Monterey, California.

Since the early 1970s, the trend in surfboard design has been toward an increase in flotation, reduction in board length, multiple posterior-fixed rudders ("skegs"), and bifurcated or "V" tails. All of these modifications have enhanced the similarity between the silhouette of a surfer and that of a pinniped, and we suggest that this may increase the probability of attack of surfers encountered by white sharks. We feel it advisable that those who surf be aware of and consider the potential risks of surfing in coastal waters known to be frequented by white sharks.

Acknowledgments

We are particularly grateful to Al Giddings, President of Ocean Images, Ltd., for financial assistance, for providing access to his film library for cinematographic analyses, and for sharing his observations of shark behavior with us. We also thank Terry Thompson, Ocean Images, Ltd., for his assistance. Additional shark data were provided by W. I. Follett (CAS), L. J. V. Compagno (CAS), J. Randall (Bernice P. Bishop Museum), and the staff of the Department of Ichthyology of the CAS. A. Dizon (NMFS, Honolulu) and I. Cooke (Bekesy Laboratory, U. of Hawaii) provided facilities during construction of our transmitters. We thank H. Tricas, C. J. Slager, K. O'Farrell, S. Middleton, and S. Nakamura for assistance with our figures; J. Ames, R. Bandar, R. Dunne, A. Giddings, S. Morrell, P. Romano, and P. Wing for allowing us to use their pictures; and Bob Britcher and Chico Chingwidden, the Master and the mate of the *Nenad.* We give special thanks to Rodney Fox, for his guidance in the field in South Australia and for helpful discussions concerning shark behavior, and to Leighton Taylor, Jr. (Waikiki Aquarium), and Phil Motta (Univ. of Montana) for their critical reading of this manuscript.

Senior authorship of this paper was determined by the outcome of a pinball match played at Port Lincoln, South Australia, in January 1980.

References

Ainley, D. G., C. S. Strong, H. R. Huber, T. J. Lewis, and S. H. Morrell. 1981. Predation by sharks on pinnipeds at the Farallon Islands. Fish. Bull., U.S. 78:941–945.

Alexander, R. McN. 1967. Functional design in fishes. Hutchinson and Co., London. 160 pp.

Ames, J. A., and G. V. Morejohn. 1980. Evidence of white shark, *Carcharodon carcharias,* attacks on sea otters, *Enhydra lutris.* Calif. Fish Game 66:196–209.

Backus, R. H., S. Springer, and E. L. Arnold, Jr. 1956. A contribution to the natural history of the white-tip shark, *Pterolamiops longimanus* (Poey). Deep-Sea Res. 3:178–188.

Balazs, G. H., and A. K. H. Kam. 1981. A review of shark attacks in the Hawaiian Islands. 'Elepaio. 41(10):97–105.

Bass, A. J., J. D. D'Aubrey, and N. Kistnasamy. 1975. Sharks of the east coast of southern Africa. IV. The families Odontaspididae, Scapanorhynchidae, Isuridae, Cetorhinidae, Alopiidae, Orectolobidae, and Rhiniodontidae. Invest. Rep. Oceanogr. Res. Inst. no. 39. 102 pp.

Bigelow, H. B., and W. C. Shroeder. 1948. Sharks. *In* Fishes of the western north Atlantic. J. Tee-Van, C. M. Breeder, S. F. Hildebrand, A. E. Parr, and W. C. Schroeder, eds. Part one. Mem. Sears Found. Mar. Res., Yale Univ. 1. 576 pp.

Bone, Q., and B. L. Roberts. 1969. The density of elasmobranchs. J. Mar. Biol. Assn. U.K. 49:913–937.

Bonham, K. 1942. Records of three sharks on the Washington coast. Copeia 1942:264–266.

Budker, P. 1971. The life of sharks. Columbia Univ. Press, New York. 222 pp.

Carey, F. G., G. Gabrielson, J. W. Kanwisher, and O. Brazier. 1982. The white shark, *Carcharodon carcharias,* is warm-bodied. Copeia 1982:254–260.

Collier, R. S. 1964. Report on a recent shark attack off San Francisco, California. Calif. Fish Game 50:261–264.

Compagno, L. J. V. 1977. Phyletic relationships of living sharks and rays. Amer. Zool. 17:303–322.

Day, L. R., and H. D. Fisher. 1954. Notes on the great white shark, *Carcharodon carcharias,* in Canadian waters. Copeia 1954:295–296.

Ellis, R. 1975. The book of sharks. Grosset and Dunlap, New York. 320 pp.

———. 1983. Chiller from the depths. Geo Magazine 5:91–97.

Fast, T. N. 1955. Second known attack on a swimmer in Monterey Bay. Calif. Fish Game 41:348–351.

Feder, H. M., C. H. Turner, and C. Limbaugh. 1974. Observations of fishes associated with kelp beds in southern California. Calif. Dept. Fish Game, Fish. Bull. 160. 144 pp.

Follett, W. I. 1974. Attacks by the white shark, *Carcharodon carcharias* (Linnaeus), in northern California. Calif. Fish Game 60:192–198.

Gilbert, P. W. 1963. The visual apparatus of sharks. Pages 283–326 *in* Sharks and survival. P. W. Gilbert, ed. D. C. Heath and Co., Boston.

Guitart, D., and J. F. Milera. 1974. El monstruo de Cojimar. Mar y Pesca 104:10–11.

Günther, A. 1870. Catalogue of fishes in the British Museum. Taylor and Francis, London.

Haller, G. 1926. Uber die Entwicklung, den Bau und die Mechanik des Kieferapparates des Dornhais (*Acanthias vulgaris*). Z. mikrosk. ant. Forsch. 5:749–793.

Hartree, W., and A. V. Hill. 1921. The nature of the isometric twitch. J. Physiol. 55:389–411.

Kalmijn, A. J. 1971. The electric sense of sharks and rays. J. Exp. Biol. 55:371–383.

———. 1974. The detection of electric fields from inanimate and animate sources other than electric organs. *In* Handbook of sensory physiology. A. Fessard, ed. Vol. III/3. Springer-Verlag, New York.

———. 1978. Electric and magnetic sensory world of sharks, skates, and rays. Pages 507–528 *in* Sensory biology of sharks, skates, and rays. E. S. Hodgson and R. F. Mathewson, eds. Off. Nav. Res., Arlington.

———. 1982. Electric and magnetic field detection in elasmobranch fishes. Science 218:916–918.

Lauder, G. V. 1980. Hydrodynamics of prey capture by teleost fishes. Biofluid Mechanics 2:161–181.

Le Boeuf, B. J., D. G. Ainley, and J. T. Lewis. 1974. Elephant seals on the Farallones: population structure of an incipient breeding colony. J. Mammal. 55:370–385.

Le Boeuf, B. J., and R. S. Peterson. 1969. Social status and mating activity in elephant seals. Science 163:91–93.

Le Boeuf, B. J., M. Riedman, and R. S. Keyes. 1982. White shark predation on pinnipeds in California coastal waters. Fish. Bull., U.S. 81:80(4):891–895.

LeMier, E. H. 1951. Recent records of the great white shark, *Carcharodon carcharias*, on the Washington coast. Copeia 1951:249.

Liem, K. F. 1978. Modulatory multiplicity in the functional repertoire of the feeding mechanism in cichlid fishes. 1. Piscivores. J. Morph. 158:323–360.

Limbaugh, C. 1963. Field notes on sharks. Pages 63–94 *in* Sharks and survival. P. W. Gilbert, ed. D. C. Heath and Co., Boston.

Luther, A. F. 1909. Untersuchungen uber die vom N. trigeminus innervierte Musculator der Selachier. (Haie und Rochen) unter Berucksichtigung ihrer Beziehungen zu benachbarten Organen. Acta Soc. Sci. Fenn. 36:1–176.

McCosker, J. E. 1981. Great white shark. Science 81 2:42–51.

Miller, D. J., and R. S. Collier. 1981. Shark attacks in California and Oregon, 1926–1979. Calif. Fish Game 67: 76–104.

Moss, S. A. 1972. The feeding mechanisms of the sharks of the family Carcharhinidae. J. Zool. Lond. 167:423–436.

———. 1977. Feeding mechanisms of sharks. Am. Zool. 17: 355–364.

Neill, W. H., R. K. Chang, and A. E. Dizon. 1976. Magnitude and ecological implication of thermal inertia in skipjack tuna, *Katsuwonnus pelamis* (Linnaeus). Env. Biol. Fish. 1:61–80.

Osse, J. W. M. 1969. Functional morphology of the head of the perch (*Perca fluviatilis* L.): an electromyographic study. Neth. J. Zool. 19:289–392.

Pratt, H. L., J. G. Casey, and R. B. Conklin. 1982. Observations on large white sharks, *Carcharodon carcharias*, off Long Island, New York. Fish. Bull., U.S. 80:153–156.

Randall, J. E. 1973. Size of the great white shark (*Carcharodon*). Science 181:169–170.

Ricker, W. E. 1973. Linear regression in fishery research. J. Fish. Res. Board Can. 30:409–434.

Roedel, P. M., and W. E. Ripley. 1950. California sharks and rays. Calif. Div. Fish Game, Fish. Bull. 75. 88 pp.

Royce, W. F. 1963. First record of white shark (*Carcharodon carcharias*) from southeastern Alaska. Copeia 1963:179.

Scattergood, L. W. 1962. White sharks, *Carcharodon carcharias*, in Maine, 1959–1960. Copeia 1962:446–447.

Schroeder, W. C. 1938. Records of *Carcharodon carcharias* (Linnaeus) and *Pseudopriacanthus altus* (Gill) from the Gulf of Maine, summer of 1937. Copeia 1938:46.

Smith, J. L. B. 1951. A juvenile of the man-eater, *Carcharodon carcharias* Linn. Ann. Mag. Nat. Hist. 4(12):729–736.

———. 1957. Sharks of the genus *Isurus* Rafinesque, 1810. Ichthy. Bull. 6:91–96.

Springer, S. 1961. Dynamics of the feeding mechanism of large galeoid sharks. Am. Zool. 1:183–185.

Squire, J. L., Jr. 1967. Observations of basking sharks and great white sharks in Monterey Bay, 1948–50. Copeia 1967: 247–250.

Thomson, K. S., and D. E. Simanek. 1977. Body form and locomotion in sharks. Amer. Zool. 17:343–354.

Tricas, T. C. 1979. Relationships of the blue shark, *Prionace glauca*, and its prey species near Santa Catalina Island, California. Fish. Bull. 77:175–182.

PROCEEDINGS
OF THE
CALIFORNIA ACADEMY OF SCIENCES

Vol. 43, No. 15, pp. 239-248, 5 figs., 1 table September 19, 1984

DENDRODOA (*STYELOPSIS*) *ABBOTTI*, SP. NOV. (STYELIDAE, ASCIDIACEA) FROM THE PACIFIC COAST OF THE UNITED STATES, AND ITS IMPACT ON SOME GONADAL CRITERIA OF ITS GENUS AND SUBGENUS

By
Andrew Todd Newberry
Cowell College, University of California, Santa Cruz, California 95064

Abstract: ***Dendrodoa*** **(*Styelopsis*)** ***abbotti*, a newly described styelid ascidian from the central and northern California coast, the San Juan Islands of Washington, and southwestern Vancouver Island, resembles *D. carnea* but differs in branchial and gonadal traits. Inclusion of *D. abbotti* in the genus *Dendrodoa* requires modification of the gonadal criteria of the genus to accommodate styelan gonadal resemblances (non-encapsulation of the testis-lobes with the ovary) and styelan or cnemidocarpan spermiducal resemblances (gonad's single vas deferens and spermipore).**

Introduction

The tunicate named and described in this paper, *Dendrodoa* (*Styelopsis*) *abbotti,* is a styelid ascidian that has long been collected along the central and northern California coast. Donald P. Abbott, who first found this ascidian in 1948 near Point Arena (Mendocino County), included it as "*Alloeocarpa* sp." in the urochordate key of the second edition of *Light's Manual* (Light et al. 1954) but, for want of more certain identification, omitted it from that handbook's third edition (Smith and Carlton 1975).

This ascidian's aggregative habit does create an appearance of budding (Fig. 1A), but adjacent zooids' tests are unfused and easily separated from one another; no evidence of budding has been found in several hundred zooids from several sites and all seasons. Apparently, then, this is a solitary ascidian and cannot be placed in the genus *Alloeocarpa.* It shows *Dendrodoa*'s restriction of the single, elongate ovary to the zooid's right side. The ovary's unbranched shape and the pharynx's simplicity place the species in the subgenus *Styelopsis* of *Dendrodoa.* The specific name, *abbotti,* honors Professor Donald P. Abbott, of the Hopkins Marine Station of Stanford University, who has shared with his students and colleagues a singular keenness of intellect and generosity of spirit, and it expresses the esteem and affection of his fellow ascidiologists.

Materials and Methods

This report is based principally on specimens collected intertidally at Pigeon Point, San Mateo County, California (lat. 37°11′0″N, long. 122°23′10″W), at intervals of roughly six weeks throughout 1977. I have also drawn on material taken over the past two decades from there; from Point Pinos, Monterey County, California (lat.

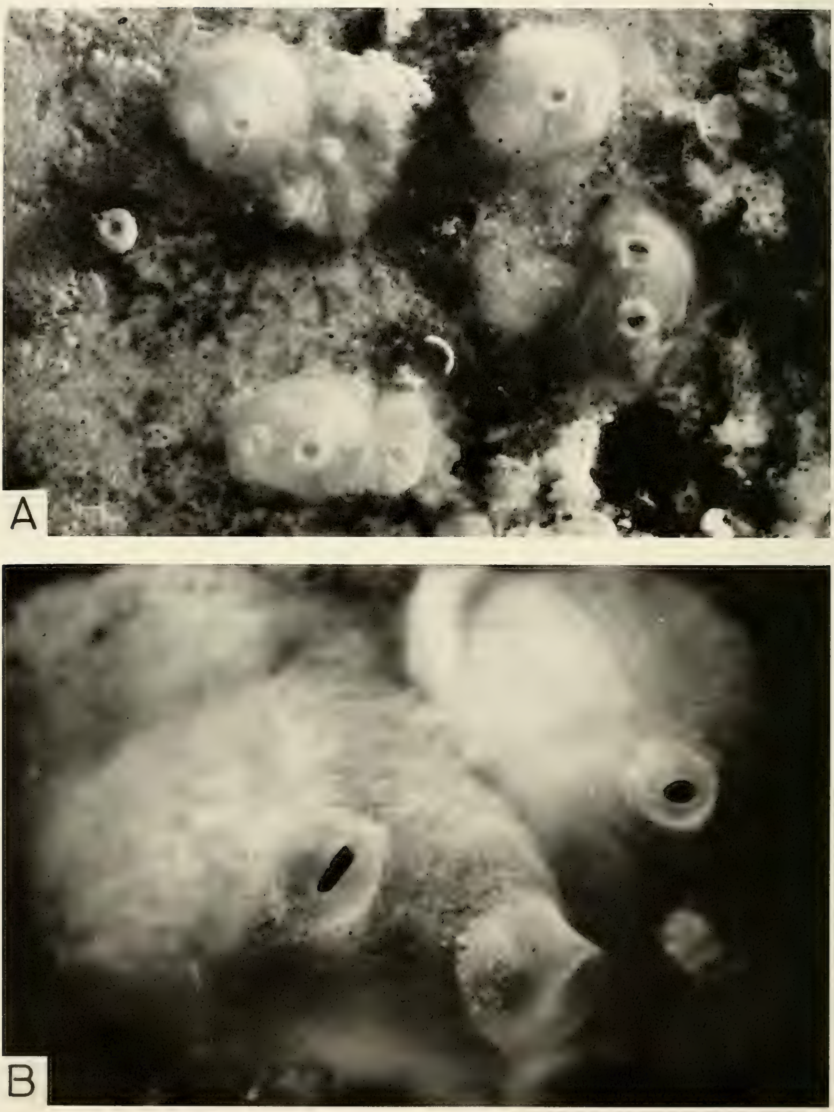


FIGURE 1. A) Living zooids of *Dendrodoa abbotti,* including one (upper left-center) that has been wounded or severely disturbed and is extremely contracted while the others remain relaxed. Zooids are about 1 cm long. B) Closer view of two slightly disturbed zooids, showing siphons in the process of bilabial closure. Brood pouch is detectable in the left zooid by inflated aspect of the posterior region of the zooid (to left in photo). Zooids are about 1 cm long.

36°38′0″N, long. 121°56′0″W); and subtidally from Peavine Pass (lat. 48°35′4″N, long. 122°45′48″W) in the San Juan Islands, Washington. I have used, as well, D. P. Abbott's unpublished notes and drawings of specimens from northern and central California.

In all, I have examined approximately 30 specimens thoroughly. I have examined several dozen more in a cursory way to verify the criteria that characterize the species. All specimens were relaxed with $MgCl_2$ or $MgSO_4$, and menthol, then fixed in seawater Bouin's fluid or 10% formalin, and all were preserved in 70% ethanol. The Bouin's-fixed material provided excellent serial sections but brittle dissections. Formalin always fixed adequately for dissections but rarely well enough for close scrutiny by serial section (which was required, for example, to trace the very fine spermiducts). Specimens were dissected in 70% ethanol. Dissected specimens usually were stained, once opened, with Grenacher's borax carmine; serially sectioned specimens were either prestained, often for prior dissection, in Grenacher's alcoholic borax carmine or stained in section with "standard alum hematoxylin" (Galigher and Kozloff 1964) and eosin. Prestaining proved satisfactory for general examination, but staining in section was necessary to reveal finer structural details or to take advantage of the better fixation achieved with Bouin's fluid than with formalin.

COORDINATES.—The endostyle designates the anterior-posterior axis and the ventral midline. Thus, the dorsal midline extends from the oral siphon through and beyond the atrial siphon. By these coordinates, the ovary lies against the right ventral margin of the zooid, and the loop of the gut dominates the left posterior region of the zooid (Fig. 2).

DESCRIPTION OF SPECIES

Dendrodoa (Styelopsis) abbotti, sp. nov.

TYPE-SPECIMENS.—Holotype at California Academy of Sciences, San Francisco, Calif. (CAS #034790). Paratypes at California Academy of Sciences, San Francisco, Calif. (CAS #034791).

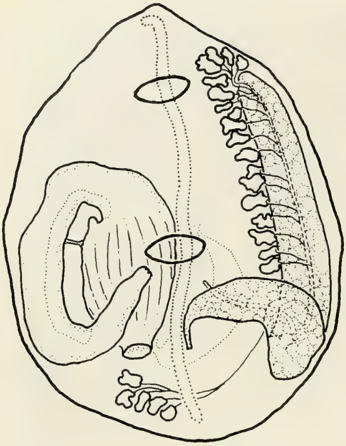
TYPE-LOCALITY.—North side of Pigeon Point, San Mateo County, California (lat. 37°11′0″N, long. 122°23′10″W).

OTHER RECORDS.—Intertidal records from Point Pinos and Hopkins Marine Reserve (Monterey County), Pigeon Point and Moss Beach (San Mateo County), Point Arena (Mendocino County), California, and near Sooke, Vancouver Island, British Columbia; subtidal records from Peavine Pass (San Juan County), Washington.

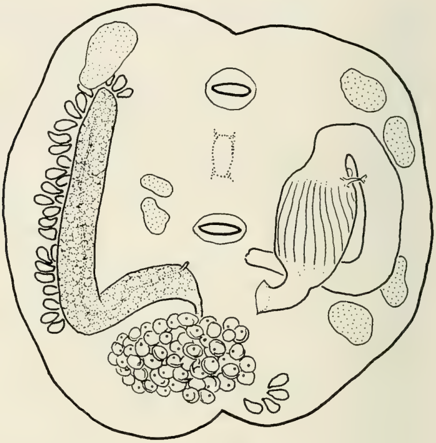
EXTERNAL APPEARANCE (Fig. 1).—Zooids round or oval (lengthened antero-posteriorly) low hemispheres; entire sub-endostylar surface applied to substrate; attached surface extends beyond ovary on right and gut-loop on left. Specimens including test reach 8 to 12 mm length, 6 to 10 mm width, 2 or 3 mm height when relaxed; zooids removed from test reach 8 to 10 mm length, 6 to 8 mm width, 2 to 3 mm height. Test clean, thin, and parchment-like, spreading as a thin apron 1 to 2 mm wide on the substrate around the zooid. Ventral test extremely thin. Color in life translucent gray tinted with ochre or very pale brownish pink, with borders of siphonal apertures sometimes slightly darker. Zooids fixed in formalin become plain translucent white-gray. Alive or fixed, zooid's branchial sac, gut, ovary, and mass of brooded young are faintly visible through dorsal and lateral regions of test. Oral siphon far anterior; atrial siphon placed centrally atop hemispheric zooid; both siphons fairly evident in relaxed living animals but reduced to obscure slits in contracted ones. Relaxed zooids have circular siphonal apertures; disturbed zooids close their siphons bilabially into transverse slits (Fig. 1B) and flatten themselves against the substrate within a delicately crumpled test. Zooids are simple and non-budding but often aggregate in pairs or trios (rarely groups of more) with young ones often settling adjacent to or even on the test "apron" around older zooids (but not on zooidal surfaces themselves). Mature zooids, even when tightly adjacent to one another, attach entirely to the substrate itself; they do not form clumps of zooids growing thickly one upon another. Adjacent zooids often are oriented similarly on the substrate.

VASCULAR ELEMENTS OF THE TEST.—Test-vessels not prominent; as revealed by staining, branching systems of test-vessels ramify toward the margin of the test. Test-vessel ramifications connect to zooid by one or more sub-zooidal circulatory junctions; tips of all branches of test-vessel ramifications end peripherally in slender, bulbous vascular ampullae.

MANTLE.—Thin, lightly muscled mantle except for extensive arrays of fibers radiating from each siphon and controlling its bilabial closure; fairly conspicuous concentric musculature surrounding oral siphon, less developed concentric musculature around atrial siphon. About a dozen endocarps project from the mantle into the atrium



2



3

FIGURE 2. Dorsal view of zooid, with pharynx removed to show disposition of ovary and testis-lobes (including far posterior group), vasa efferentia and vas deferens (including tiny spermiporal papilla near atrial siphon), mid-ventral endostyle and heart beneath it, and gut-tract (stomach, pyloric duct, caecum, intestine). Position of oral and atrial siphons indicated by ovals.

FIGURE 3. Zooid opened by mid-ventral cut to show ovary, testis-lobes (including posterior lobes), larvae in brood pouch, several endocarps (stippled), gut-tract, siphons with neural complex between them. Pharynx removed.

of most zooids; particularly large endocarps usually protrude from the atrial mantle anterior to the ovary and in the region of the gut-loop.

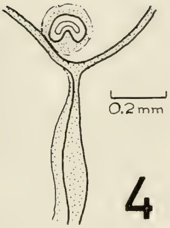
ORAL TENTACLES.—36 to 40 filiform oral tentacles of three sizes; largest ones most abundant (24–30), others about half their size intercalated irregularly, a few to many tiny papillae evident upon close examination of the band of oral tentacles. Just distal to this circle of tentacles is a siphonal flange that marks the inward limit of the test that lines the oral siphon.

ATRIAL TENTACLES.—40 to 50 tiny filiform atrial tentacles in band analogous to that of the circle of oral tentacles. Just distal to this inconspicuous circle is the atrial siphonal flange that marks the inward limit of the test lining the atrial siphon.

DORSAL TUBERCLE (Fig. 4).—Simple C-shaped slit atop a short, stout projection; concavity of the C faces posteriorly (toward the dorsal lamina). The dorsal tubercle is set slightly to the right of the dorsal midline.

NEURAL COMPLEX.—In dorsal or ventral silhouette, whole complex forms a rectangle elongated antero-posteriorly and extended somewhat at each corner. Like the dorsal tubercle, the neural complex is set slightly to the right of the dorsal midline.

BRANCHIAL SAC (PHARYNX) (Fig. 5).—Folds absent, perhaps represented by internal longitudinal branchial vessels. In dissection, 4 internal longitudinal vessels are evident on each side of the pharynx; in transverse serial sections, a fifth internal longitudinal vessel is sometimes discernible on each side close to the endostyle, and in a few specimens even a sixth vessel on each side may run only some length of the sac. Usually 9 or 10 stigmata lie between these internal longitudinal vessels. Ten to 12 transverse vessels separate the rows of longitudinally oriented stigmata, and there are about 10 parastigmatic vessels partly or entirely traversing each side of the pharynx. Along the ventral midline the branchial sac connects with the body wall by widely spaced sub-endostylar vascular trabeculae, not by a continuous sub-endostylar membrane. Other vascular trabeculae connect the branchial sac abundantly in all directions to the



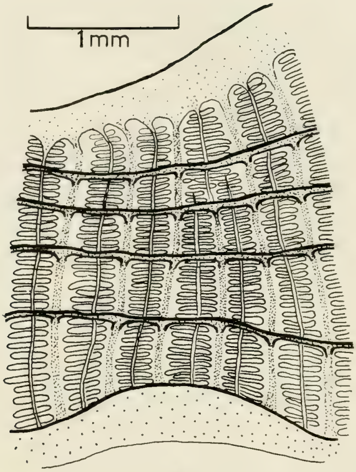


FIGURE 4. Dorsal tubercle in relation to peripharyngeal groove and dorsal lamina.

FIGURE 5. Right side of pharynx, showing several rows of stigmata and the four internal longitudinal branchial vessels of the pharynx's right side. Dorsal lamina at top, endostylar groove at bottom. Drawing based in part on unpublished notes of D. P. Abbott, in part on freshly dissected specimens.

atrial surface of the mantle and to the atrial epithelium around the gut.

DORSAL LAMINA.—Prominent, continuous, smooth-bordered dorsal lamina, without languets.

GUT (Figs. 2, 3).—Esophageal aperture far dorso-posterior in pharynx; stout esophagus bends sharply ventrally into stomach; stomach empties anteriorly into fore-intestine, which bends to left and passes posteriad on the lateral side of the stomach. Hind-intestine then curves sharply dorsad and follows the left mantle to the anus, which lies slightly to the left-posterior of the atrial siphon. Stomach has 16 to 18 moderately evident external folds corresponding to well-developed internal gastric septa. The gastric septa are reduced to low ridges in the left pyloric region of the stomach, near the pyloric caecum. Pyloric caecum is small, sometimes absent. A highly vascularized pyloric duct joins the sinusoidal sheath surrounding the stomach with that surrounding the fore-intestine. Intestine comprises a fore-intestine with a large typhlosole-like longitudinal plication of its wall and a thick sinusoidal jacket between the gut wall and its sheath of atrial epithelium, and a hind-intestine of more simply tubular section whose atrial sheath is much closer to the gut wall. Anus lies dorso-medial or slightly to the left, above the stomach; anus is cut square to the axis of the rectum; anal margin is scalloped into usually 5 lobes that fit together when the anus is tightly closed.

HEART.—Fairly straight within a somewhat curved and inflated pericardium; set at about 45° obliquely to the endostyle, oriented right-anterior to left-posterior, centered roughly beneath the endostyle in the posterior half of the zooid (site and orientation in Fig. 2).

OVARY (Figs. 2, 3).—Single, unbranched, sausage-shaped ovary along the right ventral margin of the zooid, extending almost the entire length of the zooid, curving sharply dorsad posteriorly and following the right mantle to arch halfway over the atrium, recurving dorsally to terminate in an oviduct directed posteriorly toward the brood pouch and away from the atrial siphon. Oviduct lies lateral (away from atrium) to main mass of ovary, with its lumen penetrating among the ripening gametes; lateral surface (away from germinal tissue) of oviduct heavily ciliated, other oviducal surfaces apparently not ciliated. Ovaries of all specimens examined by dissection or serial section show all stages of ovogenesis present, regardless of season.

TESTIS (Figs. 2, 3).—A dozen to more than 20 separate lobate sacs, not encapsulated with the ovary but instead lying in the mantle wall adjacent to but clearly outside the ovary's delimiting membrane. Most sacs lie medial to the ovary; some lie anterior to the ovary; few are lateral; many lobes lie partly "beneath" the ovary, in the mantle between the ovary and the ventral surface of the zooid. In many specimens, but not all, a few testis-lobes lie far posteriorly and on the left side of the ventral midline, but their spermiducts join the vas deferens of the testis-lobes that lie beside the ovary. All sacs join by vasa efferentia to a single, long vas deferens that lies between the ovary and the atrial epithelium. This duct follows the ovary to the region of the atrial siphon, and there leaves the ovarian surface to project toward the atrial siphon from the dorsal roof of the atrium while the ovary bends posteriad toward its ovipore. The ciliated vasa efferentia are extremely thin, visible only in serial section; the vas deferens, also scarcely visible except in serial section, is a compressed, ciliated channel terminating in a tiny, spermipore-bearing papilla pointing toward the atrial aperture. In all specimens examined from all seasons for gametic condition, many testis-lobes have tailed sperm, but the spermiducts contain only scattered sperm.

BROOD CHAMBER AND BROODED YOUNG (Figs. 1, 3).—The posterior region of the atrium serves as a brood chamber, occluded anteriorly by the branchial sac, on the left by the gut-loop, on the right by the ascending limb of the ovary. All specimens examined were brooding young in all stages of development from (relatively rarely) fertilized eggs and cleavage stages to (usually) tadpoles that were still curled (although many of these straightened upon removal from the brood chamber during dissections). Quantities of brooded young vary greatly—fewest (20 to 30) in midwinter specimens, most (100 to 200) in late spring to midfall specimens. The brood chamber often is so swollen with young that it is readily apparent in living animals. Young are crammed tightly into the chamber; external study of zooids divested of test may suggest only a few larvae, but dissection then reveals many dozens. The brood chamber is criss-crossed by many vascular trabeculae that connect the branchial sac and the atrial and gut wall and may keep loose young from being swept from the brood chamber by atrial water-currents.

ECOLOGICAL DISTRIBUTION IN CALIFORNIA.—Intertidal. At Point Pinos and Pigeon Point, peak abundance is at about +0.3 m, and I have found no specimens at either site above +0.6 m or below 0.0 m. This is an open-coast ascidian in California, inhabiting surf-swept rocky habitats where the full force of the waves is broken by surrounding rocks and reefs. Zooids congregate on horizontal undersides of large boulders, usually well back from the boulders' edges. Such boulders restrict waterflow underneath, so much so that at Point Pinos the rocks that harbor *Dendrodoa abbotti* may lie partially in sand that by its odor and color appears to be virtually anoxic. At Pigeon Point most rocks with this ascidian are slightly propped up by their neighbors, so that oxygen remains plentiful in waters percolating or flowing underneath. Large boulders that do not have *D. abbotti* on them may shelter smaller rocks that do. Many rocks that seem appropriate for this species do not harbor specimens. This spotty distribution of aggregated individuals may indicate a short swimming period and quick settlement by brooded larvae, or as yet unclear ecological restrictions on the adults. At Pigeon Point, other invertebrates found on surfaces with *Dendrodoa abbotti* include the anemone *Epiactis prolifera,* the polyclad *Notoplana acticola,* the polychaetes *Spirorbis* and *Salmacina,* the barnacle *Balanus glandula* (and sometimes *Chthamalus dalli*), porcelain crabs such as *Petrolisthes,* several encrusting bryozoans such as *Eurystomella bilabiata,* the asteroid *Leptasterias pusilla,* and the aplousobranch ascidian *Aplidium californicum.* But none of these associated invertebrates seems so severely kept back from the margins of boulders, so cryptic in its under-rock habitat, as *Dendrodoa abbotti.*

ECOLOGICAL DISTRIBUTION IN WASHINGTON.—Subtidal. At Peavine Pass, San Juan Islands, specimens were dredged from 10 to 12 m. The species has been sought elsewhere in rocky areas, but only Peavine Pass, which is swept to the bottom by strong tidal currents, has proved a reliable site for collecting by this method, and even there the species is rarely taken. Debris harboring *Dendrodoa abbotti* contains, as well, *Bal-*

TABLE 1. *DENDRODOA CARNEA* AND *D. ABBOTTI*: CONSISTENT DIFFERENCES.

Feature	*Dendrodoa carnea*	*Dendrodoa abbotti*
Color in life	Bright pink to blood red.	Gray to ochre, occasionally reddish around siphonal apertures.
Siphonal apertures	Bilabial.	Bilabial, somewhat more pronouncedly so than in *D. carnea.*
Dorsal tubercle	Narrow ovoid slit whose axis is oriented almost anterior-posterior.	Fairly sharply bent "C" whose long axis is oriented laterally.
Transverse branchial vessels and rows of stigmata	17 or more.	Ca. 12.
Internal longitudinal branchial vessels and folds (DL = dorsal lamina, (#) = number of vessels in fold, E = endostyle)	Left: DL0(1)0(1)0(1)0(1)0E as in *D. abbotti.* Right: DL0(4–5)0(1)0(1)0(1)0E; prominent low fold carrying at least 4 vessels on right pharyngeal wall.	Left: DL0(1)0(1)0(1)0(1)0E as in *D. carnea.* Right: DL0(1)0(1)0(1)0(1)0E; no multi-vessel fold on right pharyngeal wall.
Endocarps	Many, small, widely scattered over entire atrial wall.	Fewer, larger, more (but not entirely) confined to ventral atrial surface.
Margin of anus	"Reflected but not lobed, often somewhat two-lipped" (van Name 1912, p. 587).	Scalloped into usually 5 lobes.
Ovary	Straight along right ventral margin of body; oviduct continues so.	Along right-anterior ventral margin of body, then bends sharply into ascending limb, recurves behind atrial siphon into dorsal oviduct that projects posteriorly.
Testis	Not clearly encapsulated with ovary, testis-lobes extend somewhat into body wall, predominantly ventro-lateral to ovary; all testis-lobes close to ovary.	Clearly not encapsulated with ovary, testis-lobes lie wholly in body wall, predominantly ventro-medial to ovary; often one posterior group of testis-lobes far from ovary.
Spermiduct	(?) as in *D. grossularia,* many short spermiducts converge in multiple spermipores on atrial surface of ovary (?)	Single, long vas deferens on atrial surface of ovary receives vasa efferentia of all testis-lobes, ends mid-dorsally in spermipore-bearing papilla pointing at atrial siphon.
Brood chamber	Extensive, including right-posterior region beyond oviduct there.	More restricted to far posterior part of body.
Brooded young	(From a small sample) only a few dozen embryos brooded at a time.	Many dozens to more than 100 embryos brooded at a time.

anus nubilis (one of the best indicators that the ascidian may be present) and the hydrocoral *Allopora.* The ascidian occurs especially around the husks of dead barnacles and in crannies in large rocks. But dredging of course destroys the set of surfaces and actual relationships among members of the fauna at the site, and so no comparison can yet be made between the subtidal habitat of *Dendrodoa abbotti* at Peavine Pass and its intertidal circumstances at Pigeon Point.

The bathymetric contrast between California and Washington (San Juan Islands) records of *Dendrodoa abbotti* is striking. The species may occur subtidally in California; its inaccessibility, beneath large boulders, could account for the current lack of such records by dredging or even by diving. But *D. abbotti* does not occur in the very low intertidal zone in California, below about mean low-low tidal levels. Thus, if it does occur subtidally, there is not a continuous distribution of the species from those depths to the low- to mid-tidal habitats where it characteristically is found. In contrast, in the San Juan Islands, I have not found the species at all intertidally in habitats that resemble California's coastal sites—except, of course, for the lack of surf in the San Juans. *Dendrodoa abbotti* appears to be only a subtidal species in that archipelago. But to the west of the San Juan Islands, on the southwest coast of Vancouver Island, B.C., Dr. Ivan Goodbody has found this species "on the underside of boulders at extreme low tide . . . on the open coast north of Sooke." Dr. Goodbody reports (pers. comm.) that the site there is "a rough boulder strewn shore with many large rounded boulders indicating heavy wave action." His record thus extends the intertidal range of *D. abbotti* into those Canadian habitats where surf does resemble California's. Dr. Goodbody's Canadian specimens of *D. abbotti* are now in the collection of the California Academy of Sciences.

Discussion

A. Comparison of *Dendrodoa abbotti* with *D. carnea*

A comparison of *Dendrodoa abbotti* with the western North Atlantic species *D. carnea*—the styelopsid dendrodoan that most closely resembles *D. abbotti*—indicates an array of differences, some trivial, some marked, but all consistent. This comparison sets a great many specimens of *D. abbotti* against necessarily only a few dissected specimens of *D. carnea* (from the USNM collection) and others' reports on *D. carnea* (see van Name 1912, 1945). But differences that emerge even in this perhaps unbalanced sampling of these species gain force as they become elements in a consistent pattern of distinctions between the two taxa, and this pattern has become more persuasive with each examination of new specimens. Table 1 summarizes the comparison.

Even arguably minor distinctions (for example, the character of the brood chamber or of the endocarps) take on significance in Table 1's array. The two species are most effectively distinguished, however, by the following criteria:

1. shape and disposition of the ovary;
2. testis-ovary relationship, including *D. abbotti's* posterior group of testis-lobes;
3. structure of the spermiducts, especially of the vas deferens;
4. arrangement and number of internal longitudinal vessels of the right side of the pharynx;
5. number of transverse branchial vessels and rows of stigmata on both pharyngeal walls;
6. shape and orientation of the dorsal tubercle;
7. color in life.

B. Generic Traits

By most accounts and diagnoses, in the genus *Dendrodoa* the testis and ovary are "encapsulated" within a common sheath (Monniot and Monniot 1972), and the testis comprises many lobes that do not lie in the body wall but rather hug the parietal (away from the atrium) surface of the ovary (Huntsman 1913). Most of the gonad of *Dendrodoa grossularia* shows this condition of encapsulation and testis-ovary juxtaposition clearly, although some of the anterior testis-lobes do lie more in the body wall than wholly against the ovary. *Dendrodoa carnea* exhibits a somewhat looser gonadal arrangement: the testis-lobes apparently are still encapsulated with the ovary and lie largely against its parietal surface, but they extend into the adjacent body wall much more than do the testis-lobes of *D. grossularia,* especially to the lateral (right) side of the ovary. *Dendrodoa abbotti* carries this loosening of the testis-ovary bond further still: the testis-lobes of *D. abbotti* lie "beneath" the ovary or close by on the medial (left) side of the ovary, but they lie in the body wall itself, not against the ovarian mass, and there is no sheath enclosing these gonadal elements into a single structural unit of intimately juxtaposed parts. And although most of the testis-lobes of *D. abbotti* lie very close to the ovary, there is often a group of testis-lobes lying in the far posterior atrial floor of the zooid, and actually on the left side of the zooid, although even this separated and isolated group is still connected by a vas deferens to the common spermiduct of all the other, "ovary-affiliated" testis-lobes.

Dendrodoa carnea is so much like *D. grossularia* (Traustedt's (1883) type species of his genus *Styelopsis,* now a subgenus of *Dendrodoa*) that Ärnbäck (1922) and Hartmeyer (1903) have both suggested these could be merely geographic variants of a single species—a view not held, however, by van Name (1945). The main distinction between these two species is their different number of internal longitudinal branchial vessels, more numerous in *D. grossularia* than in *D. carnea.* But the slight gonadal contrast reported here also seems to be a consistent one. The difference takes on added taxonomic significance when *D. abbotti* joins the comparison, because the genus thereby shows a series of testis-ovary juxtapositions from a tightly joined one to an appreciably looser one—from the condition "characteristic" of the genus *Dendrodoa* to one rather akin to that of the genus *Styela.*

Perhaps the perplexing *Dendrodoa uniplicata*

Hartmeyer 1903, which Millar (1966) redesignates *Styela uniplicata* Bonnevie 1896 because "the structure of the gonad agrees better with *Styela*," extends the *grossularia-carnea-abbotti* series of gonadal arrangements further while retaining dendrodoan features of the pharnyx. Unfortunately, the meager remnants currently available of *Dendrodoa* (or *Styela*) *uniplicata* will not by themselves resolve this question.

Another dendrodoan trait from which *Dendrodoa abbotti* diverges involves the spermiduct. In the genus *Dendrodoa*, testis-lobes empty in groups into very short vasa deferentia or even more cloaca-like pits on the atrial surface of the ovary, and there are several such spermiporal loci on the ovary (Berrill 1950). The repetition of short vasa deferentia, each emptying a group of testis-lobes, is not usually as striking in *D. grossularia* as in the somewhat stylized depiction of this trait by Lacaze-Duthiers and Delage (1892), from which work many accounts of the species have been partly drawn. But Riedlinger (1902) indicates in his careful study how slight or even absent the vasa deferentia may be in that species, in place of which spermiporal loci serve the converging vasa efferentia of groups of testis-lobes. *Dendrodoa carnea* also appears to have multiple spermipores along the atrial surface of the ovary (again, though, a condition difficult to discern in dissections). In contrast, the gonad of *D. abbotti* has a single, long vas deferens, as in *Cnemidocarpa* and *Styela* (Fig. 2). All the spermiducts of this species are exceedingly fine, and their disposition difficult to trace except in serial sections. Such a close scrutiny of *D. carnea* would seem appropriate, to find out if that species is intermediate between *D. grossularia* and *D. abbotti* in this trait, as it is in testis-ovary juxtapositions.

Dendrodoa (*Styelopsis*) *abbotti* is placed in *Dendrodoa* by its possession of a single gonad, and in *Styelopsis* because of its unbranched ovary and its simple pharynx, which lacks folds and possesses few internal longitudinal vessels. *Dendrodoa abbotti* is so much like *D. carnea*, which in turn is so much like *D. grossularia*, that this placement of the new species seems indisputable. But the consequence is to relax and modify long-held gonadal criteria of *Dendrodoa*, recognizing that species with styelan gonadal patterns or cnemidocarpan spermiducal patterns occur in the genus.

ACKNOWLEDGMENTS

A grant from the Faculty Research Committee of the Academic Senate of the University of California, Santa Cruz has supported much of the research reported in this paper. I appreciate the assistance of Linda Cole, U.S. National Museum of Natural History, who guided me through the collection there, with the consequence that *Dendrodoa carnea* came into consideration at a critical moment in this study. Professor Ivan Goodbody has shared with both Professor Abbott and me several Canadian specimens of *Dendrodoa abbotti* and ecological information about their site; I am grateful for his help and for his readiness to include this important northern intertidal record in this initial paper about the new species. Donald P. Abbott, without realizing at the time the nomenclatural consequence of his generosity, shared with me his notes and drawings of many years' acquaintance with the species described in this paper, and I am most grateful for these and for many other ways in which he has encouraged me.

LITERATURE CITED

ÄRNBÄCK-CHRISTIE-LINDE, A. 1922. Northern and arctic invertebrates in the collection of the Swedish State Museum. 8. Tunicata. 1. Styelidae and Polyzoidae. *In* Kungl. Svenska Vetenskapsakad. Handlingar 63(2):1–62, pls. 1–3.

BERRILL, N. J. 1950. The Tunicata, with an account of the British species. London: Ray Society. 354 pp.

BONNEVIE, K. 1896. Ascidiae simplices og Ascidiae Compositae fra Nordhavs Expeditionen. *In* Norske Nordhavs-Expedition 23(2):1–16, pls. 3, 4.

GALIGHER, A. E. AND E. N. KOZLOFF. 1964. Essentials of practical microtechnique. Philadelphia: Lea & Febiger. 484 pp.

HARTMEYER, R. 1903. Die Ascidien der Arktis. *In* Römer, F. and F. Schaudinn, Fauna Arctica 3(2):91–412, pls. 4–14.

HUNTSMAN, A. G. 1913. The classification of the Styelidae. Zool. Anz. 41:482–501.

LACAZE-DUTHIERS, H. DE AND Y. DELAGE. 1892. Etudes sur les ascidies des côtes de France. Faune des Cynthiadées de Roscoff et des côtes de Bretagne. Mém. Acad. Sci. France (ser. 2) 45:1–323.

LIGHT, S. F., R. I. SMITH, F. A. PITELKA, D. P. ABBOTT AND F. M. WEESNER. 1954. Intertidal invertebrates of the central California coast. 2nd ed. Berkeley: Univ. Calif. Press. 446 pp.

MILLAR, R. H. 1966. Tunicata Ascidiacea. Marine invertebrates of Scandinavia, No. 1. Oslo: Universitetsforlaget. 123 pp.

MONNIOT, C. AND F. MONNIOT. 1972. Clé mondiale des genres d'ascidies. Arch. Zool. Exp. Gén. 113:311–367.

RIEDLINGER, R. 1902. Untersuchungen über den Bau von *Styelopsis grossularia* des Ostsee. Nova Acta Akad. Leop.-Carol., Halle 81:1–62, pls. 1–6.

SMITH, R. I. AND J. T. CARLTON, eds. 1975. Light's manual: intertidal invertebrates of the central California coast. 3rd ed. Berkeley: Univ. Calif. Press. 716 pp.

TRAUSTEDT, M. P. A. 1883. Vestindiske ascidiae simplices. 2. Molgulidae og Cynthiadae. Vid. Medd. Naturhist. Kjöbenh., ann. 1882:108–136, pls. 5, 6.

VAN NAME, W. G. 1912. Simple ascidians of the coasts of New England and neighboring British provinces. Proc. Boston Soc. Nat. Hist. 34:439–619, pls. 43–73.

———. 1945. The North and South American ascidians. Bull. Amer. Mus. Nat. Hist. 84:1–476, pls. 1–31.

PROCEEDINGS
OF THE
CALIFORNIA ACADEMY OF SCIENCES

Vol. 43, No. 16, pp. 249-267, 6 figs., 6 tables December 11, 1984

THREE NEW SPECIES OF SEVEN-GILLED HAGFISHES (MYXINIDAE, *EPTATRETUS*) FROM THE PACIFIC OCEAN

By

Charmion B. McMillan and Robert L. Wisner

Marine Biology Research Division, A-002, Scripps Institution of Oceanography,
La Jolla, California 92093

Abstract: Three new species of hagfishes (Myxinidae, *Eptatretus*) from the Pacific Ocean are described, and compared with *E. cirrhatus*. All four species have seven pairs of gill pouches and associated external openings. Of the new species, *E. carlhubbsi* is known from Molokai to Guam, north-central Pacific, *E. laurahubbsi* from off south-central Chile, and *E. strahani* from near Lubang Island, Philippines, South China Sea. *Eptatretus cirrhatus* occurs in the Australian-New Zealand area. Methods used in examination of hagfishes are described, and sensory (lateral line) canals are delineated and discussed briefly.

INTRODUCTION

This study of seven-gilled hagfishes (genus *Eptatretus*) from the Pacific Ocean is one of a series resulting largely from the specimens and data accumulated under direction of the late Carl L. Hubbs. Herein we describe three new species, present new data on *E. cirrhatus* (Bloch and Schneider 1801), offer suggestions for initial preservation of myxinids to provide good study material, and discuss methods useful in the taxonomic study of hagfishes. We also offer figures and a brief description of the sensory canals found in the ocular regions of two of the four species.

DISCUSSION

Our examinations have shown that species of *Eptatretus* from the Pacific Ocean have six to fifteen pairs of gill pouches and corresponding external apertures. The three new species described below, with *Eptatretus cirrhatus*, comprise a group having seven pairs of gill pouches. One aberrant specimen has eight pouches on each side, but with corresponding apertures arranged abnormally. Our rather limited counts (22 pairs) from the three new species may not reflect extremes of variation, but the number of gill apertures in *Eptatretus cirrhatus* appears to be constant—seven pairs in 48 specimens. In 44 counts from 22 specimens of the three new species, the only variation from seven was the specimen cited above (further discussed and figured below).

Counts of six apertures for *Eptatretus cirrhatus* recorded in the literature apparently resulted from a confusion of species. Günther (1870) stated that the species had "six or seven gill openings on each side," but he listed specimens from South Africa (*E. hexatrema* Müller, 1834) and Japan (*E. burgeri* Temminck and Schlegel, 1850). Species from these areas commonly have six pairs of gill openings. Referring to *Eptatretus cirrhatus*, Waite (1909) stated, "The gill-openings appear to be seven in number, but I have seen an example in which there were but six openings on one side, though seven were present on the other." A variation of one per side is common in species having ten or more gill pouches, such as *E. deani* (Evermann and Goldsborough 1907) and *E. stoutii* (Lockington 1878). Also, it is possible that Waite had an abnormal specimen in which two pouches shared the same opening (see above). Strahan's (1975) finding of "seven (rarely six) pairs of branchial apertures" for *Eptatretus cirrhatus* may have been influenced by Günther's or Waite's accounts.

Regan (1912) listed a species with "7 gill openings: on each side two rows of 8 teeth. Southern Pacific" as *Heptatretus banksii,* and placed in its synonymy *Homea banksii* Fleming 1822, and *Bdellostoma heptatrema* Müller (1834). Regan's total count of 32 teeth is much lower than that of any of the four species treated herein (Table 6), and may indicate an erroneous count or an undescribed species. Regan may have counted three fused median teeth (multicusps) on each row as one, thus reducing the count to 32 from a possible 40. This would have been much nearer our minimal count of 43 for *Eptatretus cirrhatus,* under which we synonymize the above three names.

Species of *Eptatretus* having seven gill apertures are not restricted to the Pacific Ocean. Fernholm and Hubbs (1981) listed a species having seven apertures from the Caribbean Sea. Fernholm (1982) has further described it as new.

In general, we concur with Fernholm and Hubbs in terminology, with but minor variations. We believe the term "dental muscle" is more appropriate than "tongue," "lingual," or "club-shaped muscle" in reference to the firm elongate complex of muscles and cartilages which constitutes the feeding mechanism of myxinids. Apparently the term "tongue" was first used by Müller (1834), but we concur with Ayers and Jackson (1900) that the entire apparatus in no way resembles a tongue. They stated, "The homology of this organ with the vertebrate tongue has never been discussed, nor do we know of any effort to determine the true nature of this organ." Dawson (1963:248, fig. 11) provided a detailed analysis and figure of the structure, and of the "teeth" and "jaw apparatus." She concluded (p. 253) that it was unwise to make any definite assumptions concerning homologies of the cartilages and muscles.

There are two pairs of anterior and posterior sets (series) of sharply pointed, laterally flattened, horny structures in the oral cavity which are embedded in a dental plate. These structures cut and scrape food into ingestible portions when everted and retracted by the dental muscle. Although the term "teeth" has been widely used in reference to these structures, they are unlike the teeth of other vertebrates, being composed entirely of keratin and devoid of calcification. Dawson (1963:247) concluded that, "It is most likely that there is no phylogenetic connection between these teeth and calcified teeth, and that they are an individual adaptation to a parasitic mode of life."[1] For descriptive and statistical purposes, we prefer the terms unicusps and multicusps to differentiate between single and composite teeth—the latter formed by the fusion of two or three unicusps. We consider the number and arrangements of both the multicusps and unicusps to be a significant species character.

MATERIALS

Collection data and disposition of specimens examined in this study are listed in the treatment of each species. Institutions which have furnished study material, or in which type specimens have been deposited, are: Bernice P. Bishop Museum, Honolulu, Hawaii (BPBM); United States National Museum, Washington, D.C. (USNM); Scripps Institution of Oceanography, La Jolla, California (SIO); California Academy of Sciences, San Francisco (CAS); Museum National d'Histoire Naturelle, Paris, (MNHN); University of the Philippines Zoological Museum, Diliman, Quezon City, Philippines (UPZM); Australian Museum, Sydney (AMS); Zoological Institute, Academy of Sciences, Leningrad (ZIN).

METHODS

The methods of measuring and counting described herein represent original methods as well as some used by prior authors including Dean (1904), Nani and Gneri (1951), Richardson (1953), and Strahan (1975). Fernholm and Hubbs (1981) reported many of these methods in their study of the eastern Atlantic *Eptatretus.* When

---

[1] Hagfishes are not parasitic; they scavenge dead or moribund fishes and invertebrates.

the senior author, in collaboration with the late Carl L. Hubbs, began work on the myxinids (in 1969), it was obvious that no standard criteria existed for the study of hagfishes, which lack the jaws, opercula, rayed fins, scales, gill rakers, and bones found in most fishes. Early workers applied different names to the same anatomical characters, defining them differently or not at all, and often not mentioning the methods used in measuring and counting. Therefore, it was difficult to correlate or compare data of different authors, and taxonomic confusion resulted. We hope that the methods proposed and defined below will provide future investigators with a standard by which hagfish species and specimens may be readily compared and identified.

Proper treatment immediately after capture is of particular importance in rendering specimens suitable for study. Often too many live hagfish are crowded in jars of preservative, resulting in coiled or bent bodies, usually heavily coated with slime (mucus) and difficult to measure or count. The copious secretion of slime, characteristic of the family Myxinidae, is dramatically curtailed by prompt immersion in fresh water, preferably warm. This rapidly kills the hagfish and prevents further extrusion of slime, which otherwise continues for several minutes even in formalin. Any remaining slime may be removed with paper or cloth towels, and the specimens should then be laid straight in a suitably large container of formalin until fixed. If a specimen is too large for a flat pan, it should be coiled smoothly in a 3–5-gallon container, taking care not to deform the snout or twist the body, and covered with formalin. This treatment produces fairly straight specimens with a minimal coating of slime, and greatly facilitates accurate counts and measurements.

Since fresh hagfishes deteriorate rapidly, preservation should be prompt. Color photos or notes should be made to record pigmentation, and tissue or blood desired for biochemical or chromosomal studies should be taken prior to immersion in formalin. We find that initial freezing prior to chemical preservation may cause softening of the tissue and collapse of eggs and internal organs, but it may be preferable to crowding into a too-small container. Due to the many body openings, we consider it unnecessary to slit the skin or to inject preservatives; hagfishes are so soft that the skin may tear and some underlying tissues may come apart, causing difficulty in subsequent measures and counts.

Abbreviations

PCD: external opening of the pharyngocutaneous duct; ordinarily confluent with the posteriormost left gill aperture, and much larger than all other apertures.

GA: gill (branchial) aperture; external opening of the efferent duct leading from a gill pouch.

GP: gill pouch; rounded, serially arranged structures along and posterior to the dental muscle.

DM: dental muscle; the firm, elongate, cylindrical complex of muscles and cartilages that moves the dental plates and sets of cusps during feeding. Posterior portions of DM are shown in Figure 3.

VA: ventral aorta; the portion between the heart (ventricle) and where it branches to each side of DM.

ABA: afferent branchial artery; one of the small blood vessels that lead to each gill pouch from VA or its branches.

Measurements

If the specimen is distorted due to preservation, it should be moderately straightened to approximate its normal form. Measurements are taken from the left side with the fish lying on a meter stick; dividers or dial calipers are advisable for shorter lengths. We arbitrarily divided the body into four major sections (Fig. 1): prebranchical, branchial, trunk, and caudal. These are particularly apropos to genera *Eptatretus* and *Paramyxine,* as each has more than one GA, thus a branchial section. In *Myxine, Neomyxine,* and *Nemamyxine,* there is only one GA on each side, that on the left being confluent with PCD.

Synonymous terms appearing in the literature are: "head" or "pectoral" for prebranchial, "gill" for branchial, and "abdominal" for trunk. The term "mucus" has often been used for slime, "teeth" for cusps, "tongue" or "lingual muscle" for dental muscle, and "outer" and "inner" for posterior and anterior in referring to the series of cusps.

Body measurements we have found particularly useful are:

Total length (TL): snout (anterior tip of rostrum, excluding barbels) to posteriormost margin of tail or caudal fin.

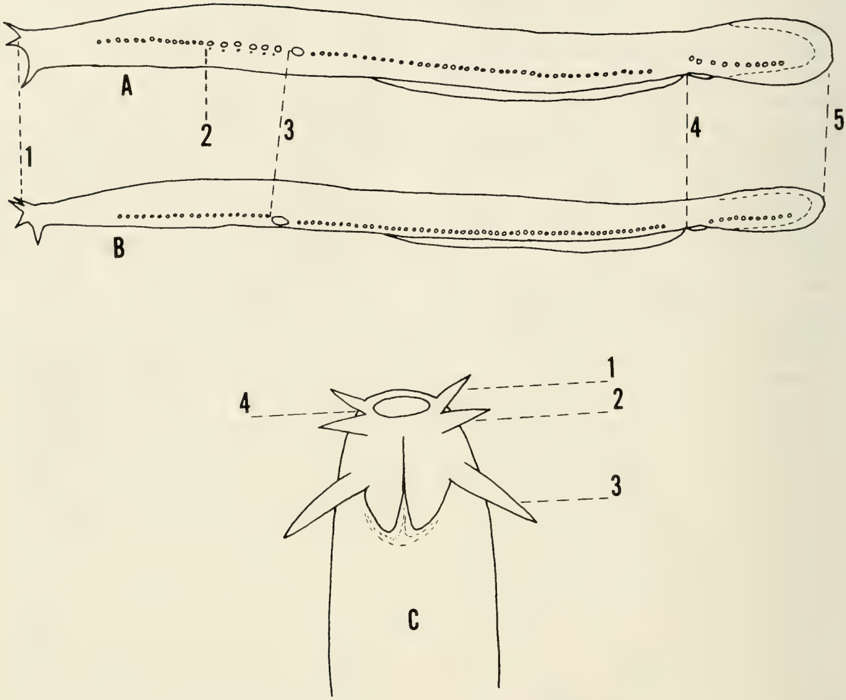


FIGURE 1. A–B: Sketches of an *Eptatretus* and a *Myxine,* showing regions of body used in study of myxinids: 1 to 5, total length; 1 to 2, prebranchial; 2 to 3, branchial; 3 to 4, trunk; 4 to 5, caudal. C: sketch of head region of a myxinid, showing barbel pairs 1, 2, and 3, and nasopharyngeal opening, 4.

Preocular length: snout to center of eyespot, unpigmented area (if present) marking the ocular region.

Prebranchial length: snout to front of first, or only, GA.

Branchial length: front of first to front of last GA (PCD). The anterior edge of the last GA is used because the posterior margin is often too vague and poorly defined to provide a definite reference point.

Trunk length: front of PCD to origin of cloaca.

Body width: maximum dimension about midway between rostrum and PCD.

Body depth: maximum vertical depth in trunk region, including finfold if present; depth excluding finfold should be taken at the same place. In both width and depth measurements the body should be molded into a seemingly natural shape if necessary.

Depth at cloaca: vertical depth at origin of cloaca.

Tail depth: maximum vertical depth of flattened tail, with any roll-up or fold of the thin tail margin uncurled and flattened.

Barbel length: from center of base to tip of each barbel (Fig. 1). The distance between bases of each pair may be measured from the inside edge of each base. Barbels are often curled and difficult to measure accurately, but in certain species barbel length may be a significant character, and is worth measuring.

Dental muscle length (DM): snout to tip of DM, as revealed by a midventral incision in the prebranchial region.

Dental muscle width: measured at a straight-sided portion well anterior to tapering end.

Dental muscle depth: measured at same place as width measure. Rather than using the total length, we have found it convenient to compare the length (or width) with the unbranched portion of the VA with measurements of the DM. This is a significant ratio in certain species, but varies greatly between specimens of other species.

Weight: may be taken, but we have not found it to be a reliable or useful character, principally because of the uncertainty in determining if all the entrapped fluid was drained, and because of dehydration of body fluids during preservation.

COUNTS

Ordinarily the branchial openings (GA) are the first items examined to ascertain the genus and possible species. The gill pouches are usually counted after the teeth (cusps) when the oral cavity incision is extended midventrally to the region of the PCD. Before counting the slime pores, we gently scraped away any coagulated slime overlying the line of pores; an air jet greatly facilitated location of pores. Because so few specimens were available for this study, both sides were counted to obtain wider range of variation. Counts we have found particularly useful are:

Slime pores:

Prebranchial—from anteriormost slime pore to last one before first GA.

Branchial—those pores in immediate association with (usually below and to the right of) each GA; often one less than GA count in *Eptatretus,* and much less, or absent entirely, in *Paramyxine.* There is usually no slime pore associated with PCD, but this varies with species and individual specimens. In this study all species except *E. strahani* have a branchial pore count equal to or higher than the number of GA; the extra pores vary in location and number.

Trunk—the series posterior to PCD and terminating anterior to end of cloaca, distinctly separate from cloacal series.

Cloacal—the pores distinctly before a vertical from posterior end of cloaca, usually starting somewhat anterior to and elevated from origin of cloaca.

Caudal—from first pore distinctly behind a vertical from posterior end of cloaca to last pore on tail. For statistical purposes we combine counts of cloacal and caudal pores under the heading "tail pores" (Table 2).

Cusps (teeth): We refer to a single "tooth" as a cusp, or unicusp, if it is not fused to one or more adjoining cusps. A unit of two or more cusps fused together at some point prior to its embedment in the cartilaginous dental plate is a multicusp.

FIGURE 2. Cusps and basal plates, in excised and spread condition, of *E. carlhubbsi,* paratype USNM 233742, 955 mm TL.

The two paired sets of cusps (the outer and inner rows of Fernholm and Hubbs [1981] and Fernholm [1982]) are examined from the ventral aspect. They are revealed by a midline incision from the base of the oral cavity through the cartilaginous pharynx until the sets are free and easily turned outward for viewing. There are disadvantages to this method. It is easy to misjudge the midline (if the "face" has been distorted in preservation) and cut through the median teeth, making counts difficult; also, the resulting view presented to the observer is a reversed image of the actual arrangement. The inner left row appears on the outer right side and vice versa. To avoid this confusion, the incision may be made from either side of the oral cavity to just under the third barbel, then extended laterally downward through the thin membrane, exposing the paired sets of cusps which, when spread apart, appear as shown in Figure 2.

On most specimens the count of multicusps may be determined by placing a dissecting or air jet needle under the first two cusps and gently

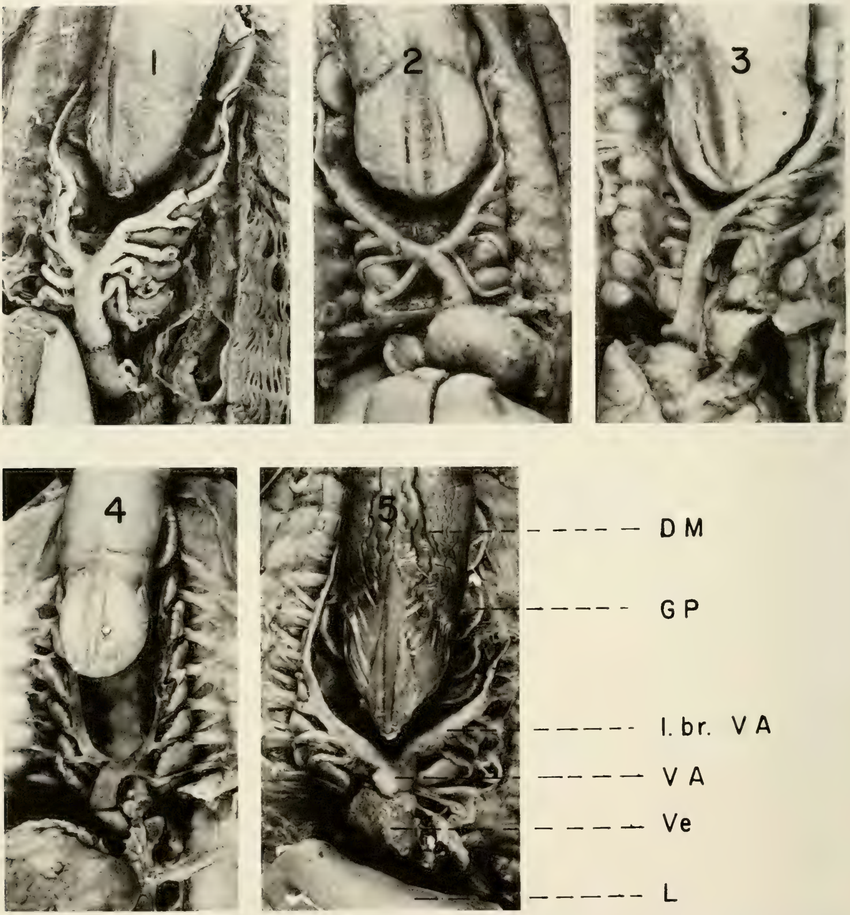


FIGURE 3. Ventral view of branchial region of: 1, *E. carlhubbsi*: 2–3, *E. laurahubbsi*, showing diversity in afferent branchial arteries (ABA) leading off from branches of ventral aorta (VA); 4, *E. strahani*; 5, *E. cirrhatus*.

lifting; the multicusp usually lifts and separates from the adjacent unfused cusp. However, in the nine largest specimens examined by us (*E. carlhubbsi*), lifting often raised the entire dental plate and set of cusps. Even if cusps are unquestionably fused, a line may extend among the fusion to the plate or "gum line;" in such instances perhaps the only valid criterion for separating multicusps from unicusps is the distinctness of this line as seen under magnification. Such lines are in marked contrast to the condition shown by scanning electron microscopy of *E. springeri* (Fernholm and Hubbs 1981: fig. 2), wherein no lines are evident in the multicusps.

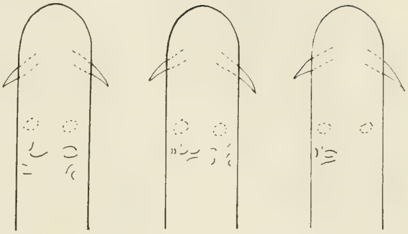
Gill apertures and pouches: In genera *Myxine, Neomyxine, Nemamyxine,* and *Notomyxine,* dissection is necessary to determine the number of gill pouches, since only one pair of efferent ducts leads to the exterior. A midventral incision is made from the single pair of GA anteriorly until all pouches are revealed (Fig. 3). The cut should be deep enough to expose VA and ventricle, taking care not to sever branches of VA or any ABA, or to destroy the origin of the ventral finfold if it is present anterior to PCD.

There are multiple, readily visible GA in genera *Eptatretus* (5–15 pairs) and *Paramyxine* (5–7 pairs). Although the number of internal pouches ordinarily is the same as the external apertures, there may be variation; thus, it is desirable to count the pouches and examine the arrangement of the GP relative to DM and branched and unbranched portions of VA (Fig. 3). The arrangement is often of taxonomic importance, although variation occurs (see *E. laurahubbsi*).

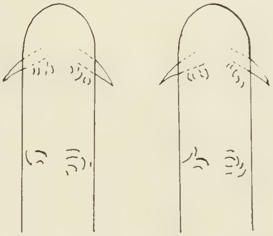
Sensory canals (lateral lines): Ayers and Worthington (1907:331, figs. 5–10), in a study of the skin-end organs of the trigeminal and lateralis nerves of *Bdellostoma dombeyi* (=*Eptatretus stoutii* [Lockington 1878]), described and figured lateral line canals, associated dermal grooves, and nerve endings. They showed the canals as short lines occurring only dorsally and somewhat laterally on the "head" and in two groups, one before and one behind the eyespots. Plate (1924: 66, fig. 61D) accepted the interpretation by Ayers and Worthington that the short lines constituted lateral line canals, but considered the dermal grooves to be artifacts. Ross (1963:155) cited both these studies and stated that the lateral lines had not been described in *Myxine glutinosa.* To our knowledge these are the only prior references to lateral line canals of hagfishes.

We concur with Ayers and Worthington that the canals occur only on the head (in the ocular area of the prebranchial region). However, they are lateral only in that a few occur on the side of the head, with most on the dorsal surface (Fig. 4), and none at all on the rest of the body. Assuming that the canals are indeed sensory in function, we prefer the term "sensory" to "lateral." Sensory canals occur in only two of the four species discussed here (*E. strahani* and *E. cirrhatus,* Fig. 4), but not on all specimens, and are irregular in number and form. The erratic occurrence in location and in numbers of canals is intriguing, as is their total absence in two of the four species.

Due to the limited number of specimens available, it is difficult to draw any firm conclusions regarding the taxonomic value of sensory canals. Ayers and Worthington (1907) stated that these canals were difficult to find because they were very small and the surface indications faint, and that any apparent erratic appearance might be due to the observer. However, on the specimens examined by us the canals, when present, were readily visible under adequate magnification and lighting, and often by the unaided eye. They appear as thin lines, about 1–3 mm long, variably straight or curved (Fig. 4), often very slightly raised above the skin, and sometimes covered with a coating of coagulated slime. Histological examination was not done, nor have we attempted to observe these canals on unpreserved fishes.



E. cirrhatus



E. strahani

FIGURE 4. Sketches (not to scale) of head regions of *Eptatretus cirrhatus* and *E. strahani* showing arrangements of sensory canals. The first two pairs of barbels are omitted.

Old, healed scars are often present in areas occupied by the sensory canals, and elsewhere on the body, mostly anteriorly. These are identifiable as shallow depressions, usually wider and longer than the sensory canals. Many scars occur singly, but often they are in groups of parallel lines, the spacing closely resembling that of the anterior cusps. Possibly this scarring occurs when many hagfishes are feeding in close proximity competing for food, or when crowded in a trap.

TABLE 1. AVERAGES AND RANGES (IN THOUSANDTHS OF TOTAL LENGTH) OF SELECTED BODY PROPORTIONS FOR FOUR SPECIES OF SEVEN-GILLED HAGFISHES (GENUS *EPTATRETUS*) FROM THE PACIFIC OCEAN.

	E. carlhubbsi	*E. laurahubbsi*	*E. strahani*	*E. cirrhatus*
N (size range in mm)	9 (813–1160)	8 (240–375)	5 (265–520)	8 (481–655)
	Avg. (range)	Avg. (range)	Avg. (range)	Avg. (range)
Preocular length	38 (36–54)	50 (44–59)	63 (57–68)*	60 (52–67)
Prebranchial length	184 (168–197)	193 (184–204)	220 (210–231)	225 (214–239)
Branchial length	68 (55–77)	55 (52–59)	77 (69–83)	76 (69–89)
Trunk length	602 (577–623)	561 (545–585)	521 (500–537)	550 (525–563)
Tail length	160 (145–176)	198 (181–213)	182 (174–202)	154 (135–168)
Tail depth	97 (89–105)	90 (82–99)	117 (109–125)	83 (77–91)
Body depth with finfold	No finfold	89 (74–97)	111 (101–117)	89 (69–102)
Body depth without finfold	93 (78–106)	81 (73–91)	98 (94–105)	88 (69–102)
Body depth at cloaca	73 (65–85)	70 (61–80)	87 (77–94)	67 (57–75)

* Due to lack of visible eyespots, the preocular length was taken from center of uncovered pupil.

Waite (1909) placed three adult *E. cirrhatus* in a bucket of formalin and observed them savagely attacking each other. One was bitten at least 15 times by the other two.

KEY TO SEVEN-GILLED SPECIES OF *Eptatretus* FROM THE PACIFIC OCEAN

1a. Slime pores of trunk 60–70, low, well below mid-lateral aspect. Total cusps 61–71. Eyespots present 2

1b. Slime pores of trunk 45–53, high, near mid-lateral aspect. Total cusps 43–53. Eyespots present or absent 3

2a. Ventral finfold absent. Two (rarely three) fused cusps on anterior multicusps, three on the posterior. Eyespots large, prominent .... *E. carlhubbsi* n.sp.

2b. Ventral finfold prominent. Two (rarely three) fused cusps on each of the four multicusps. Eyespots present .... *E. laurahubbsi* n.sp.

3a. Ventral finfold readily visible. Eyespots absent. Ventral margin of tail forming a nearly straight line from cloaca to abrupt beginning of curve around tail. Anterior few gill apertures small, slitlike. No pale rings around slime pores or gill apertures. Three fused cusps on each of the four multicusps .... *E. strahani* n.sp.

3b. Ventral finfold vestigial. Eyespots present. Tail margin smoothly ovate. All apertures rounded. Pale rings around slime pores and gill apertures. Three fused cusps on each of the multicusps .... *E. cirrhatus*

Eptatretus carlhubbsi new species

HOLOTYPE.—SIO 68-473, mature female, 961 mm TL, taken at 19°18′N, 166°33.5′E, near Wake Island, in a free-vehicle trap on bottom at 1574 m, 12–13 Sept. 1968.

PARATYPES.—SIO 68-473, female, 810 mm TL, taken with the holotype; SIO 82-63 (formerly BPBM 27850), female, 1125 mm TL, taken at Brooks Banks, between French Frigate Shoals and Gardner Pinnacles, Leeward Islands, Hawaii, Nov. 1981, *Mokihana* Cruise 81-12, set 35, shrimp trap, depth not given; BPBM 27848, male, 1160 mm TL, taken at 12°56′N, 166°22′W, French Frigate Shoals, Leeward Islands, Hawaii, 7 Nov. 1981, shrimp trap at 684 m; BPBM 27851, male, 830 mm TL, taken off the north shore of Molokai Island, Hawaii, 26–27 Dec. 1981, shrimp trap at 659 m; USNM 227440, male, 900 mm TL, taken at 24°48′N, 167°14′W, R/V *Cromwell* Cruise 80-05, Station 57, in a shrimp trap at 835 m; USNM 233742 (formerly NMFS P-0289), male, 955 mm TL, taken at 14°59′N, 145°13′E, Esmeralda Bank, Guam, 5–6 April 1981, Cruise *Typhoon* 81-01, Station 151, in a shrimp trap at 1061 m; CAS 50705 (formerly BPBM 27847), male, 1064 mm TL, Leeward Islands, Hawaii, Nov.–Dec. 1981, depth and method of capture not given; CAS 50706 (formerly BPBM 27849), male, 980 mm TL, taken at French Frigate Shoals, East Plateau, north side, Leeward Islands, Hawaii, 19 Nov. 1981, in a shrimp trap at 481 m.

DIAGNOSIS.—A seven-gilled *Eptatretus* having no ventral finfold, very large eyespots, two (rarely three) fused cusps on the anterior multicusps and three on the posterior.

DESCRIPTION.—Counts: Those of holotype given first (left and right sides), followed by ranges for all specimens in parentheses: gill apertures 7, 7 (all); prebranchial slime pores 15, 16 (12–17); branchial pores 7, 7 (6–8); trunk pores 60, 61 (60–70); cloacal pores 2, 2 (1–3); caudal pores 11, 11 (11–13); tail pores 13, 13 (12–16); total slime pores 95, 97 (93–110). Cusps on anterior multicusps 2, 2 (rarely 3); posterior multicusps 3, 3 (all); anterior unicusps 16, 16 (15–17); pos-

TABLE 2. PREBRANCHIAL, BRANCHIAL, AND TAIL SLIME PORES OF FOUR SPECIES OF SEVEN-GILLED HAGFISHES (GENUS *EPTATRETUS*) FROM THE PACIFIC OCEAN.

	Prebranchial slime pores									
	12	13	14	15	16	17	18	19	20	N
E. carlhubbsi	1	7	2	5	2	1				18
E. laurahubbsi			2	3	8	3				16
E. strahani		1	4	2	3					10
E. cirrhatus					4	17	17	4	1	43

	Branchial slime pores			
	6	7	8	N
E. carlhubbsi	4	12	2	18
E. laurahubbsi	7	6	3	16
E. strahani	10			10
E. cirrhatus	7	34	2	43

	Tail slime pores[1]							
	10	11	12	13	14	15	16	N
E. carlhubbsi			2	4	3	8	1	18
E. laurahubbsi					2	12	2	16
E. strahani	3	4	2					9
E. cirrhatus	1	6	16	14	6			43

[1] Tail count is the total of the cloacal and caudal slime pores.

terior unicusps 12, 13 (11–13); total cusps 68 (64–71).

Morphometry: In thousandths of total length; values for holotype given first, followed by ranges for all specimens: preocular length 38 (36–54); prebranchial length 184 (168–197); branchial length 68 (55–77); trunk length 602 (577–623); tail length 160 (145–176); tail depth 97 (89–105); body depth 90 (78–112); depth at cloaca 74 (62–86).

All specimens from Hawaii were frozen initially; the body proportions of these may not be closely comparable to the other collections, which were initially preserved in formalin. It is not known what effect freezing may have on subsequent shrinkage, but it is possible that the soft tissues of hagfishes are greatly affected by the expansion of cells in freezing. It is known that length of time in preservative significantly affects the total length; a shrinkage of 10% is not uncommon. However, to our knowledge no study has been done showing the changes in other body proportions. Body proportions (Table 1) and counts (Tables 2–6) are compared with similar data for other seven-gilled *Eptatretus* from the Pacific Ocean.

Body robust; prebranchial region slightly deeper than wide; body increasingly compressed laterally to tail, varying in greatest depth from 8% to 11% of TL. Two to four GP anterior to tip of DM, which is somewhat flattened posteriorly. Length of DM 19% (17–21%) of TL, its width 15% (9–19%) of its length, its depth 66% (57–87%) of its width. VA short, wide, its width

TABLE 3. TRUNK SLIME PORES OF FOUR SPECIES OF SEVEN-GILLED HAGFISHES (GENUS *EPTATRETUS*) FROM THE PACIFIC OCEAN.

	Trunk slime pores																									
	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	N
E. carlhubbsi																1	2			3		1	4	5		2	18
E. laurahubbsi																3	1	2	2		1	2	5				16
E. strahani	2	2	2	3																							9
E. cirrhatus		5	2	10	11	3	5	2	5																		43

TABLE 4. TOTAL SLIME PORES OF FOUR SPECIES OF SEVEN-GILLED HAGFISHES (GENUS *EPTATRETUS*) FROM THE PACIFIC OCEAN.

	Total pores																																			
	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	100	101	102	103	104	105	106	107	108	109	110	N
E. carlhubbsi																		1		1		2			3	1	2		2	4		1			1	18
E. laurahubbsi																						2		1	3	3		3	2	2						16
E. strahani	2	1	1	2	3																															9
E. cirrhatus								4	7	7	8	5	5	4	3																					43

39% (35–43%) of its length. Distance between DM and branching of VA 17% (12–22%) of DM length. GA rather evenly spaced in a line often sloping or curving slightly downward posteriorly, with the exception of paratype BPBM 27851, apparently an aberrant specimen. It has eight GP on each side, but with corresponding apertures arranged abnormally (Fig. 6); there are eight GA on the left side, but only seven on the right, with two gills sharing one aperture.

Head blunt, face sloping at about 30° from the vertical. Eyespots large, prominent, ranging from nearly round to square or rectangular. Removal of overlying integument shows the embedded eyes varying from under to well behind center of eyespots. Eyes nearly round, about 5 by 6 mm, slanting ventrodorsally at about 45°. The first two pairs of barbels of nearly equal length on the holotype, the second pair slightly shorter than the first. Proportions of the barbel pairs on the paratypes show great variation, with some of the first pairs shorter than the second. The second barbel, right side, of paratype SIO 68–473 is bifurcate to the base, both halves of about equal length. No sensory canals are present on any of the specimens.

There is no ventral finfold, but an intermittent, vague line resembling a median suture extends from well behind PCD nearly to cloaca. The thin margin of the tail, common on other hagfishes, is not readily evident in these large specimens. If a caudal finfold is present, it is very thick, tapering steeply from the tail musculature. This may be a species character or merely the result of age or size; no juveniles are known. In the other three species discussed below (particularly the juvenile specimens of *E. laurahubbsi*) the tail margins are notably deeper and thinner. The average tail length in the nine specimens of *E. carlhubbsi* is about twice (1.9–2.5) the body depth at the origin of the cloaca, but the shapes of the tails vary considerably (Fig. 5). The deep notch on the dorsal surface of the tail of the holotype is apparently an old, entirely healed injury; no notch is present on any paratype. The tail depths average 58% (49–65%) of the lengths; shape varies from that of a truncated club (No. 7) with no evidence of finfolds to the very deep, expanded form of No. 3, which has a notably less thickened margin.

The holotype and three paratypes are tan in color; two are from Wake Island, and one each

TABLE 5. UNICUSPS IN THE ANTERIOR AND POSTERIOR SETS OF CUSPS OF FOUR SPECIES OF SEVEN-GILLED HAGFISHES (GENUS *EPTATRETUS*) FROM THE PACIFIC OCEAN.

	Anterior unicusps										
	8	9	10	11	12	13	14	15	16	17	N
E. carlhubbsi								5	10	3	18
E. laurahubbsi						1	1	4	7	3	16
E. strahani		2	4	4							10
E. cirrhatus	7	28	7	1							43
	Posterior unicusps										
	7	8	9	10	11	12	13	14	15	16	N
E. carlhubbsi					3	8	7				18
E. laurahubbsi					1	10	4			1	16
E. strahani		2	5	3							10
E. cirrhatus	2	26	15								43

from French Frigate Shoals and Molokai, Hawaii. Five paratypes (one from Guam, four from Leeward Islands, Hawaii) are a purplish brown; the Guam specimen has a more brownish overtone. Scattered, irregularly shaped pale areas of varying sizes occur mainly on the anterior portions of the body and occasionally as small patches on the other parts; these light spots are more visible on the purplish-brown specimens. Small, very dark brown blotches occur randomly on all but one of the tan specimens. Pale rings surround the GA, but not the slime pores. The color differences are striking, but such variation is known in other species wherein blotching, lighter shades, and even albinism occur (Dean 1903; Jensen 1959).

The color variations discussed above and the striking differences in tail shapes and barbel ratios, as well as wide ranges in other body proportions and differences, often indicate the presence of more than one species, but we find no definite correlation between these characters and those of counts, sex, other body proportions, or geographical areas. Further collections may show that subspecies or other taxa occur within or between the three areas—Hawaii, Wake Island, and Guam.

The first few prebranchial pores curve gently downward on the holotype, but on all paratypes they are in an essentially straight line (occasionally the first one or two are slightly depressed). There are seven or eight slime pores in the branchial region, one or two more than expected, which is one less than the number of GA.

Eggs: The holotype contained at least 21 eggs, the largest 58.5 by 14.4 mm. These eggs had been removed and bottled separately by an earlier investigator, and it is not known that all were preserved. None were in the specimen when examined by us. Paratype BPBM 27848 contained 32 eggs, the largest 75.5 by 16.5 mm. Some eggs were damaged by freezing, the original preservative, and were loose in the body; these are now bottled separately. Eight eggs, the largest 58.5 by 14.4 mm, were packaged separately within a larger pack containing a male and a female (SIO 82-63, formerly BPBM 27850). The female contained only 13 eggs, the largest 63.0 by 12.6 mm.

TABLE 6. TOTAL CUSPS OF FOUR SPECIES OF SEVEN-GILLED HAGFISHES (GENUS *EPTATRETUS*) FROM THE PACIFIC OCEAN.

	Total cusps																													
	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	N
E. carlhubbsi																					1	2	1		2	1	1		1	9
E. laurahubbsi																			2		1		4			1				8
E. strahani					1			1		3																				5
E. cirrhatus	1	2	2	8	2	3	1	2	1																					22

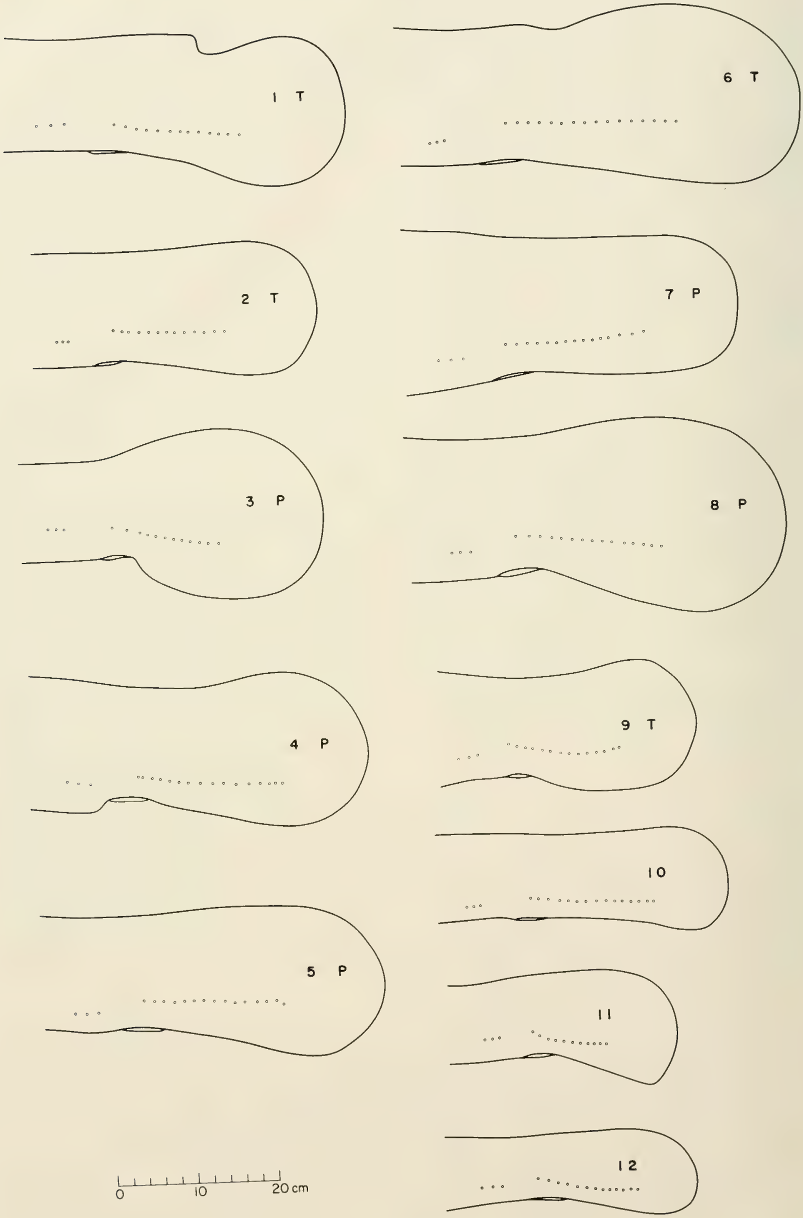

1 T
6 T
2 T
7 P
3 P
8 P
4 P
9 T
10
5 P
11
12
0
10
20 cm

FIGURE 6. Sketch of abberrant arrangement of gill apertures of a specimen of *E. carlhubbsi*, paratype BPBM 27851, 830 mm TL.

Although there was no identifying label with the separate eggs, we assume they had been taken from the same female. Since the Hawaiian specimens apparently were all frozen as initial preservative, these eggs could have been stripped prior to immersion in preservative; the specimen had not been cut open anywhere on the body. Although all were extremely large, none of the eggs cited above had the terminal hooks of fully ripe eggs (Dean 1899; Jespersen 1975).

ETYMOLOGY.—With great respect and admiration we dedicate this species of giant hagfish to the late Carl L. Hubbs, himself a giant in ichthyology.

Eptatretus laurahubbsi new species

HOLOTYPE.—SIO 65-643, juvenile female, 375 mm TL, taken at 33°31′S, 78°50′W, near Más a Tierra, Islas Juan Fernández, in a free vehicle trap on bottom at 2400 meters, between hours of 2030 and 0830, 12–13 Dec. 1965, Cruise 12 of R/V *Anton Bruun*.

PARATYPES (remaining material examined).—Seven juveniles (sex questionable) taken with the holotype, are deposited as follows: SIO 65-643, two, 369 and 287 mm TL (deposited with the holotype); CAS 49125, two, 287 and 358 mm TL; USNM 227441, two, 240 and 265 mm TL, Museo Nacionál de Chile, Santiago, one, 240 mm TL.

DIAGNOSIS.—A seven-gilled *Eptatretus* having a well-developed finfold and only two (rarely three) fused cusps on each of the four multicusps.

DESCRIPTION.—Counts: Those of the holotype given first (left and right sides), followed by ranges for all specimens in parentheses: gill apertures 7, 7 (all); prebranchial slime pores 17, 16 (14–17); branchial pores 7, 7 (6–8); trunk pores 67, 66 (60–67); cloacal pores 2, 3 (2–3); caudal pores 12, 12 (11–14); tail pores 14, 15 (14–16); total slime pores 105, 104 (97–105). Cusps on anterior multicusps 2, 2 (2, 3); posterior multicusps 2, 2 (2–3); anterior unicusps 15, 16 (13, 17); posterior unicusps 12, 12 (11–16); total cusps 63 (61–68).

Morphometry: Values in thousandths of TL given first for the holotype, followed by ranges for all specimens (left side): preocular length 53 (52–59); trunk length 560 (545–585); tail length 189 (181–213); maximum body depth including finfold 89 (74–97), excluding finfold 84 (73–91); body depth at cloaca 69 (61–80); tail depth 82 (82–89). Morphometric data (Table 1) and counts (Tables 2–6) are compared with similar data for other seven-gilled *Eptatretus* from the Pacific Ocean.

Body deeper than wide, width at midbody about 1.6 in depth. Tail broadly ovate, its depth slightly greater than body depth. Ventral finfold well developed, originating well behind PCD; a broad, thin finfold from posterior margin of cloaca around tail and dorsally until about over anterior margin of cloaca (Fig. 5–1). Dorsal profile of head sloping to a very blunt, nearly straight-across rostrum; width of nasopharyngeal orifice about equal to length of third barbels. First pair of barbels about 63% of length of third pair; second pair about 75%.

Color notes were not taken at time of capture (December 1965); all specimens are now a uniform yellowish color, no doubt a result of fading. The eyespots are no longer discernible, but preocular measurements were recorded by the senior author in November 1973. Removal of integument over the right eye of a 287-mm specimen shows the eye to be round, about 2.5 mm in diameter, with a small triangular pupil with its base dorsad and slanting forward at a slight angle to horizontal axis of body. No sensory canals are evident on any specimen.

Despite the faded condition of all specimens, the branchial apertures and most slime pores have whitish borders. Usually one pore, plus an occasional extra one, occurs adjacent to each BA. Two pores are near the opening of PCD on four specimens; three have one pore, and one has none near PCD (as is the usual condition on other

←

FIGURE 5. Tail shapes (to scale) and patterns of occurrence of the last four trunk pores and cloacal and tail slime pores of four species of seven-gilled *Eptatretus* from the Pacific Ocean: 1–9 *E. carlhubbsii* (T = tan color, P = purplish color); 1—Holotype, SIO 68-473, 961 mm TL; 2–9 Paratypes: 2—SIO 68-473, 813 mm TL; 3—USNM 227440, 900 mm TL; 4—USNM 233742, 955 mm TL; 5—CAS 50705, 1064 mm TL; 6—BPBM 27848, 1160 mm TL; 7—CAS 50706, 908 mm TL; 8—SIO 82-63, 1125 mm TL; 9—BPBM 27851, 830 mm TL; 10—Holotype, *E. laurahubbsi*, SIO 65–643, 375 mm TL; 11—Holotype, *E. strahani*, MNHN 1978-462, 520 mm TL; 12—*E. cirrhatus*, 655 mm TL.

Eptatretus). Space between the last trunk pore and first cloacal pore is about equal to length of cloaca (Fig. 1). Two or three slime pores lie over cloaca in a straight line and equally spaced with caudal pores. Prebranchial pores in a fairly straight line; occasionally the first one to three slightly depressed.

There is great variation in the arrangement of GP and afferent branchial arteries (ABA) with respect to the DM and branching of VA (Figs. 3-2 and 3-3). The number of GP along DM are far more variable than in the other three species, ranging from two to five. Also, length of VA varies notably; in six specimens VA averages 8.1% (6.3–9.3%) of length of DM, but in one 240-mm specimen the length of VA was 14.4% of DM, with three ABA leading off the left side and two off the right. This variation is in marked contrast to the regular arrangement of the branchial apparatus of the three other species discussed herein.

The eight specimens of *E. laurahubbsi* are unusual within genus *Eptatretus* in the appearance of the multicusps, apparently having only two fused cusps in each series. Indeed, it is often a highly subjective decision as to whether any of the anteriormost cusps are fused as multicusps. One specimen appears to have three fused cusps in each of the anterior series and two in the posterior series. In two specimens it is questionable as to whether two or three cusps are fused in the posterior rows. In other *Eptatretus* known from the southern hemisphere the usual configuration is three fused cusps on each of the four multicusps; all *Eptatretus* known from the North American Pacific coast have three in the anterior and two in the posterior row, which are distinct and clearly seen even in juveniles. A juvenile (188 mm) *E. stoutii* (Lockington 1878) clearly shows hard, well-developed cusps with the pattern 3/2. Also, a 100-mm specimen of *E. polytrema* (Girard 1855) from Chile has three distinctly fused cusps in each multicusp; adults of this species attain a total length of at least 550 mm. Thus, the presence of only two fused cusps in most specimens of *E. laurahubbsi*, and the uncertainty regarding the number fused in the others, is apparently not due to immaturity or small size.

All of our study specimens are juveniles, but it is highly probable that adults exceed one meter in length. The longest (holotype), although 373 mm TL, contains minute eggs, seen with difficulty under magnification. In another *Eptatretus* (undescribed) from the Gulf of California, a specimen of this size may have fully developed gonads and large eggs. Gumersindo Revuelta, a former student at the University of Chile, Valparaíso, in an unpublished thesis (1976), sketched and gave limited data on a very large hagfish, slightly exceeding a meter in length (from scale provided with sketch). He tentatively identified it with the giant *Eptatretus* taken at Wake Island (from data sent to him by Hubbs), probably because of its gigantic size compared to other species from Chilean waters. Revuelta had at least two females, both apparently very large, for he sent to Hubbs (in 1976) two large eggs: one 68 by 16.5 mm from Valparaíso, and one 72 by 16.8 mm from "Juan Fernandez" (presumably the island). We presume these large specimens to be adults of *E. laurahubbsi* because Revuelta reported the multicusps as 2/2, and his limited data are in close agreement to those of our specimens taken in the same vicinity. Also, in *E. carlhubbsi* the ventral finfold is entirely absent, but Revuelta's sketch shows a ventral finfold originating a little behind the anterior third of the body. In our juveniles a pronounced finfold originates variably between the midpoint and anterior third of the body; the exact point of origin is indeterminate because of wrinkling during preservation.

Etymology.—We dedicate this unique species to our friend and and co-worker, Laura Clark Hubbs, who contributed in so many ways to the life and works of her husband, Carl Leavitt Hubbs.

Eptatretus strahani new species

Holotype.—MNHN 1978-462, female, 520 mm TL, containing eggs of about 4.5 mm in length, taken at 14°00′N, 120°18′.2″E, South China Sea near Lubang Island, Philippines, in a trap net at 189 meters, Station 22 *Musorstom* Expedition, 21–22 March 1976, 1800–0600 hours.

Paratypes (and remaining material examined; all taken with the holotype).—MNHN 1981-722, female, 420 mm TL; SIO 81-116, female, 265 mm TL, male, 450 mm TL; USNM 227442, male, 465 mm TL.

Additional Material.—UPZM 1981-809, 400 mm TL; UPZM 1981-811, 480 mm TL. Total lengths, comparisons, and identifications were made by Prof. Reynaldo de La Paz, University of the Philippines, Diliman, Quezon City, Philippines, based on methods and data provided by us.

Diagnosis.—A seven-gilled *Eptatretus* having no eyespots, a well-developed ventral finfold, and three fused cusps on each of the four multicusps.

Description.—Counts: Those of the holotype given first, followed by ranges in parentheses for all five specimens (both sides counted): gill apertures 7, 7 (all); prebranchial slime pores 14, 16 (13–16); branchial pores 6, 6 (6–7); trunk pores 45, 47 (45–48); cloacal pores 4, 3 (3–4); caudal pores 7, 7 (6–8); total tail pores 11, 11 (10–12); total slime pores 76, 79 (76–80). Cusps on multicusps 3, 3 (all); anterior unicusps 11, 11 (9–11); posterior unicusps 9, 9 (8–10); total cusps 52 (47–52).

Morphometry: Values for holotype given first, followed by ranges for all five specimens, in thousandths of total length: preocular length (no eyespots); prebranchial length 231 (210–231); branchial length 81 (69–83); trunk length 500 (500–537); tail length 196 (174–202); body depth including finfold 115 (101–117); excluding finfold 95 (94–105); body depth over anterior margin of cloaca 88 (77–94); tail depth 119 (109–125). Morphometry (Table 1) and counts (Tables 2–6) are compared with similar data for other seven-gilled *Eptatretus* from the Pacific Ocean.

Body deeper than wide, deepest at midsection. Ventral finfold well developed, extending from about midbody to cloaca, its length about 31% of TL. Tail margin quite thin posterior to cloaca, extending around tail to dorsal surface, ending at about a vertical from posterior end of cloaca. Ventral outline of tail forms a nearly straight line, ending with an abrupt curvature up and around end to dorsal aspect. This shape is in marked contrast to the gradual curvature of tails of the other three species treated herein (Fig. 5).

Dorsal profile of head sloping steeply to snout; rostrum more rounded than in *E. carlhubbsi* or *E. laurahubbsi*; width of nasopharyngeal opening about 60–80% of length of first pair of barbels. First two pairs of barbels nearly equal in length; respectively, about 66% and 72% of length of third pair. First barbel, left side, of a 420-mm female is bifurcate to near base, with posterior branch shorter. Since we have occasionally seen this bifurcation in other hagfishes (usually near the tip, and always on only one barbel of the six), we assume this form is the result of an injury rather than some genetic malformation.

No eyespots are visible on any specimen (about 30 months after capture). Since the body color is still fairly dark we have assumed that little or no fading has occurred, and that the unpigmented eyespot area should still be visible if present in life. No notes regarding eyespots were made at time of capture. Removal of overlying integument on holotype shows eye to be ovate (3.4 by 2.4 mm) and slanted ventrodorsally at about a 45° angle; pupil more rounded (1.4 by 1.1 mm).

Sensory canals are present in two groups on each side of the head before and behind the area where eyespots normally occur (Fig. 4). One group of sensory canals is found near the bases of the third pair of barbels, anterior to embedded eyes, another group slightly posterior to eyes. Anterior group consists of five more-or-less longitudinal lines 1–3 mm long; canals of posterior group both longitudinally and horizontally arranged, those on top of head tending to be more horizontal. No canals extend across dorso-medial line.

Color of holotype (in preservative) a light brown, all paratypes a darker brown, the smallest the darkest. No discernible whitish rings around slime pores or GA on larger specimens, but the GA of the smallest one has distinctly pale margins. Finfold anterior to cloaca is same color as body, but tail has a very narrow, pale margin extending a short distance forward on the dorsal surface.

The line of the anterior prebranchial slime pores is straighter in this species than in the other three discussed; two specimens have only slight curvature, and no anterior pores are markedly elevated above adjacent ones in the prebranchial series. Space between last trunk and first cloacal pore about 65% of length of cloaca; spacing is variable with degree of slant or elevation of first cloacal pore (Fig. 5). Cloacal pores form a distinct dorsoventral slant on left side of holotype, but not on right; slanting is variable on paratypes.

Most GA are shaped as slits, slanting ventrodorsally; this shape could be an artifact of preservation, but the GA may be made to assume a rounded form only by considerable pulling and squeezing of surrounding flesh; all the slime pores below GA are rounded.

Three to five GP lie anterior to tip of DM (Fig. 3); two to four lie between that tip and branching of VA, and none posterior, although one GP of the smallest specimen (265 mm TL) lies just at the branching. Length of VA 6.4% (5.4–7.6%) of DM length; DM length 26% (25–27%) of TL, its width 15% (13–16%) of its length. Distance between tip of DM and branching of VA 9% (7.2–10.9%) of DM length.

ETYMOLOGY.—We are pleased to dedicate this new species to Ronald Strahan in acknowledgment of his important contributions to the study of Myxinidae.

Eptatretus cirrhatus (Bloch and Schneider, 1801)

Petromyzon cirrhatus Bloch and Schneider, 1801:532 (original description fide Forster ms II:24 [habits: New Zealand]).

Homea banksii Fleming, 1822:374 (South Seas [presumptive]).

Bdellostoma Forsteri Müller, 1834:71, 80 (anatomy; characters in key; reference to *Petromyzon cirrhatus* Bloch); Schneider, 1880:115 (status uncertain; based on a poor specimen).

Bdellostoma heptatrema Müller, 1834:7 (original description; New Zealand).

Bdellostoma cirrahatum Günther, 1870:511 (synonymy, in part; diagnosis, in part; distribution [New Zealand only]); Hutton, 1872:87 (characters; color reddish brown, white around mouth; common Australia and South Africa [misidentified with *E. heptatrema*]); Putnam, 1874:156 (in part; New Zealand; 7 gill slits); Schneider, 1880:115 (in part; doubts on status); Adam and Strahan, 1963:6 (6 or 7 pairs of gills; average length 480 mm; South Pacific, common off New Zealand).

Homea cirrhata Garman, 1899:341, 345, 349, 419 (synonymy; nomenclature); Dean, 1904:21 (in part; synonymy; New Zealand).

Heptatrema cirrata [sic] Hutton, 1904:55 (listed; New Zealand).

Eptatretus cirrahatus Berg, 1906:173 (in part; New Zealand); Waite, 1909:2 (description; behavior; average length 680 mm; Timaru and Chatham Islands; New Zealand); Graham, 1965:67 (plentiful on North Otago Shelf, New Zealand; often takes baited hooks); Heath and Moreland, 1967:30 (shore to 1800 ft; more abundant south of Hawke Bay than elsewhere in New Zealand); Whitley, 1968:4 (synonymy); Scott, Glover, and Southcott, 1974:19 (New Zealand, New South Wales, S.E. Australia); Fernholm, 1974:351 (in shallow water, New Zealand); Fernholm and Holmberg, 1975:253 (structure of eye, comparative; Kaikoura, S. Island, New Zealand); Strahan, 1975:145 (key; description; ranges of counts and body proportions).

Heptatretus banksii, Regan, 1912:534, 536 (comparisons; synonymy; diagnosis; D'Urville Is., Queen Charlotte Sound, New Zealand.).

Material Examined (counts and measurements both taken).—SIO 81-105, two males, 488 and 655 mm TL, three females 481–636 mm TL, 42°24′S, 173°41′E, no data on depth or date of capture, received from J. A. F. Garrick, Zoology Department, Victoria University of Wellington, New Zealand, 1 Nov. 1972; SIO 62-482-4A, two females, 577 and 580 mm TL, received from L. R. Richardson, Wellington, New Zealand, 25 March 1959, no data on depth of capture; ZIN 717-966, male, 595 mm TL, 40°19′S, 172°15′E, 160–172 meters, 18 Jan. 1965.

Counts only taken: AMS I 15527-001, three males, 254–452 mm TL, 26°32′S, 153°51′E, agassiz trawl, 175 fms (320 m), 27 July 1968; AMS Kapala Station 71-07-03, female, 505 mm TL, 33°33′–37′S, 152°01′–151°57′E, 205 fms (375 m), 21 April 1971; AMS Kapala Station 71-08-05, male, 265 mm TL, female, 552 mm TL, 33°11′S, 152°23′E, otter trawl, 310 fms (567 m), 29 April 1971; AMS Kapala Station 71-11-07, two females, 491, 514 mm TL, 34°40′–35°01′S, 151°10′–07′E, otter trawl, 300 fms (549 m), 7 July 1971; AMS Kapala Station 71-11-08, female, 410 mm TL, 34°56′–35°02′S, 151°06′–05′E, otter trawl, 160 fms (194 m), 8 July 1971; AMS Kapala Station 71-11-10, male, 447 mm TL, 35°11′–37′S, 150°45′–42′E, otter trawl, 230 fms (421 m), 8 July 1971; AMS Kapala Station 71-12-04, female, 546 mm TL, 33°41′–49′S, 151°53′–47′E, otter trawl, 245–250 fms (448–457 m), 20 July 1971; AMS Kapala Station 71-12A-06, three females, 374–503 mm TL, 35°25′–29′S, 150°50′–48′E, otter trawl, 300 fms (549 m), 2 Aug. 1971.

Diagnosis.—A seven-gilled *Eptatretus* having a vestigial ventral finfold, small but prominent eyespots, white around the mouth, pale rings around branchial apertures and slime pores; three fused cusps on each multicusp; sensory canals may occur.

Description.—Despite its being the first hagfish described from the Pacific Ocean, the literature contains minimal data on morphology and counts. Waite (1909) and Graham (1965) provided descriptions and accounts of behavior, but no meristic data. Strahan (1975) listed only ranges of counts and percentages of total length for certain body measurements for 13 specimens. We offer morphometry based on only the eight specimens available to us, but include counts on 22 specimens examined by Carl L. Hubbs in 1971 at the Australian Museum, Sydney.

Counts: Averages followed by ranges in parentheses, both sides counted: gill apertures 7 (all); prebranchial slime pores 17–18 (16–20); branchial pores 7 (6–8); trunk pores 48–49 (46–53); cloacal pores 3 (2–5); caudal pores 9 (6–11); total tail pores 12 (10–14); total slime pores 86 (83–90). Three fused cusps on each of the four multicusps; anterior unicusps 9 (8–11), posterior unicusps 8 (7–9); total cusps 46 (43–51).

Morphometry: Averages followed by ranges in parentheses, in thousandths of TL, for eight specimens: preocular length 60 (52–67); prebranchial length 225 (214–239); branchial length 76 (69–89); trunk length 550 (525–563); tail length 154 (135–168); maximum body depth including finfold 93 (84–102); excluding finfold 91 (81–102); body depth over cloaca 67 (57–74); tail depth 82 (77–91); body width at mid-prebranchial section 50 (46–55).

Dorsal profile of head sloping gently downward, face sloping at about a 45° angle; nasopharyngeal opening about equal to or slightly less than length of first barbel. Average length of first pair of barbels about 69% and second pair about 75% of the length of the third pair. Body rounded anteriorly, becoming more laterally compressed and deeper posteriorly; tail bluntly rounded, spatulate, its depth slightly less than greatest depth of body (Table 1). Ventral finfold narrow and relatively short, its length about 30% of TL, extending from well behind midbody to cloaca.

Color of our specimens in preservative varies from light chocolate to dark brown; the most lightly colored one is strongly mottled anteriorly with small, irregular pale spots and patches. Waite (1909) stated that "the colour varies from blue to bluish violet [presumably fresh material]. Some examples show irregular white spots and markings; the ventral finfold and the margin of the tail may also be white." On our material, preserved at least ten years prior to our examination, the poorly developed finfold has a narrow pale margin on two specimens, but not on the other six; color is highly variable. Tail of one specimen is irregularly margined with pale areas; pale rings around most of the gill apertures and slime pores.

Small but plainly visible eyespots are present on all specimens. Removal of integument covering right eyespot of a specimen 577 mm TL reveals the embedded eye as elliptical (6.3 by 3.2 mm) and slanting forward ventrodorsally at about a 45° angle; pupil small, more rounded (about 1.9 by 1.4 mm).

Sensory canals, only as posterior series (in the specimens available to us), are located close behind eyespots (Fig. 4). Canals are readily identifiable on only three of eight specimens (488–655 mm TL) and only on the left side of largest one; they are similar in size, form, and arrangement to those of *E. strahani.* On two specimens (580 and 597 mm TL) positive identification of canals is prevented by presence of much scarring.

The anterior prebranchial slime pores on all specimens form a downsloping curve; a high incidence of irregular spacing of these pores occurs. On left side of four specimens, first or third pore is notably elevated or very closely spaced. On one specimen four pores form an almost-square pattern; all apparently lead from a single slime gland. In most *Eptatretus* from the Pacific Ocean, the usual number of branchial slime pores is one less than the number of GA, since ordinarily there is no pore associated with the PCD. In *E. cirrhatus* there is a high incidence of extra pores and irregular spacing of slime glands in the branchial region, especially near the PCD.

Posterior two or three GA, left side, curve gently downward on seven of eight specimens, but only on the right side of one. On a 480-mm juvenile female the normally confluent openings of the seventh GA and PCD are distinctly separate; such separation also occurs infrequently in other species of *Eptatretus.* Usually five, occasionally four, GP lie anterior to tip of DM. Length of DM 27% of TL, its width 13% (12–14%) of its length; somewhat flattened posteriorly, depth is 80% (75–88%) of its width. The shape of the tip of the DM varies somewhat from that of the other three species discussed herein (Fig. 3). Distance between tip of DM and branching of VA about 7.4% (4.8–10.8%) of DM length; VA usually greater in width than in length, in contrast to that of the other three species. No ABA lead off before branching of VA in the eight specimens available to us.

A 655-mm TL female contains about 50 large eggs, ranging from 29 to 32 mm long by about 10 mm in diameter; this is an unusually large number of maturing eggs. All are still in the mesentery which is attached to the body wall; terminal anchor filaments and hooks are not present on any egg.

ACKNOWLEDGMENTS

We are deeply grateful to the late Carl L. Hubbs for his efforts in amassing much of the material on hagfishes, without which this study might never have been accomplished. Also, we are most grateful to the following persons and agencies: Jacques Forest, Museum National d'Histoire Naturelle, Paris, and Professor Reynaldo M. de La Paz, University of the Philippines, Diliman, Quezon City, for material of *E. strahani*; J. A. F. Garrick, Victoria University, Wellington, New Zealand, and L. R. Richardson, Wellington, for specimens of *E. cirrhatus*; and Richard H. Rosenblatt, for the holotype and one paratype of *E. carlhubbsi.* Other material of *E. carlhubbsi* was provided by Steven Kramer, National Marine Fisheries Service, Hawaii; Robert Moffitt, NMFS Field Station, Mangilāo, Guam; Paul Strushaker, Honolulu; and John E. Randall and Arnold Suzumoto, Bernice P. Bishop Museum, Honolulu.

All specimens of *E. laurahubbsi* were taken by the junior author on Cruise 12, R/V *Anton Bruun,* Southeastern Pacific Biological Oceanography Program, sponsored by the National Science Foundation. The holotype and one paratype of *E. carlhubbsi* were taken on the Scripps Styx expedition, sponsored by the National Science Foundation through a grant (GB-7596) to R. H. Rosenblatt and W. A. Newman. We greatly appreciate the efforts of all persons involved. R. H. Rosenblatt critically read the manuscript.

References Cited

Adam, H., and R. Strahan. 1963. Notes on the habitat, aquarium maintenance, and experimental use of hagfishes. Chapter 1, pages 1–8 *in* The Biology of *Myxine*. A. Brodal and R. Fänge, editors. Universitetsforlaget, Oslo. 588 pp.

Ayers, H., and C. M. Jackson. 1900. Morphology of the Myxinidae 1. Skeleton and musculature. Bull. No. 1, University of Cincinnati 185–224.

———, and J. Worthington. 1907. The skin-end organs of the trigeminal and lateralis nerves of *Bdellostoma dombeyi*. Am. J. Anat. 7:327–336.

Berg, L. 1906. Übersicht der Marsipobranchii des Russischen Reiches. Bull. Acad. Sci. de St. Petersbourg, V^{e} Ser., 24(3): 173–197.

Bloch, M. E., and J. G. Schneider. 1801. Systema ichthyologiae iconibus ex illustratium. Post obitum auctoris opus inchoatum absolvit, correxit, i interpolovit Jo. Gotlob Schneider Saxo, Berlin:1–584.

Dawson, J. A. 1963. The oral cavity, the "jaws," and the horny teeth of *Myxine glutinosa*. Chapter 5, pages 231–255 *in* The Biology of *Myxine*. A. Brodal and R. Fänge, editors. Universitetsforlaget, Oslo. 588 pp.

Dean, B. 1899. On the embryology of *Bdellostoma stoutii*. A general account of myxinoid development from the egg and segmentation to hatching. Fest. zum Siebensigsten Geburstag von Carl von Kuppfer, Jena. 221–276.

———. 1903. Albinism, partial albinism, and polychromism in hagfishes. Am. Naturalist 37(437):295–298.

———. 1904. Notes on Japanese myxinoids. A new genus, *Paramyxine*, and a new species, *Homea okinoseana*, reference also to their eggs. Jap. Coll. Sci., Imperial Univ., Tokyo 19(2):1–23.

Evermann, B. W., and E. L. Goldsborough. 1907. The fishes of Alaska. Bull. U.S. Bur. Fish. 26(for 1906):219–360.

Fernholm, B. 1974. Diurnal variations in the behavior of the hagfish, *Eptatretus burgeri*. Mar. Biol. 27:351–356.

———. 1982. *Eptatretus caribbeaus*: A new species of hagfish (Myxinidae) from the Caribbean. Bull. Mar. Sci. 32(2):434–438.

———, and K. Holmberg. 1975. The eye in three genera of hagfish (*Eptatretus, Paramyxine*, and *Myxine*)—a case of degenerative evolution. Vision Research 15:253–259.

———, and C. L. Hubbs. 1981. Western Atlantic hagfishes of the genus *Eptatretus* (Myxinidae), with descriptions of two new species. Fish. Bull. 79(1):69–83.

Fleming, J. 1822. The philosophy of zoology; or a general view of the structure, functions, and classification of animals. Fishes. Edinburgh 2:305–397.

Garman, S. 1899. Reports on an exploration off the west coasts of Mexico, Central and South America, and off the Galápagos Islands in charge of Alexander Agassiz, by the U.S. Fish Commission Steamer *Albatross* during 1891, Lieut. Commander Z. L. Tanner, U.S.N., commanding. XXVI. The Fishes. Mem. Mus. Comp. Zool. 24:1–431.

Girard, C. F. 1855. Abstract of a report to Lieut. Jas. M. Gillis, U.S.N., upon the fishes collected during the U.S.N. Astronomical Expedition to Chile. Proc. Acad. Nat. Sci. Philadelphia 7(11):197–199.

Graham, J. 1965. The North Otago Shelf fauna. VI. Chordata, subclass Cyclostomata. Trans. Royal Soc. New Zealand 6(6):67–68.

Günther, A. 1870. Catalogue of the Physostomi, containing the families Gymnotidae, Symbranchidae, Muraenidae, Pegasidae, and of the Lophobranchii, Plectognathi, Dipnoi, Ganoidei, Chondropterygii, Cyclostomata, and Leptocardii, in the British Museum. Catalogue of the fishes in the British Museum, London 8:1–549.

Heath, E., and J. Moreland. 1967. Marine fishes of New Zealand. A. H. and A. N Reed, Wellington, Auckland, and Sydney. 1–56.

Hutton, F. W. 1872. Fishes of New Zealand: Catalogue with diagnosis of the species. Colonial Museum and Geological Survey Dept., Wellington. 1–93.

———. 1904. Index Faunae Novae Seelandiae. Dulau and Co., London. 1–372.

Jensen, D. 1959. Albinism in the California hagfish, *Eptatretus stoutii*. Science 130(3378):798.

Jespersen, A. 1975. Fine structure of spermiogenesis in eastern Pacific species of hagfish (Myxinidae). Acta Zool., Stockholm 56:189–198.

Lockington, W.N. 1878. Walks around San Francisco. No. III—Lake Honda and Seal Rock. Am. Nat. 12:786–793.

Müller, J. 1834. Vergleichende Anatomie der Myxinoiden, der Cyclostomen mit durchbohrtem Gauman. Erster theil. Osteologie und Myologie. Abhandlungen der Königlichen Akademie der Wissenschaften zu Berlin, Jahre, 1834, 1836: 65–340.

Nani, A., and F. S. Gneri. 1951. Introducción al estudio de los mixinoideos Sudaméricanos. I. Un nuevo género de "Babosa de Mar," "*Notomyxine*" (Clase Myxini, Familia Myxinidae). Rev. Inst. Nac. Invest. Ciencias Nat. 1(4):183–224.

Plate, L. 1924. Allgemeine Zoologie und Abstammungslehre. Teil 2. Die Sinnesorgane der Tierre, Jena. 1–806.

Putnam, F. W. 1874. Notes on the genus *Bdellostoma*. Proc. Boston Soc. Nat. Hist. 16:156–160.

Regan, C. T. 1912. A synopsis of the myxinoids of the genus *Heptatretus* or *Bdellostoma*. Ann. Mag. Nat. Hist., ser. 8, 9: 534–536.

Revuelta, G. 1976. Informe de datos y observaciónes: Revisíon del genero *Eptatretus* en Chile (Agnatha: Myxinidae). Unpublished thesis. Departamento de Oceanología, Universidad de Chile, Valparaíso.

Richardson, L. R. 1953. *Neomyxine*, n.g. (Cyclostomata) based on *Myxine biniplicata* Richardson and Jowett, 1951, and further data on the species. Trans. Royal Soc. New Zealand 31(3):379–383.

Ross, D. M. 1963. The sense organs of *Myxine glutinosa* L. Chapter 2, pages 150–160 *in* The Biology of *Myxine*. A. Brodal and R. Fänge, editors. Universitetsforlaget Oslo. 588 pp.

Schneider, A. 1880. Über die Arten von *Bdellostoma*. Arch. Naturgesch. 46(1):115–116.

Scott, T. D., C. J. M. Glover, and R. V. Southcott. 1974. The marine and freshwater fishes of South Australia (2nd ed.). Gov't. Printer, S. Australia. 1–329.

Strahan, R. 1975. *Eptatretus longipinnis*, n.sp., a new hagfish (family Eptatretidae) from South Australia, with a key to the 5–7 gilled Eptatretidae. Australian Zool. 18(3):137–148.

Temminck, C. J., and H. Schlegel. 1842–1850. Pisces. Pages 1–345 *in* Fauna Japonica. Siebold, Fr. de. A. Arns et Socios, Lugdini. Plates and Suppl. Batavorium (=Leiden).

Waite, E. R. 1909. Scientific results of the New Zealand Government trawling expedition, 1907. Rec. Canterbury Mus. 1(2):1–26.

Whitley, G. P. 1968. A check-list of the fishes recorded from the New Zealand region. Australian Zool. 15:1–102.

CALIFORNIA ACADEMY OF SCIENCES
Golden Gate Park
San Francisco, California 94118

PROCEEDINGS
OF THE
CALIFORNIA ACADEMY OF SCIENCES

Vol. 43, No. 17, pp. 269-282, 5 figs. December 11, 1984

NEW AND NOTEWORTHY ADDITIONS TO THE MELASTOMATACEAE OF PANAMA

By
Frank Almeda
Department of Botany, California Academy of Sciences,
Golden Gate Park, San Francisco, California 94118

ABSTRACT: Descriptions, discussions, diagnostic illustrations, and distributional notes are provided for five new species of Melastomataceae (*Clidemia tetrapetala, C. trichosantha, Graffenrieda bella, Miconia arboricola,* and *Topobea calophylla*). Based on a study of the first known flowering collections, *Topobea elliptica* is transferred to *Blakea* and provided with an amplified description. Notes are also presented on the size and delimitation of these genera with special reference to Panama.

INTRODUCTION

The first and only floristic treatment of the Panamanian Melastomataceae was published some 25 years ago (Gleason 1958). The manuscript for that study was completed several years before it appeared in print. Gleason's study is a very useful account that unfortunately suffers from a lack of adequate field study and a paucity of local material for many of the species attributed to Panama. The many new collections of Melastomataceae generated by the heightened botanical exploration of Panama during recent years has underscored the need for an updated supplement. Such an undertaking is still premature in view of the many undescribed taxa represented by collections that are too incomplete to serve as a basis for formal descriptions.

In this interim report I propose new species in *Clidemia, Graffenrieda, Miconia,* and *Topobea,* present a new combination in *Blakea,* and provide brief notes on the size and delimitation of these genera in Panama.

Blakea P. Browne

Blakea and the closely related *Topobea* constitute the tribe Blakeae, which is characterized by baccate fruits, ovoid to pyramidal seeds, and axillary, 6-merous flowers that are individually subtended by two pairs of decussate bracts inserted at the base of the hypanthium. These genera exhibit many parallel variations in foliar characters, floral bract morphology, and calyx development. The traditional distinction between *Blakea* and *Topobea* is based on the androecial characters summarized in the following couplet:

Anthers short, oval, oblong, or elliptic, blunt or broadly rounded at the summit with two typically well-separated (often minute) apical pores .... *Blakea*
Anthers linear-oblong to lanceolate or subulate, the dorsally inclined apical pores approximate and often confluent at anthesis .... *Topobea*

In addition to the three species of *Blakea* described by Almeda (1974, 1980) and the generic transfer presented below, *Blakea tuberculata* Donn.-Smith of Costa Rica has recently been collected in western and central Panama (Chiriquí: *Folsom et al. 4838,* CAS; Coclé: *Knapp 5334,* CAS; Panamá: *Sytsma 1154,* CAS). These additions increase the number of described Panamanian species to thirteen.

Blakea elliptica (Gleason) Almeda, comb. nov.

Topobea elliptica Gleason, Phytologia 3:353. 1950.

Type.—**Panama.** Bocas del Toro, Robalo Trail, northern slopes of Cerro Horqueta, elevation 6000–7000 ft [1828–2133 m], 5–7 Aug. 1947, *Allen 5001* (holotype MO!; photo CAS!). The type collection of this species consists of a branch with four leaves and four more or less mature berries (one of which is detached). When Gleason described this species from incomplete material he was impressed by its sessile, clasping leaves, which are reminiscent of those of *Topobea brenesii* Standley, a rare Costa Rican endemic. Two recent flowering collections from near the type locality in western Panama are an exact vegetative match for the species that Gleason placed in *Topobea.* The uniform, bluntly ovoid anthers of these new collections are characteristic of *Blakea,* thus necessitating the generic transfer proposed herein. Because all available descriptions of this taxon are based on the fragmentary type collection, an amplified description is presented below to facilitate recognition of this little-known cloud forest epiphyte.

Epiphytic shrub reportedly 2–4 m tall. Cauline internodes glabrate, terete, becoming striate to furrowed or cracked in age. Distal branchlets and floral pedicels sparsely covered with a deciduous indument of slender, spreading, glandular trichomes and stoutly conic trichomes, the latter typically copious on distal nodes and vegetative buds. Mature leaves sessile, blades chartaceous to coriaceous, entire, somewhat revolute on drying, 5–11.5 cm long and 3–7.5 cm wide, elliptic-ovate to obovate, obtuse to rounded apically and auriculate to cordate-clasping basally, 3-nerved with an additional but less conspicuous submarginal pair, essentially glabrous throughout or with a sparse scattering of conic and glandular trichomes at the base of the blade below. Flowers 6-merous, solitary or paired in the axils of distal branches, pedicels 2.5–4.3 cm long. Floral bracts foliaceous, sparsely covered with a mixture of blunt conic and spreading glandular trichomes on the inner and outer surfaces; outer bracts 3–5-nerved, essentially free to the base, 12–14 mm long and 13–15 mm wide, broadly elliptic-ovate to suborbicular, obtuse to rounded or somewhat retuse apically; inner bracts (at anthesis) connate basally for about 4–5 mm to form a collar that tightly envelops the ovary, the free lobes ± semicircular, 7 mm long and 12–13 mm wide basally between sinuses. Hypanthia (at anthesis) glabrous, campanulate, 8–11 mm long to the torus. Calyx lobes triangular, ± entire, mostly recurved, 5–6 mm long and 5 mm wide basally, apically beset with a mixture of spreading glandular and sessile globular trichomes. Petals thin and ± translucent on drying, mostly glabrous with a moderate but somewhat concentrated abaxial patch of brown verrucose excrescences, reportedly white with pink blotches, elliptic-ovate to obovate and rounded apically, entire to irregularly ciliolate, 20–23 mm long and 14–18 mm wide. Stamens isomorphic, free and declined to one side of the flower, filaments glabrous, 4.5–6 mm long and 1.5 mm wide; anthers yellow, ovoid, laterally compressed, biporose and rounded apically, 5 mm long and 1.5–2 mm wide, connective thickened dorsally and dilated basally about 0.5 mm above point of filament insertion into a short deflexed truncate appendage about 0.5–1 mm long. Style straight, glabrous, conspicuously exserted, 11–14 mm long; stigma truncate. Berry 13–15 mm long to the torus and 14–15 mm in diameter, glabrous and subglobose. Seeds beige, cuneate to clavate, or narrowly pyriform, mostly 1 mm long.

Additional Specimens Examined.—**Panama.** Chiriquí: Bocas del Toro border along Continental Divide NE of Cerro Pate Macho, above Palo Alto in windswept elfin forest. 8°47′N, 82°21′W, 2200 m, 15 Mar. 1982, *Knapp et al. 4233* (MO); end of road past Palo Alto NE of Boquete in forest along ridge; elev. 6200–6800 ft [1890–2073 m], 8 Feb. 1979, *Hammel 6048* (MO).

Distribution.—Western Panama. Known only from the northern slopes of Cerro Horqueta and the region NE of Cerro Pate Macho above Palo Alto at elevations of about 1800–2100 m.

This species is apparently rare and localized, as evidenced by the few specimens collected over the past three decades. It is among the most distinctive of the Central American species by virtue of its sessile, clasping leaves, and deciduous indument of spreading glandular and blunt conic trichomes on distal branchlets, pedicels, floral bracts, and vegetative buds. The petals of this species are remarkably thin and translucent when dry and have a peculiar abaxial cluster of brown verrucose excrescences. Additional collections and field observations will be needed to determine whether this petal feature is a consistent diagnostic character or an artifact of pressing and drying.

Clidemia D. Don

Clidemia is one of approximately 30 genera constituting the tribe Miconieae. The generic classification of this complex tribe is difficult because it contains species groups that intergrade across generic lines that have been defined on the basis of one or few characters. The evolutionary development of characters used in generic delimitation of the Miconieae is unclear, and some of the genera as currently delimited are probably polyphyletic. Until a reassessment of generic limits can be accomplished, *Clidemia* is defined in the traditional sense to include those berry-fruited species with axillary inflorescences, more or less obtuse petals, linear to subulate anthers, wingless hypanthia, and flowers that are not individually subtended by two pairs of decussate bracts.

Of the approximately 165 species of *Clidemia* recorded for tropical America, 30 are now known from Panama. This count includes the two new taxa proposed below.

Clidemia tetrapetala Almeda, sp. nov.

(Figure 1)

Frutex 1–2 m. Ramuli teretes sicut petioli inflorescentia foliorum subtus venae primariae pilis stipitato-stellatis densiuscule ornati et pilis stellatis sessilibus modice vel dense induti. Petioli 10–27 mm longi; lamina 5–9.5 × 2.1–3.9 cm ovato-elliptica apice gradatim acuminato basi rotundata vel subcordata, chartacea et integra, 5–7-plinervata. Inflorescentiae pauciflorae in foliorum superiorum axillis oppositis, axe plerumque 1.5–2.5 cm longo; flores 4-meri plerumque subsessiles (pedicellis supra articulationem 0.5 mm longis), bracteolis 1–1.5 mm longis linearibus. Hypanthium (ad torum) 1.5 mm longum dense stellato-puberulum et pilis laevibus glanduliferis patentibus 0.5–1 mm longis modice intermixtus; lobis 1 mm longis triangularibus, dentibus exterioribus subulatis 3 mm eminentibus. Petala 5–6 × 1.5–2 mm oblonga glabra (apice late obtuso). Stamina isomorphica glabra; filamenta 2 mm longa; antherarum thecae 1.5 × 0.5 mm oblongae, poro dorsaliter inclinato; connectivum nec prolongatum nec appendiculatum. Stylus 5.5 mm glaber; stigma truncatum; semina 0.5–1 mm pyriformia.

Shrubs 1–2 m tall. Older cauline internodes glabrate and terete. Distal branchlets, vegetative buds, juvenile leaves, and inflorescences copiously covered with sessile, and stipitate-stellate trichomes, the distal cauline internodes sparingly intermixed with spreading glandular hairs. Leaves of a pair slightly unequal in size, otherwise identical in shape and vestiture. Leaf blades flat to somewhat bullate above when dry, chartaceous, entire, 5–9.5 cm long and 2.1–3.9 cm wide, ovate-elliptic, acuminate apically and rounded to subcordate basally, 5–7-plinerved with a network of secondary and tertiary nerves below, sparsely pubescent above with a mixture of appressed simple trichomes and spreading stalked stellate trichomes, lower leaf surfaces copiously stellate pubescent on the elevated primary nerves but with a moderate to sparse mixture of sessile and stalked stellate trichomes on and between the secondaries; petioles 10–27 mm long and 1–1.5 mm broad. Inflorescence axillary, typically a lax few-flowered modified dichasium 1.5–2.5 cm long; bracteoles sessile, 1–1.5 mm long and mostly less than 0.5 mm wide, linear-lanceolate to linear-oblong, mucronate apically, glabrous above and sparsely stellate pubescent below. Pedicels terete, mostly less than 0.5 mm long and disarticulating at the tribracteolate node closely subtending each flower. Hypanthia (at anthesis) narrowly campanulate, 1.5 mm long to the torus, copiously covered with a mixture of stellate and spreading glandular trichomes. Calyx lobes (on fruiting hypanthia) widely spreading, persistent, triangular, entire, 1 mm long and 1 mm wide basally; exterior calyx teeth subulate, mostly 3 mm long, stellate pubescent and completely obscuring external surface of the calyx lobes. Petals 4, glabrous, reportedly white, linear-oblong, broadly obtuse apically, entire, 5–6 mm long, 1.5–2 mm wide. Stamens 8, isomorphic, erect at anthesis; filaments glabrous, ligulate but abruptly constricted distally, 2 mm long; anthers 1.5 mm long and 0.5 mm wide, yellow when dry, linear-oblong, truncate to rounded distally with a circular dorsally inclined apical pore; connective simple, somewhat thickened dorsally but not dilated or prolonged below the thecae. Ovary totally inferior, 4-celled, essentially glabrous at the summit but sparsely setose surrounding the stylar scar. Style 5.5 mm long; stigma truncate. Ber-

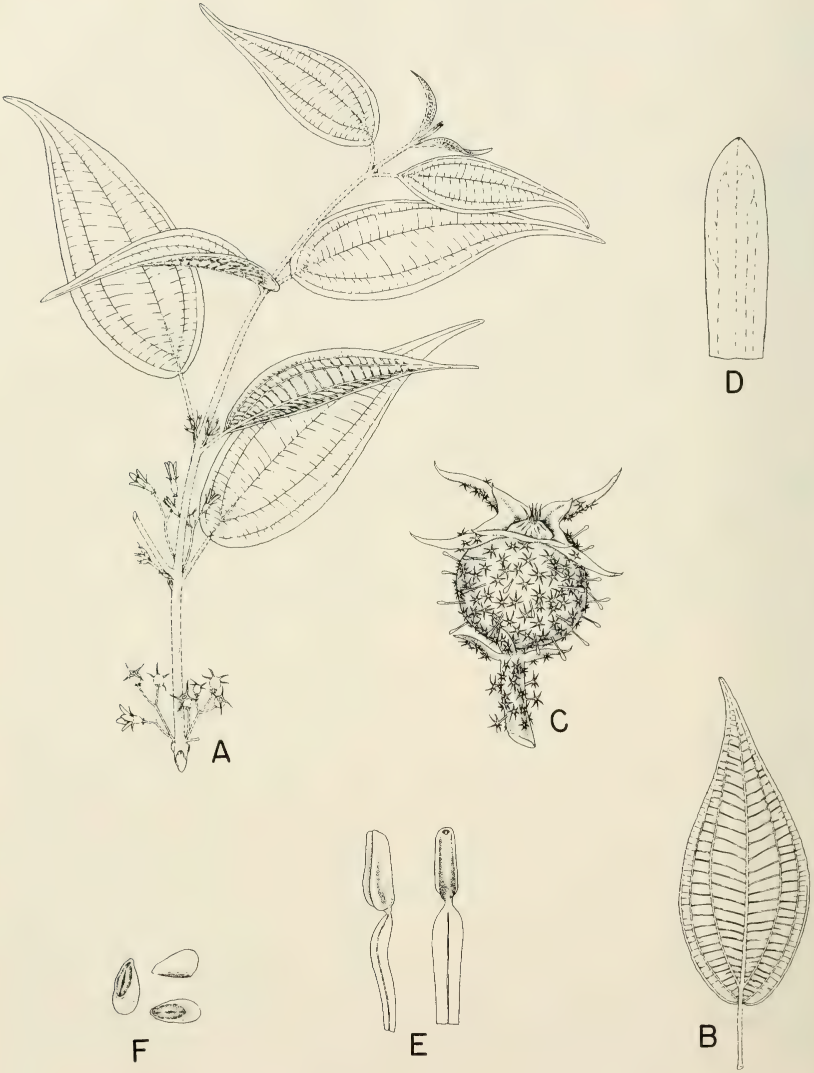


FIGURE 1. *Clidemia tetrapetala* Almeda. *A,* habit, × ca. ¾; *B,* representative leaf (lower surface), × ca. ¾; *C,* mature berry, × ca. 4; *D,* petal, × ca. 6; *E,* stamens, ¾ lateral view (left) and dorsal view (right), ×9; *F,* seeds, × ca. 7. (*A* from *Folsom 4871*; *B–F* from *Folsom 6106.*)

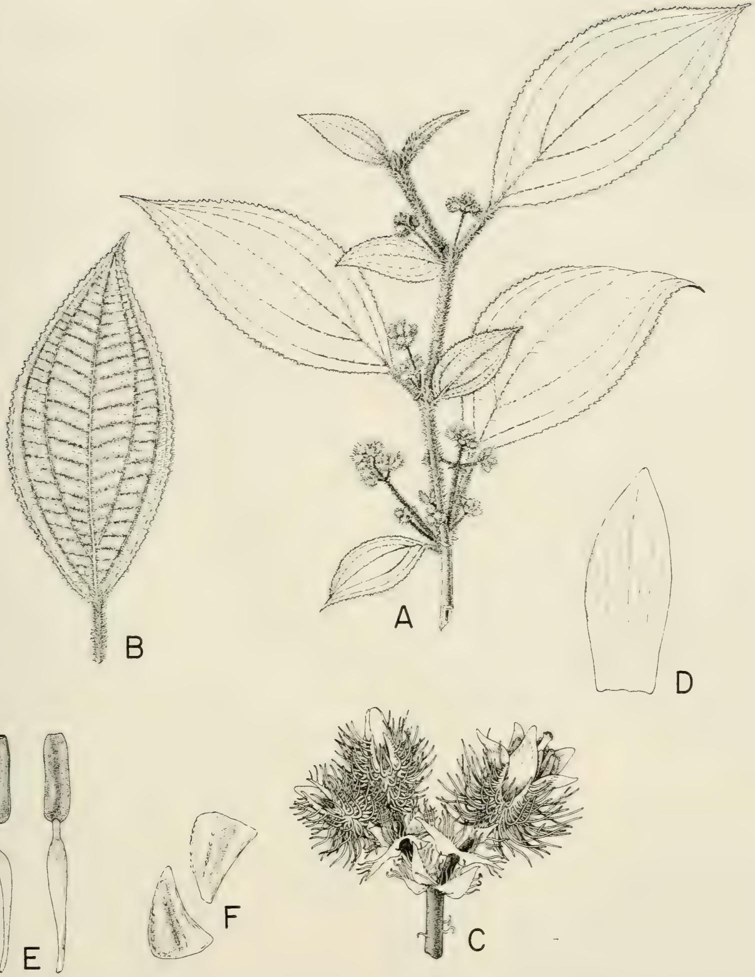


Figure 2. *Clidemia trichosantha* Almeda. *A,* habit, × ca. ¾; *B,* representative leaf (lower surface), × ca. ¾; *C,* representative flower, buds, bracts and bracteoles, × ca. 4; *D,* petal, ×7; *E,* stamens, lateral view (left) and ventral view (right), ×9; *F,* seeds, × ca. 14. (*A–E* from the holotype; *F* from *Hammel 965.*)

ry reportedly opaque green but turning translucent red at maturity, globose, 5–6 mm long to the torus, 5–6 mm in diameter. Seeds narrowly pyriform, brown, smooth, vernicose, and mostly 0.5–1.0 mm long.

Type.—**Panama.** Bocas del Toro/Chiriquí Border: Cerro Colorado, along intersection of Bocas Road with main ridge road, 11.8 km from Chami along path headed into Bocas del Toro, elevation 1400–1700 m, 24 Oct. 1977, *Folsom 6106* (holotype: CAS!; isotype: MO).

Additional Specimens Examined.—**Panama.** Bocas del

Toro/Chiriquí Border: Cerro Colorado, 11.2 km along ridge road from main road to Escopeta, 1700 m, 16 Aug. 1977, *Folsom 4871* (CAS, MO). Chiriquí: Cerro Colorado on Continental Divide, 1400 m, 25 Jul. 1979, *Antonio 1416* (CAS).

Distribution.—Known only from Cerro Colorado in western Panama at elevations of 1400–1700 m. All cited specimens are in flower; only the type has mature fruits.

Among Panamanian species of *Clidemia* with 4-merous flowers, *C. tetrapetala* is distinguished by its lance-ovate, 5–7-plinerved leaves, linear-oblong petals, and mixture of spreading glandular and stellate hypanthial trichomes. The inflorescence of this species is also notable for its elongate distal peduncles that can readily be mistaken for floral pedicels. The actual pedicels in this species are very short and disarticulate at tribracteolate nodes that closely subtend the flowers.

On the basis of its 4-merous flowers, well developed calyx teeth, and equal to subequal principal leaves in each pair, this species is provisionally placed in section *Sagraea* as defined by Cogniaux (1891). Among species of this section, *C. tetrapetala* bears a superficial resemblance to *C. saltuensis* Wurdack of Venezuela which is reportedly known only from the type (Wurdack 1973). The latter species differs most conspicuously in having ovate-elliptic, basally obtuse leaves, stellate-pinoid hypanthial trichomes, shorter (0.7 mm), erect calyx teeth, narrowly oblong anther thecae, and abaxially mucronate petals.

Clidemia trichosantha Almeda, sp. nov.

(Figure 2)

Frutex 1–2.5 m. Ramuli teretes primum sicut petioli laminae subtus inflorescentia hypanthiaque dense setosi pilis 1–3(–4) mm longis demum glabrati. Folia in quoque pari in dimensionibus disparilia (2:1); petioli 0.2–2.2 cm longi; lamina 3–14.3 × 1.5–5.8 cm elliptica apice acuminata basi interdum obtuse vel rotundata vel paulo asymmetrica, chartacea et denticulata, 5–7-plinervata, supra sparse vel modice strigosa. Inflorescentiae ca. 1.5–3 cm longae in foliorum superiorum axillis; flores 5-meri, pedicellis 1–1.5 mm longis, bracteolis 1.5–3 mm longis lanceolatis amplexicaulibus. Hypanthium (ad torum) 2–2.5 mm longum; lobis interioribus late deltoideis, dentibus exterioribus setosis 1–2 mm eminentibus. Petala glabra 4–4.5 × 1.5 mm oblongo-lanceata. Stamina isomorphica glabra; filamenta 2.5 mm longa; antherarum thecae 1.5 × 0.75 mm oblongae, connectivum nec prolongatum nec appendiculatum. Stylus 4.5 mm glaber; stigma punctiforme; semina 0.5 mm cuneata.

Slender shrubs 1–2.5 m tall. Internodes terete, glabrate at maturity, but vegetative buds, young leaves, and distal branchlets moderately to densely covered with smooth, eglandular, spreading trichomes mostly 1–3(–4) mm long. Leaves of a pair usually unequal in size, otherwise identical in shape and vestiture. Leaf blades chartaceous, denticulate, elliptic, acuminate apically, acute varying to obtuse, rounded or conspicuously oblique basally, 5–7-plinerved with a network of secondary and tertiary nerves, the innermost pair of primary nerves diverging from the median nerve (0.6–)1.0–1.6 cm above the petiole/laminar junction, moderately to sparsely strigose or hirtellous above and moderately to copiously hirsute below. Larger leaf at each node 5.8–14.3 cm long and 2.5–5.8 cm wide with petioles mostly 0.5–2.2 cm long. Smaller leaf 3–9.5 cm long and 1.5–4.1 cm wide with petioles mostly 2–4 mm long. Inflorescence an axillary, multiflowered, modified dichasium with flowers borne in pedunculate terminal glomerules; rachis terete, 1.5–3 cm long, moderately to sparsely hirsute; bracts and bracteoles sessile, paired and often fused basally into an amplexicaul nodal collar, 1.5–3 mm long and 0.5–1.5 mm wide, lanceolate to naviculiform, glabrous but irregularly fringed with spreading setose trichomes. Pedicels hirsute, 1–1.5 mm long. Hypanthia (at anthesis) ± ovoid, 2–2.5 mm long to the torus, copiously covered with smooth spreading trichomes. Calyx lobes (on fruiting hypanthia) inconspicuous, erect, persistent, broadly deltoid, entire, 1 mm long and 1.5 mm wide basally between sinuses; exterior calyx teeth setiform, 1–2 mm long, sparsely hirsute. Petals 5, glabrous, reportedly translucent white, elliptic-lanceolate, acute apically, entire, 4–4.5 mm long, 1.5 mm wide. Stamens 10, isomorphic, apparently erect at anthesis; filaments glabrous, ± linear-oblong but constricted distally, 2.5 mm long; anthers 1.5 mm long and 0.75 mm wide, linear-oblong, truncate distally; connective simple, not dilated or prolonged below the thecae. Ovary ca. ⅔ inferior, 5-celled. Style 4.5 mm long; stigma punctiform. Berry purple at maturity, globose, 4–6 mm long and 4–5.5 mm in diameter. Seeds cuneate, ± smooth with verruculose angles and a prominent ± translucent lateral raphe, 0.5 mm long.

Type.—**Panama.** Coclé: sawmill above El Cope, in forest along stream east of sawmill on the Atlantic drainage, elevation 2300 ft (701 m), 27 July 1978, *Hammel 4133* (holotype, CAS!; isotype, MO).

Additional Specimens Examined.—**Panama.** Coclé: above El Petroso sawmill at Continental Divide, N of El Cope, 13 May 1981, *Sytsma & Andersson 4624* (CAS); area surrounding Rivera sawmill, Alto Calvario, 7 km N of El Cope at Continental Divide, 25 Nov. 1977, *Folsom & Collins 6473* (CAS); near Continental Divide along lumbering road 8.4 km above El Cope, 19 Jan. 1978, *Hammel 965* (CAS); 7 km N of El Cope around Rivera sawmill, 21 Dec. 1977, *Folsom et al. 7093* (CAS); El Cope on Pacific side about ½ hour walk from the sawmill, 16 Oct. 1979, *Antonio 2116* (CAS). Panamá: forested slope along El Llano-Cartí road, 12 km from Panamerican Highway, 10 Sept. 1976, *D'Arcy 10617* (CAS). San Blas: El Llano-Cartí road, 12 mi from Panamerican Highway, 10 May 1981, *Sytsma & Andersson 4493* (CAS). Veraguas: Cerro Tute, 30 Nov. 1979, *Antonio 2928* (CAS).

Distribution.—Presently known from wet forests and stream margins at elevations from 700–1300 meters in central Panama. Flowering specimens have been gathered in January, May, July, and September.

The epithet for this species draws attention to its most remarkable feature—the dense covering of spreading, lustrous trichomes on the flowers and peduncles of the inflorescence. The trichomes, which are often basally flattened when dry, are so copious that it is difficult to examine the structure and posture of bracteoles and other floral parts without a dissection of hydrated material. Other characters that readily separate *C. trichosantha* from its congeners include the modified dichasial inflorescence of pedunculate terminal glomerules, the distally constricted filaments, the cuneate seeds with verruculose angles, and the sessile, paired bracts and bracteoles that are often fused into amplexicaul collars.

A fruiting collection from Cerro Habú, San Blas (*Sytsma et al. 2673,* CAS) appears to be a variant or closely related, undescribed taxon but its essentially glabrous leaves, glabrate berries, and short (0.5 mm) calyx teeth fall outside the range of variation here attributed to *C. trichosantha.*

The 5-merous, short-pedicellate flowers and anisophylly of the new species dictate placement into Cogniaux's section *Calophysoides. Clidemia trichosantha* is unlike any of the species currently placed in that section. I am, therefore, reluctant to include it with an assemblage that may prove to be artificial and can only suggest that no close relatives are apparent. The combination of smooth, spreading trichomes and elongate calyx teeth is vaguely suggestive of the copiously hirsute variants of *C. petiolaris* (Schlecht. & Cham.) Schlecht. ex Triana which, otherwise, differ markedly in their lax, divaricately branched inflorescence, subulate, apically notched anthers, and pyriform, papillate seeds.

Graffenrieda DC.

Graffenrieda, a genus of about 40 species, is one of five closely related merianioid genera occurring in Panama. Gleason (1958) reported one species (under the generic synonym *Calyptrella* Naud.) in his treatment of Panamanian Melastomataceae. The escalated botanical exploration of Panama in the past two decades has increased this total to about eight. In addition to the species proposed below, *G. galeottii* (Naud.) L. Wms., *G. gracilis* (Triana) L. Wms., and *G. micrantha* (Gleason) L. Wms. are known from Panama. Collections of about four additional entities probably represent undescribed taxa or range extensions of South American species. These remain unnamed because of incomplete material.

In the field, the superficial resemblance of Panamanian species of *Graffenrieda* to *Miconia* is striking. *Graffenrieda* is readily distinguished by the combination of capsular fruits, calyptrate calyx, dorsally spurred, arcuate anthers, and linear, pyramidate seeds.

Graffenrieda bella Almeda, sp. nov.

(Figure 3)

Arbor parva 5 m. Ramuli glabri et teretes. Petioli 0.5–1.6 cm; lamina 4.7–8 × 2.1–4 cm elliptica apice breviter subabrupteque acuminato basi acuta vel cuneata vel biauriculata, supra glabra vel sparse lepidota, subtus modice lepidota, 3(–5)-nervata, coriacea et integra. Panicula 5–7 cm longa multiflora; flores 5(–6)-meri subsessiles (vel pedicellis 0.5–1 mm longis) ad ramulorum apices glomerati (floribus ca. 3–6 in quoque glomerulo), bracteolis 0.5–1 mm longis subulato-setosis evidenter mox caducis. Hypanthium (ad torum) 3 mm longum; calyx in alabastris maturis clausus 3–3.5 mm longus ad anthesim irregulariter supra torum dehiscens. Petala 7–9 × 4–6 mm elliptico-ovata glabra. Stamina isomorphica glabra; filamenta 2.5–3 mm longa; an-

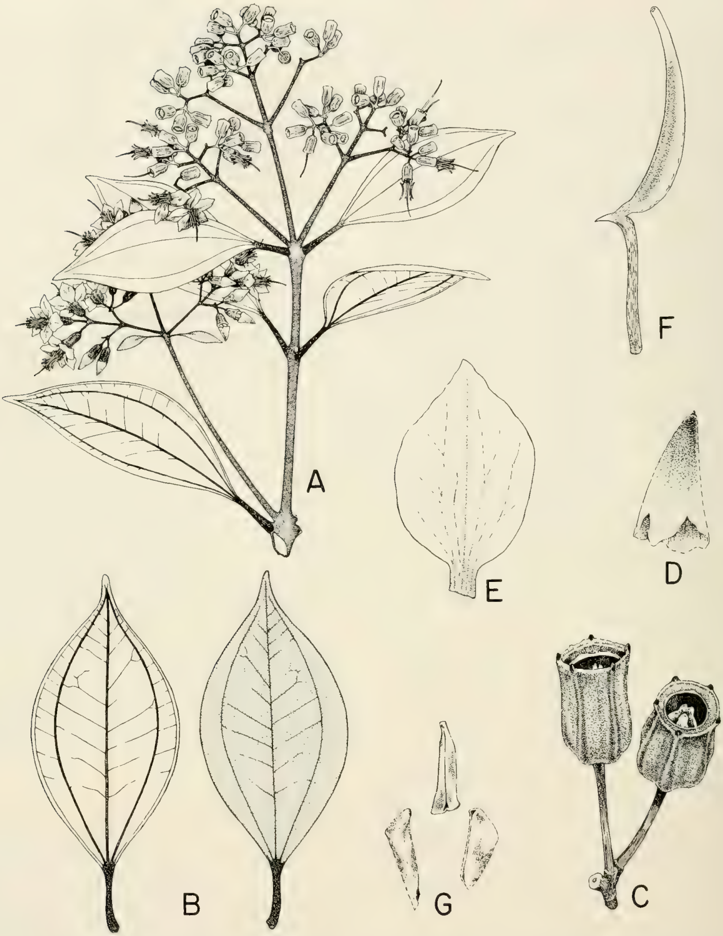


FIGURE 3. *Graffenrieda bella* Almeda. *A*, habit, × ¾; *B*, representative leaves, lower surface (left) and upper surface (right), × ca. ¾; *C*, mature hypanthia, × ca. 4; *D*, calyptrate calyx, × ca. 8; *E*, petal, × ca. 5; *F*, stamen (lateral view), × ca. 10; *G*, seeds, × ca. 14. (*A–B, D–F* from the holotype; *C* & *G* from *Mori et al. 7581*.)

therarum thecae 3–4.5 × 0.5 mm oblongo-subulatae; connectivum vix (0.25 mm) prolongatum, dente dorsali 0.5 mm longo acuto. Stylus 7.5–9.5 mm glaber; stigma punctiforme; semina numerosa 1 mm longa, recta paulo angulata.

Trees to 5 m tall. Cauline internodes glabrous and terete; the nodes on defoliated branchlets somewhat swollen with age. Leaf blades coriaceous, entire, 4.7–8 cm long and 2.1–4 cm wide, broadly elliptic, apically acuminate basally acute to cuneate or biauriculate with well-developed reflexed marginal lobes ca. 2 mm above the petiole-laminar junction, glabrous to sparsely lepidote above and moderately lepidote below at maturity, uniformly 3-nerved (excluding the inconspicuous submarginal pair); petioles 0.5–1.6 cm long and 1–1.5 mm broad. Inflorescence a multiflowered panicle mostly 5–7 cm long (including the peduncle), the uppermost units commonly glomerulate; bracteoles sessile, narrowly subulate to acicular, 0.5–1 mm long, apparently early deciduous and mostly absent at anthesis. Pedicels 0.5–1 mm long. Hypanthia (at anthesis) narrowly campanulate to subcylindric, 3 mm long to the torus. Calyx acute, apiculate and closed in bud, 3–3.5 mm long rupturing near the torus and falling away as a unit at anthesis. Calyx teeth (on mature hypanthia) evident as blunt tuberculiform projections mostly 0.25–0.5 mm long. Petals mostly 5, but varying to 6 in some flowers, glabrous, white, elliptic to ovate, entire, acute apically, cuneate to clawed basally, 7–9 mm long and 4–6 mm wide. Stamens mostly 10 but sometimes 12, isomorphic; filaments glabrous, ligulate, 2.5–3 mm long and 0.5 mm wide; anthers 3–4.5 mm long and 0.5 mm wide, yellow, subulate, the apical pore ± truncate; connective prolonged ca. 0.25 mm below the thecae and modified dorsally (at filament insertion) into an acute spur mostly 0.5 mm long. Ovary ¼ inferior, 3-celled, ovoid, glabrate but copiously lepidote distally. Style straight to somewhat curved, glabrous, 7.5–9.5 mm long; stigma punctiform. Hypanthia (at maturity) prominently costate, 5 mm long and 3 mm wide. Seeds linear-pyramidate, brown, mostly 1 mm long.

TYPE.—**Panama.** Chiriquí: along road between Gualaca and the Fortuna Dam site at 10.1 m; NW of Los Planes de Hornito, elev. 1300 m, 8 Apr. 1980, *Antonio 4078* (holotype: CAS!; isotype: MO).

ADDITIONAL SPECIMENS EXAMINED.—**Panama.** Chiriquí: Cerro Hornitos, 40 km NW of Gualaca in cloud forest dominated by *Quercus* spp., *Podocarpus*, and *Drimys*, 26 Jul. 1975, *Mori & Bolten 7486* (CAS). Veraguas: Cerro Tute, ca. 10 km NW of Santa Fe on ridgetop in cloud forest, 19 May 1975, *Mori 6255* (CAS), 3 Aug. 1975, *Mori et al. 7581* (CAS).

DISTRIBUTION.—Known only from cloud forests on Cerro Tute in Veraguas province and Cerro Hornitos and vicinity in Chiriquí province at elevations from 1000–2238 m. Flowering specimens have been collected in April, May, and July. This species is reportedly (fide *Mori 6255*) one of the most common trees in an area about 10 km northwest of Santa Fe on Cerro Tute.

Graffenrieda bella is most closely related to *G. micrantha* (Gleason) L. Wms. which differs in its longer leaf blades (13–20 cm) with five prominently elevated abaxial nerves, longer petioles (2.5–5 mm), shorter (2–3 mm) narrowly lanceolate petals, and smaller fruiting hypanthia (2–2.5 mm). My circumscription of *G. bella* includes two morphological entities representing geographically distinct populations. The collections from Chiriquí in western Panama have 5-merous flowers and foliar margins with bilaterally developed reflexed auricles about 2 mm above the petiole/laminar junction. Collections from Veraguas in central Panama have 5(–6)-merous flowers and lack the conspicuous foliar auricles. Except for these differences, the few available specimens from each area are identical and exhibit parallel ranges in foliar size, hypanthial and staminal length, and petal width. More collections, especially from intervening areas, are needed to determine whether this bimodal variation shows a consistent geographical correlation.

Miconia Ruiz & Pavon

As presently circumscribed, *Miconia* with approximately 1000 species is the largest genus in the family and one of the largest among flowering plants. It is generally characterized by its terminal inflorescences and apically rounded, obtuse, or retuse petals. *Miconia* occupies a central position in the complex of genera comprising the taxonomically difficult tribe Miconieae. Through its broad neotropical range *Miconia* displays great diversity in habit, foliar characters, inflorescence organization, trichome and androecial morphology, and seed structure. Success in identifying species, however, inevitably requires examination of anther structure because the current sectional classification relies heavily on this character. *Miconia* is greatly in need of monographic study to evaluate character variation, assess the status of satellite groups, and redefine sectional limits based on character correlations. Some 60 species of *Miconia* occur in Panama. These represent all twelve currently recognized sections. In addition to the species proposed below, several new taxa await formal description pending collection of complete material.

Miconia arboricola Almeda, sp. nov.
(Figure 4)

Caulis scandens primum sicut foliorum subtus venae primariae inflorescentia hypanthiaque dense vel modice pilis stipitato-stellatis 0.5–1 mm

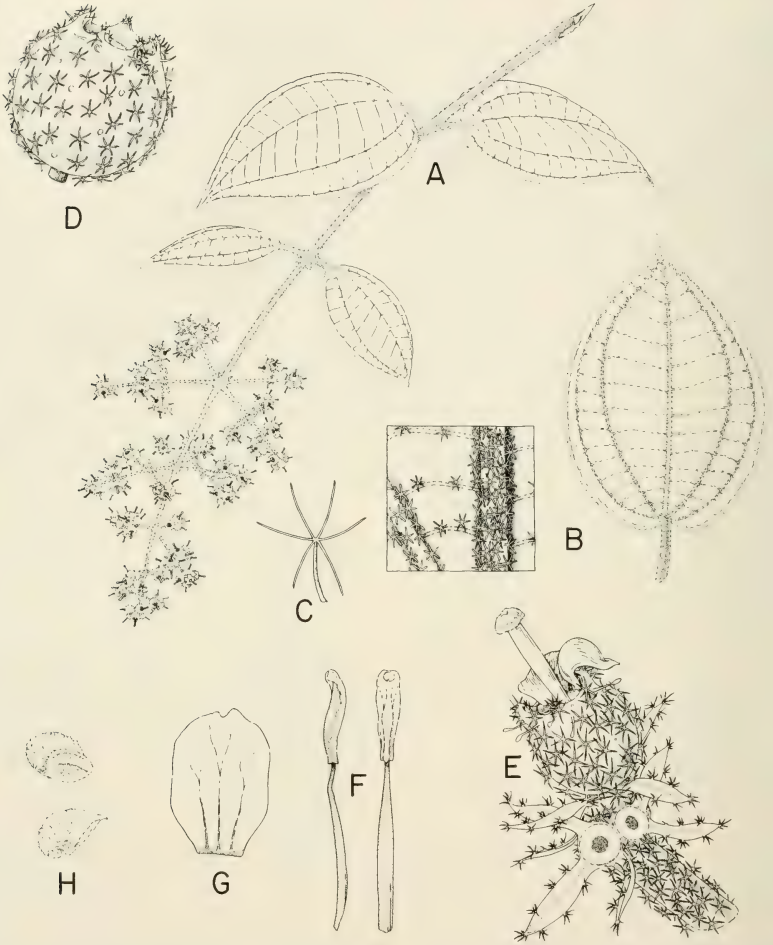


FIGURE 4. *Miconia arboricola* Almeda. *A,* habit, × ca. ⅓; *B,* representative leaf (lower surface) with enlargement (left), × ca. ½; *C,* stipitate-stellate trichome, × ca. 17; *D,* mature berry, × ca. 5; *E,* representative flower showing young hypanthium, two petals, style, bracteoles, and pedicellar scars, × ca. 7; *F,* stamens, lateral view (left) and dorsal view (right), × ca. 9; *G,* petal, × ca. 7; *H,* seeds, × ca. 20. (*A–C* from the holotype; *D, F, G* from *Knapp 5735*; *E* & *H* from *Croat 49151.*)

latis indutus. Petioli 8–23 mm longi; lamina 5.5–11.4 × 3.5–7.1 cm late ovata vel cordata, apice breviter acuminato basi subcordata vel cordata, 5–7-nervata, firme coriacea et integra. Panicula 11.5–25 cm longa multiflora; flores 5-meri subsessiles in glomerulis interruptis vel ad ramulorum apices aggregati, bracteolis 1–2.5 × 0.25–0.5 mm anguste oblongis persistentibus. Hypanthium (ad torum) 1.5–2 mm longum; calycis tubus non eminentibus, lobis interioribus 0.5 mm longis deltoideis, dentibus exterioribus crassis lobos interiores aequantibus. Petala 2–3 × 1.5–2 mm glabra obovata apice retuso. Stamina isomorphica glabra; filamenta 2.5 mm longa;

antherarum thecae 1.5 × 0.5 mm oblongo-cuneatae; connectivum nec prolongatum nec appendiculatum. Stylus 4 mm glaber; stigma capitatum; semina 0.5 mm galeiformia.

Pendent woody vines or hemiepiphytes adhering to bark of host tree by adventitious roots. Older cauline internodes terete and ± glabrate. Distal branchlets, petioles, vegetative buds, juvenile leaves, and inflorescences moderately to copiously covered with ferrugineous stipitate-stellate trichomes. Leaves of a pair essentially equal in size; blades coriaceous at maturity, entire, 5.5–11.4 cm long and 3.5–7.1 cm wide, broadly ovate to cordate, short acuminate apically and subcordate to cordate basally, 5–7-nerved with a prominulous reticulate network of secondaries and tertiaries below, mostly glabrate and vernicose above at maturity or with stipitate-stellate trichomes persisting to varying degrees in the furrows created by the impressed primary nerves, sparsely to moderately stipitate-stellate below; petioles 8–23 mm long and 2–2.5 mm wide. Inflorescence basically paniculiform with ultimate branchlets terminating in multiflowered congested glomerules; bracts of the rachis nodes paired, linear-oblong, 2.5–5(–10) mm long, 1–1.5 mm wide, glabrous adaxially and stipitate-stellate to glabrate abaxially; bracteoles 3–5 per pedicel, sessile, linear-oblong, acute to obtuse or rounded apically, 1–2.5 mm long, 0.25–0.5 mm wide, entire, glabrous adaxially and stipitate-stellate abaxially. Pedicels 0.5 mm long but typically inconspicuous and concealed by congested glomerules. Hypanthia (at anthesis) subcylindric to narrowly campanulate, 1.5–2 mm long to the torus, moderately to copiously beset with short stalked-stellate trichomes and occasionally with a sparse scattering of spreading glandular trichomes on or near basal portions of the calyx teeth; adaxial rim of the torus minutely glandular-puberulent. Calyx lobes (on young fruiting hypanthia), glabrous, hyaline, and erect, deltoid, 0.5 mm long and 1 mm wide basally; calyx teeth bluntly subulate, copiously stellate, adnate to and ± equaling subtending calyx lobes. Petals 5, glabrous, white, obovate to oblong-obovate, strongly reflexed, irregularly retuse apically, 2–3 mm long and 1.5–2 mm wide. Stamens 10, isomorphic, filaments straight to somewhat incurved distally, glabrous, subulate, 2.5 mm long; anthers 1.5 mm long and 0.5 mm wide distally, linear-oblong to narrowly cuneate, typically recurved distally; connective thickened dorsally but not dilated or prolonged below the point of filament insertion. Ovary (young fruiting hypanthia) ca. ⅓ to ¼ inferior, 3-celled, coarsely papillate to farinaceous, caducously glandular-puberulent along the bluntly fluted stylar collar that becomes depressed and inconspicuous on mature fruits. Style straight, glabrous, 4 mm long; stigma broadly capitate. Berry reportedly blue at maturity, globose, 3–4 mm long and 3–4 mm in diameter. Seeds galeiform, white, papillate to costate-papillate, 0.5 mm long.

TYPE.—**Panama.** Chiriquí: slope NW of confluence of Río Hornito and Río Chiriquí, ca. 8°44′N, 80°07′W, elev. 1050–1100 m, 11 Nov. 1980, *Stevens 18266* (holotype: CAS!; isotype: MO).

ADDITIONAL SPECIMENS EXAMINED.—**Costa Rica.** Cartago: Pejibaye, 30 May 1924, *Lankester 877* (US). Limon: Cerro Urén, Cordillera Talamanca, 1 Sept. 1898, *Pittier 12683* (US). **Panama.** Coclé: hills N of El Valle, E slope and ridges leading to Cerro Gaital, 8°40′N, 80°07′W, 27 June 1982, *Knapp 5735* (MO); Alto Calvario, above sawmill on Continental Divide, 5.2 mi above El Cope, 6 Dec. 1979, *Croat 49151* (CAS).

DISTRIBUTION.—This little-collected cloud forest species ranges from the Caribbean slopes of the Cordillera Talamanca in south-central Costa Rica south and east to the hills surrounding El Valle de Anton in central Panama at elevations from 300–1100 m. Flowering specimens have been collected in June, September, and November.

Labels on collections of this species describe it as a pendent woody vine. The notes on *Croat 49151* describe it as a hemiepiphyte with the stem rooted in the ground but closely attached to a tree trunk. It seems likely that plants of this species are typically hemiepiphytes that ultimately become scandent vines requiring the support of host trees. The specific epithet refers to this discordant habit among species of *Miconia.*

Miconia arboricola is quite unlike all other species of *Miconia* from Central America. In addition to the unusual habit, it is distinctive in its coriaceous leaves, stipitate-stellate pubescence, paniculiform inflorescence, congested, polybracteolate flowers, and sculptured, galeiform seeds. As pointed out on the label of *Pittier 12683,* in Cogniaux's monograph, this species comes closest to *M. mollicula* Triana and *M. cordata* Triana in section *Miconia.* In foliar shape, internodal pubescence, and inflorescence structure, *M. ar-*

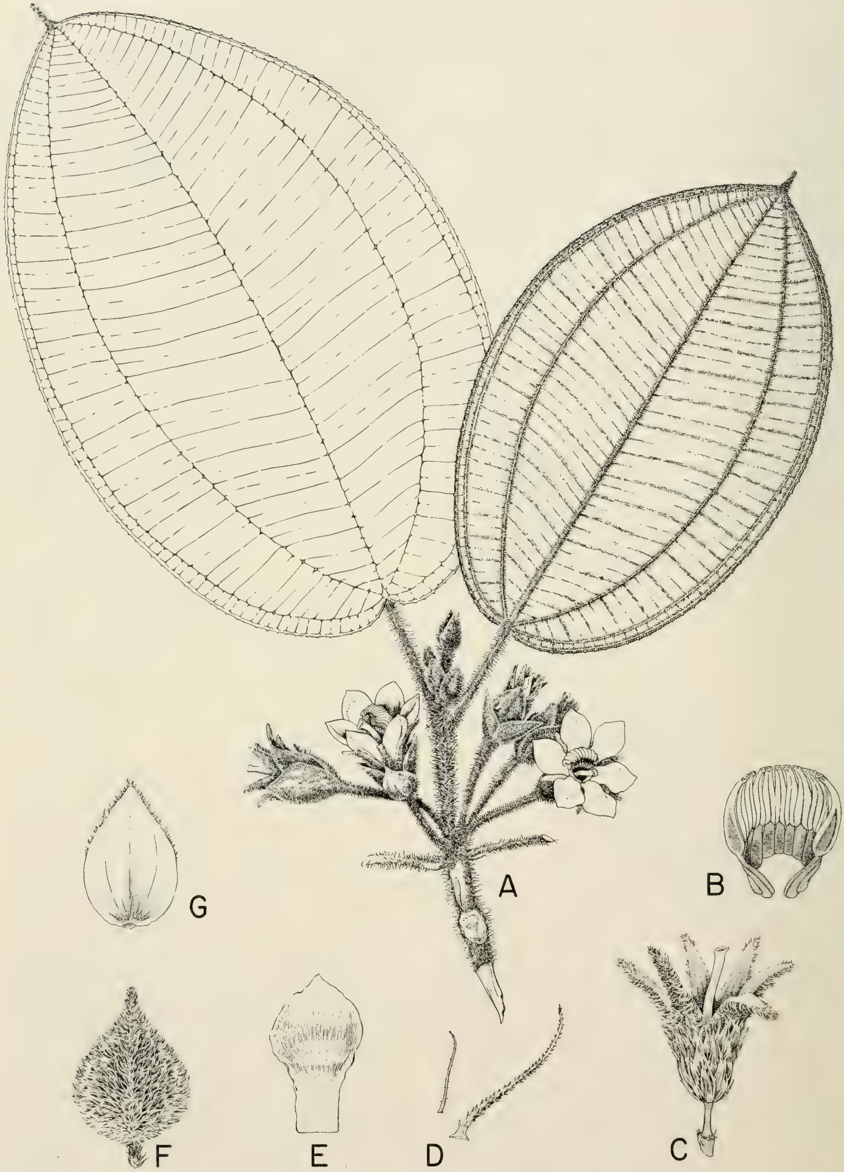


FIGURE 5. *Topobea calophylla* Almeda. *A,* habit, ×½; *B,* stamens, ventral view, ×1; *C,* hypanthium with floral bracts removed, × ca. 1½; *D,* cauline trichomes, × ca. 4; *E,* petal, × ca. 1¼; *F,* outer floral bract (outer surface), × ca. 1; *G,* inner floral bract (inner surface), × ca. 1. (*A & D* from *Nee 9873*; *B, C & E* from *Mori & Kallunki 5353*; *F–G* from the holotype.)

boricola resembles these two shrubby species. They differ most notably from the new species in having irregularly denticulate leaves, sessile stellate or stellate-furfuraceous hypanthial pubescence, and a differentiated androecium in which the larger stamens are inserted opposite the petals.

Topobea Aublet

The species proposed below represents the first new *Topobea* to be described from Panama since the appearance of Gleason's (1958) summary. The following description of *T. calophylla,* the transfer of *T. elliptica* to *Blakea* (also proposed herein) and the discovery of *T. pittieri* Cogn. in Chiriquí province (Cerro Colorado, *Folsom & Collins 1770,* CAS) now brings the number of Panamanian species to nine.

Topobea calophylla Almeda, sp. nov.
(Figure 5)

Frutex epiphyticus. Ramuli primum obscure quadrangulati demum teretes sicut petioli laminarum subtus venae primariae pedicelli bracteaeque pilis barbellatis ca. (1–)3–9 mm longis induti. Petioli 2.2–5 cm longi; lamina 14.5–37.5 × 8.6–17.8 cm, elliptico-ovata, apice abrupte caudato-acuminato basi rotundata vel paulo cordata, supra ad maturitatem glabra, subtus modice setosa (pilis ca. 1–3 mm longis). Flores 6-meri in foliorum superiorem axillis oppositis plerumque 2–4; bracteae liberae; bracteae exteriores 1.7–2.3 × 1.5–1.7 cm late ovatae; bracteae interiores 1.6–1.9 × 1.3–1.7 cm elliptico-ovatae. Hypanthium (ad torum) 1.1–1.3 cm longum extus dense strigosum pilis 2–4 mm longis, calycis lobis 14–17 mm longis triangularibus. Petala glabra 2 × 1 cm spathulata apice hebeti-acuto vel obtuso. Filamenta 5 mm longa; antherae 8 × 1.5 mm subulatae inter se cohaerentes, poris binis terminalibus; connectivum ad basim dorsaliter minute calcaratum. Stigma capitellatum vel truncatum; stylus 11–14 mm glaber in ovarii collo 5–6 mm immersus.

Coarse spreading epiphytic shrub. Cauline internodes ± terete to subquadrangular. Distal branchlets, vegetative buds, pedicels, and floral bracts covered with a hirsute indument of rusty brown barbellate trichomes mostly 3–9 mm long. Mature leaves firmly chartaceous to coriaceous, inconspicuously dentate, 14.5–37.5 × 8.6–17.8 cm, elliptic-ovate, abruptly caudate-acuminate apically, rounded to subcordate basally, 5–7-nerved with conspicuous elevated secondaries, glabrous above, moderately hirsute below with barbellate trichomes mostly 1–3 mm long; petioles 2.2–5 cm long and 3–5 mm diam. Flowers 6-merous, erect to widely spreading, paired or borne in clusters of three or four in axils of the distal branches; pedicels 2.8–4 cm long. Floral bracts foliaceous, entire, 3–5-nerved free basally, each pair closely subtending one another or separated on the pedicel by a distance of 3–4 mm, outer bracts 1.7–2.3 × 1.5–1.7 cm, broadly ovate, acuminate apically; inner bracts 1.6–1.9 × 1.3–1.7 cm, elliptic-ovate, acute to acuminate apically. Hypanthia (at anthesis) campanulate, 1.1–1.3 cm long to the torus, copiously appressed-strigose with barbellate trichomes 2–4 mm long. Calyx lobes lance-triangular, often involute to uncinate apically when dry, entire, hirsute to hirtellous, 14–17 mm long and 5–6 mm wide basally between sinuses. Petals glabrous, reportedly pink, ± spathulate but acute to obtuse apically, entire to sparingly glandular-ciliate, 2 cm long and 1 cm broad distally. Stamens isomorphic and strongly declined to one side of the flower, filaments glabrous, connivent, 5 × 1.5 mm; anthers linear-subulate, 8 × 1.5 mm, laterally coherent but free distally, strongly incurved at anthesis, each anther tipped with two somewhat dorsally inclined confluent pores; connective thickened dorsally near the point of filament insertion into a blunt callosity. Style ± straight, glabrous, 11–14 mm long and 1 mm wide; stigma capitellate to truncate, the surface appearing somewhat crateriform. Ovary inferior, 6-celled, distended apically into a glandular puberulent fluted cone and stylar collar mostly 7–9 mm long. Mature berry not seen.

Type.—**Panama.** Veraguas: 5 mi W of Santa Fe on road past Escuela Agricola Alto Piedra on Pacific side of divide, elev. 800–1200 m, 18 Mar. 1973, *Croat 23000* (holotype: CAS!; isotype: MO).

Additional Specimens Examined.—**Panama.** Veraguas: 6–7 km W of Santa Fe on new road past agriculture school, 18 Feb. 1974, *Nee 9873* (CAS); NW of Santa Fe, 4.2 km from Escuela Agricola Alto de Piedra, 25 Feb. 1975, *Mori & Kallunki 4833* (CAS); NW of Santa Fe, 2.7 km from Escuela Agricola Alto de Piedra along stream on road to Calovebora, 30 Mar. 1975, *Mori & Kallunki 5353* (CAS).

Distribution.—Known only from montane forests NW of Santa Fe in Veraguas province at elevations of 800–1200 m. Available material, all of which is in flower, was collected in February and March.

Like so many epiphytic species in the Blakeae that grow in wet forests, this species has a restricted distribution and does not appear to be closely related to any described taxon in *Topobea*. As emphasized by the specific epithet, *T. calophylla* has large, handsome leaves that are glabrous above and moderately hirsute below. It is also striking because of the copious indument of brown barbellate trichomes that gives distal branches, floral bracts, and hypanthia a coarse bristly appearance.

Among the species of *Topobea* recorded for Panama by Gleason (1958), this species also differs in the following combination of characters: its leaves are inconspicuously dentate; the inner and outer floral bracts are separate to the base, copiously pubescent abaxially, and essentially equal in length; and the ovary is elaborated apically into a prominent glandular-puberulent, fluted cone crowned by several setiform lobules that envelop the style basally for 5–6 mm.

No information is available on the size of individual plants in this species. Judging from foliar size and the coarseness of its branches, I suspect that *T. calophylla* can become an epiphyte of massive proportions comparable to *Topobea durandiana* Cogn. and *Blakea tuberculata* Donn.-Smith, both of which can obscure and overtake the crowns of their host trees. Casual collectors unfamiliar with the propensity for epiphytism in *Topobea* and *Blakea* frequently describe the epiphytic species in these genera as trees. Labels for all except one of the few available collections of *T. calophylla* indicate that it is an epiphyte. Although *Nee 9873* is described as a small tree, additional field study is needed to confirm this observation.

ACKNOWLEDGMENTS

I am grateful to Terry Bell for preparing the line drawings, to Colleen Sudekum for technical assistance, and to J. J. Wurdack for critical review of the manuscript. I also thank curators of the following herbaria who provided special loans and/or made their facilities available for study: BM, CR, DUKE, F, MO, US.

LITERATURE CITED

ALMEDA, F. 1974. A new epiphytic *Blakea* (Melastomataceae) from Panama. Brittonia 26:393–97.

———. 1980. Central American novelties in the genus *Blakea* (Melastomataceae). Rhodora 82:609–15.

COGNIAUX, C. A. 1891. Melastomaceae. Pages 1–1256. *In* A. and C. de Candolle, eds., Monographiae phanerogamarum, vol. 7. G. Masson, Paris.

GLEASON, H. A. 1958. Melastomataceae. *In* R. E. Woodson, Jr. and R. W. Schery, Flora of Panama. Ann. Missouri Bot. Gard. 45:203–304.

WURDACK, J. J. 1973. Melastomataceae. *In* T. Lasser, ed., Flora de Venezuela 8:1–819.

CALIFORNIA ACADEMY OF SCIENCES
Golden Gate Park
San Francisco, California 94118

PROCEEDINGS
OF THE
CALIFORNIA ACADEMY OF SCIENCES

Vol. 43, No. 18, pp. 283-300, 10 figs., 1 table. December 11, 1984

MARINE AND FRESHWATER STINGRAYS (DASYATIDAE) OF WEST AFRICA, WITH DESCRIPTION OF A NEW SPECIES

By

Leonard J. V. Compagno

Tiburon Center for Environmental Studies, San Francisco State University,
P.O. Box 855, Tiburon, California 94920

and

Tyson R. Roberts

California Academy of Sciences, Golden Gate Park, San Francisco, California 94118

Abstract: Three genera and 12 species of stingrays, all members of the family Dasyatidae, are known from West Africa. A key is provided for their identification. The two most common species in shallow coastal waters (including lagoons, estuaries, and river mouths) are the closely related *Dasyatis margarita* (Günther, 1870) and *Dasyatis margaritella* new species, which differ in disc shape, meristic features, and adult size. Two species occur mainly or exclusively in fresh water: *Dasyatis garouaensis* (Stauch and Blanc, 1962) and *Dasyatis ukpam* (Smith, 1863). *Dasyatis garouaensis,* a small, thin-bodied species previously known only from the lower Niger and a tributary, the Benue, is reported from Lagos and the Cross River. It is closely related to *D. margarita* and *D. margaritella. Dasyatis ukpam,* a large thick-bodied species with a vestigial sting previously known only from fetal specimens obtained at Old Calabar (without precise information on habitat), is now reported from the Ogooué and the lower Zaire or Congo rivers. It is perhaps related to the genus *Urogymnus.*

Introduction

This study was undertaken to clarify the systematics, distribution, and relationships of West African freshwater stingrays. Although widely distributed and familiar to local fishermen, stingrays inhabiting the larger rivers of West Africa are poorly known scientifically. There are at least two species. One, *Dasyatis ukpam,* was described more than a century ago, but the two fetal type-specimens obtained at Old Calabar lacked precise habitat data, and the species was not reported again or recognized as valid until the junior author obtained specimens in the Ogooué basin in 1978. We have also identified a specimen of this species collected in the lower Zaire (Congo) River in 1937.

The other West African freshwater dasyatid, *D. garouaensis,* was described originally as a species of *Potamotrygon,* a genus of the otherwise exclusively Neotropical freshwater family Potamotrygonidae. Evidence that it is actually a member of the family Dasyatidae was advanced by Thorson and Watson (1975). Our own observations fully support this conclusion. Reid and Sydenham (1979) suggested that *D. garouaensis* may be identical with the coastal species *D. mar-*

garita. Our studies, however, indicate that it is a valid species, albeit a close relative of *D. margarita* and the previously undescribed *D. margaritella. Dasyatis garouaensis* was known only from the Benue and lower Niger, but the junior author collected a specimen in the Cross River, Cameroun, in 1980, and we have also identified a specimen from Lagos, Nigeria (habitat unknown). So far as we have been able to determine, *D. margarita* and *D. margaritella* occur only in marine and estuarine habitats.

The key below should permit identification of all stingrays now known from West Africa. Following the key we present a definition of the genus *Dasyatis* and detailed descriptions of *D. margarita, D. margaritella, D. garouaensis,* and *D. ukpam.*

MATERIALS AND METHODS

This paper is based on material deposited in the American Museum of Natural History (AMNH); British Museum (Natural History) (BMNH); California Academy of Sciences (CAS and CAS-SU); Institut für Seefischerei, Hamburg (ISH); Muséum National d'Histoire Naturelle, Paris (MNHN); Musée Royale de l'Afrique Centrale, Tervuren, Belgium (MRAC); and Smithsonian Institution (USNM).

Disc width (measured at widest point) is our standard measure of size, and proportional measurements (unless otherwise indicated) are expressed as percent of disc width. Definitions or explanations of some other terms are as follows:

Disc length—midline measurement from snout-tip to a transverse line parallel to posteriormost extension of pectoral fins

Disc depth—greatest height or depth of disc (usually at scapulocoracoid)

Preorbital length—midline measurement from snout-tip to a transverse line parallel to anterior margin of eyes

Prenarial length—midline measurement from snout-tip to a transverse line parallel to anterior border of nostrils

Prebranchial length—midline measurement from snout-tip to a transverse line parallel to opening of first gill slits

Head length—midline measurement from snout-tip to a transverse line parallel to opening of fifth gill slits

Pectoral fin inner margin—from posterior insertion to posteriormost extension of pectoral fin

Pelvic fin span—distance between apices of pelvic fins when maximally extended

Upper and lower tooth rows—maximum number of tooth rows across upper and lower jaws

Vertebral counts in stingrays are complicated by the extraordinary specialization of the vertebral column as a support for the pectoral fins, and by its termination in an elongate tail, which is frequently damaged. Anteriorly the column is fused into two synarcuals incorporating a variable number of centra. In Dasyatidae the anteriormost 23–40 vertebrae are incorporated into the first synarcual. In most of these vertebrae the centra are completely fused, but their number can be determined by counting the spinal nerve foramina. The second synarcual frequently is separated from the first by a small number of intersynarcual vertebrae; in most of the *Dasyatis* herein reported, however, there is only a joint between the two synarcuals. In the second synarcual the centra, although fused, retain their form and are readily counted in radiographs. Sometimes the posteriormost centrum in the second synarcual is sharply distinguished from the monospondylous trunk centra succeeding it. In specimens in which the end of the second synarcual cannot be determined, we give a combined count of second synarcual plus monospondylous trunk vertebrae. This is usual in late fetal or newborn specimens with poor calcification and in heavily denticulated specimens in which this portion of the vertebral column is obscured in radiographs (e.g., in *D. ukpam*). Posteriorly the vertebral column ends in a long series of diplospondylous tail centra followed by a highly flexible, unsegmented rod (apparently consisting of the notochord and a heavily calcified notochordal sheath). The monospondylous and diplospondylous sections of the vertebral column are usually sharply demarcated in radiographs.

For terminology and illustrations of dasyatid clasper morphology see Compagno and Roberts (1982).

Family DASYATIDAE Jordan, 1888

We follow Bigelow and Schroeder (1953) in restricting Dasyatidae to the whiptailed stingrays, and tentatively recognize the following genera: *Dasyatis, Himantura, Hypolophus, Taeniura, Urogymnus,* and *Urolophoides* (see also Compagno and Roberts 1982).

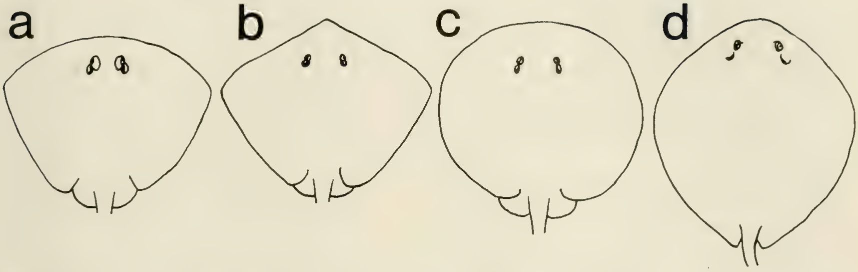


FIGURE 1. Disc shape in West African Dasyatidae. (a) *Dasyatis violacea* (trapezoidal); (b) *Dasyatis centroura* (diamond-shaped); (c) *Taeniura grabata* (circular); (d) *Urogymnus asperrimus* (oval).

KEY TO DASYATIDAE OF WEST AFRICA

1a. Disc oval (Fig. 1d); tail without dermal folds; sting invariably absent .... *Urogymnus africanus* (Bloch and Schneider, 1801)

1b. Disc variable in shape, tail with dermal fold or folds, sting usually present (absent in some *Dasyatis ukpam*) 2

2a. Ventral tail fold extending to end of tail; disc circular (Fig. 1c) .... *Taeniura grabata* (E. Geoffroy Saint-Hilaire, 1817)

2b. Ventral tail fold ending far anterior to end of tail (*Dasyatis*) 3

3a. Disc trapezoidal or diamond-shaped (Fig. 1a–b) 4

3b. Disc oval or circular 9

4a. Disc trapezoidal, anterior margin broadly rounded, snout not projecting as an angular lobe from disc (Fig. 1a); upper and lower surfaces of disc dark .... *D. violacea* (Bonaparte, 1832)

4b. Disc diamond-shaped, anterior margin angular, snout projecting as an angular lobe from disc (Fig. 1b); lower surface of disc light 5

5a. Upper surface of disc with a dark reticular pattern; ventral tailfold very short, about twice length of sting .... *D. marmorata* (Steindachner, 1892)

5b. Upper surface of disc plain; ventral tailfold long, much more than twice sting length 6

6a. Entire dorsal surface of disc covered with small denticles; no middorsal row of enlarged denticles or thorns; adults with over 100 rows of teeth in each jaw; disc very broad, about 1.5 times as wide as long in adults .... *D. rudis* (Günther, 1870)

6b. Dorsal surface of disc only partially covered with small denticles, along middle of back, or naked except for a middorsal row of enlarged denticles or thorns; adults with much less than 100 rows of teeth in each jaw; disc narrower, 1.0–1.3 times as wide as long 7

7a. Anterior margin of disc anterior to spiracles nearly straight behind snout-tip, with tip projecting; posterior parts of pelvic fins projecting well rearward beyond rear tip of pectoral fins .... *D. pastinaca* (Linnaeus, 1758)

7b. Anterior margin of disc anterior to spiracles slightly concave behind snout-tip, with tip not conspicuously projecting; posterior parts of pelvic fins extending slightly behind rear tips of pectoral fins 8

8a. Ventral tailfold high, about as deep as tail above it; a dorsal ridge present on tail behind sting; disc and tail in large juveniles and adults without enlarged, heavy, broad-based denticles, but with moderately enlarged middorsal and scapular denticles only .... *D. americana* (Hildebrand and Schroeder, 1928)

8b. Ventral tailfold low, half as deep as tail above it; no dorsal ridge on tail behind sting; disc and tail in large juveniles and adults with scattered enlarged, heavy, broad-based denticles, forming a middorsal row at center of disc and tail .... *D. centroura* (Mitchill, 1815)

9a. Anterior margins of disc broadly convex anterior to spiracles, with tip of snout not projecting from them; dorsal disc surface in juveniles to subadults completely covered with denticles, with flattened large denticles on midbelt, small pointed denticles laterally, and large, conical, erect, sharp-cusped denticles on thorns scattered on disc and tail base; sting reduced or absent; no dorsal keel on tail; base of tail circular in cross section; ventral surface of disc light with a broad dusky marginal band .... *D. ukpam* (Smith, 1863)

9b. Anterior margins of disc concave anterior to spiracles, with tip of snout conspicuously projecting from them; dorsal disc surface partially naked, with a midbelt of flattened denticles and often a midscapular pearl spine, or naked; no large conical thorns on disc and tail base; sting large; a low dorsal keel on tail behind sting; base of tail horizontally oval in cross section; ventral surface of disc light without a broad dusky marginal band 10

10a. Back flattened, without an enlarged midscapular pearl spine (sometimes a row of up to 4 moderately enlarged flattened spines in its place); midbelt of flattened denticles reduced or absent, disc sometimes entirely naked; snout long, preorbital length 2.8–3.2 times interorbital space (down to 2.3 in late fetuses or newborn specimens) and 27–32% of disc width; disc very flat, thickness at scapulocoracoid 8–11% (usually less than 11%) of disc width; lateral prepelvic processes of pelvic girdle greatly expanded .... *D. garouaensis* (Stauch and Blanc, 1962)

10b. Back somewhat arched, with an enlarged midscapular pearl spine; midbelt of flattened denticles well developed in large juveniles and adults; snout shorter, preorbital length 1.5–2.4 times interorbital space and 19–26% of disc width; disc thicker, 11–15% of disc width over scapulocoracoid; lateral prepelvic processes slightly expanded 11

11a. Upper jaw strongly undulated, with teeth greatly enlarged on prominent lateral projections; teeth less numerous, in 26–29/31–34 rows; snout more broadly pointed; pearl spine usually larger and circular, length about 5–6 mm; pectoral radials 133–135; size larger, adults to 65 cm .... *D. margarita* (Günther, 1870)

11b. Upper jaw moderately undulated, with teeth moderately enlarged on low lateral projections; teeth more numerous, in 36–42/38–50 rows; snout usually more acutely pointed; pearl spine usually smaller and often axially oval, length 2–4 mm; pectoral radials 116–127; size smaller, adults to 26 cm .... *D. margaritella* new species

Dasyatis Rafinesque, 1810

Dasyatis Rafinesque, 1810:16 (type-species *Dasyatis ujo* Rafinesque, 1810 [=*Raja pastinaca* Linnaeus, 1758], by monotypy).

For full generic synonymy of *Dasyatis* see Bigelow and Schroeder (1953).

Diagnosis.—Dasyatidae with disc circular, oval, trapezoidal, or diamond-shaped (Fig. 1), its dorsal surface smooth or variably covered with small, flat or prickle-like denticles; large, sharp, spine- or plate-like denticles present or absent on dorsal surface; snout angular or broadly rounded, its projecting tip variably developed; pectoral fins rounded or angular; pelvic bar moderately arched; tail long, slender, with dorsal and ventral folds or ventral folds only; ventral fold not reaching tip of tail; sting usually present (reduced or absent in *Dasyatis ukpam*). Teeth small, rhomboidal, thin-crowned.

Dasyatis as here recognized is a large, heterogeneous assemblage of about 33 species and may be polyphyletic. *Dasyatis margarita, D. margaritella,* and *D. garouaensis* are not far removed morphologically from the generic type-species *D. pastinaca. Dasyatis ukpam,* however, is distinct, approaching *Urogymnus* Müller and Henle, 1837 in general morphology, heavy den-

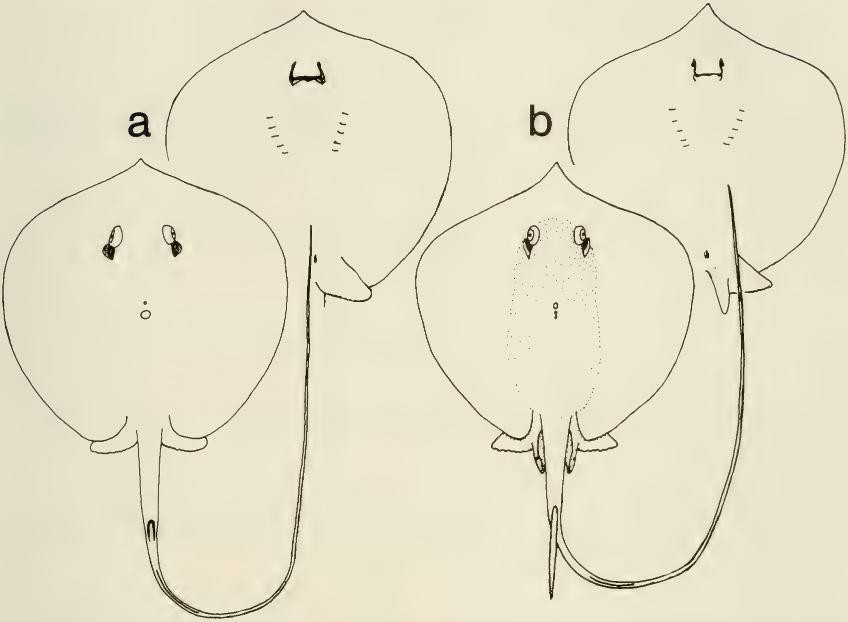


FIGURE 2. (a) *Dasyatis margarita,* lectotype, 200-mm immature female, West Africa (BMNH 1865.7.4:1); (b) *Dasyatis margaritella,* 226-mm mature male, Conakry, Guinea (ISH 183/63).

ticulation, and sting reduction. *Urogymnus* species invariably lack the sting, while specimens of *D. ukpam* either lack the sting or have a very small one. Smith (1863) noted that *D. ukpam* seemed intermediate between *Urogymnus* and *Trygon* (=*Dasyatis*), at least in the nature of its sting, but included it in *Hemitrygon* Müller and Henle, 1837 (=*Dasyatis*) because it has a short ventral tail fold and no dorsal tailfold. We retain *D. ukpam* in *Dasyatis* pending modification of the limits of *Dasyatis* and other dasyatid genera. The species is readily distinguished from known *Urogymnus* species in having a ventral tailfold, much longer tail (less than 1.5 times disc width in *Urogymnus*), a less thick, more circular disc, darker dorsal coloration (dorsal surface pale brown in all *Urogymnus* examined), a dark marginal band on ventral surface of disc, smaller flat denticles on dorsal surface of disc, and in some specimens a small sting.

Dasyatis margarita (Günther, 1870)

(Figure 2a)

Trygon margarita GÜNTHER, 1870:479 (type-locality West Africa).

Dasyatis sp. BLACHE ET AL., 1970:53, fig. 117.

MATERIAL EXAMINED.—BMNH 1865.7.4:1, 200-mm immature female, West Africa (formerly syntype of *D. margarita*; designated lectotype below); USNM 222589, 130-mm late fetal or newborn male, Sierra Leone; BMNH 1930.3.24:3, 212-mm immature male, Accra, Ghana; BMNH 1936.8.20:2–3, 216-mm and 315-mm immature females, Lagos, Nigeria; BMNH 1899.2.20:35, 206-mm immature female, Banana, Congo River mouth, Zaire; AMNH 40408, 235-mm female, Angola.

LECTOTYPE DESIGNATION.—In the original description of *D. margarita* Günther (1870:479) listed two specimens from West Africa without indicating either as holotype:

> a. Disk 8½ inches long, tail 19 inches. Purchased of Mr. J. Wood.
>
> b. Young. From the collection of the Zoological Society.

These two specimens are therefore syntypes, but our studies indicate they are not conspecific. Specimen *a* is BMNH 1865.7.4:1, a 200-mm immature female with a single, large, round pearl

TABLE 1. PROPORTIONAL MEASUREMENTS (AS % DISC WIDTH) AND COUNTS IN FOUR WEST AFRICAN *DASYATIS*.

	D. margarita		*D. margaritella*		*D. garouaensis*			*D. ukpam*		
	Lectotype 200 mm	Non-types 5:130–315 mm	Types 3:170–191 mm	Non-types 27:109–262 mm	Benue R. 8:68–340 mm	Cross R. 342 mm	Lagos 255 mm	Old Calabar 266 mm	Ogooué R. 3:499–650 mm	Zaire R. 360 mm
Proportional measurements:										
Total length	335	293–337	318	253–344	290–345		288	378	290–313	
Disc length	103	93–104	100–107	86–111	105–114	112	111	107	100–103	100
Disc depth	13.0	13.1–14.5	12.6–15.3	11.0–15.3	8.7–11.0	10.5	9.8	14.3	14.8–15.7	13.3
Eyeball	5.5	5.6–7.0	7.3–8.2	6.5–9.2	4.8–9.0	5.8	5.9	5.6	4.0–4.6	5.0
Cornea	4.5	3.4–3.8	5.2–5.5	3.0–6.0	2.9–7.7	4.1	3.9	4.1	2.6–2.9	2.8
Interorbital width	12.5	10.0–12.7	11.0–12.7	9.2–12.6	9.0–11.8	9.9	10.2	12.0	12.0–13.8	13.6
Spiracle	7.0	6.9	5.2–6.5	5.9–7.4	5.6–7.4	6.4	5.5	9.0	7.4–8.0	7.5
Interspiracular width	19.0	16.2–20.3	17.8–19.3	14.5–20.0	11.3–22.1	15.2	16.1	18.0	17.4–18.4	18.3
Nasal curtain	6.0		5.2–5.9		4.2–5.9	5.3	4.7	4.5	5.8–6.2	5.3
Internarial width	8.0	7.3–8.5	8.4–10.0	6.9–11.4	4.8–6.3	6.1	6.7	9.0	8.8–9.4	8.9
Mouth width	8.5	9.2	6.6–8.4	7.6–9.2	5.9–7.7	7.0	7.5	8.3	8.1–9.4	8.6
1st gill slit	3.0	3.1	2.1–2.4	2.4–3.4	1.5–3.0	2.3	2.4	3.0	3.3–3.5	3.3
5th gill slit	2.5	2.3	1.0–1.8	1.6–2.3	1.3–2.1	2.3	1.6	3.0	2.7–2.9	2.5
1st interbranchial width	23.0	20.8	19.9–22.9	20.7–22.5	16.4–23.5	17.3	18.4	23.7	23.6–23.8	23.1
5th interbranchial width	14.0	12.3	11.0–12.9	12.8–15.5	10.9–16.7	11.1	11.8	16.2	16.2–16.6	15.8
Preorbital length	23.0	19.4–22.8	23.6–25.4	19.8–25.8	27.8–32.2	28.7	29.4	22.9	21.4–22.5	23.1
Prenarial length	18.0	15.9–17.5	20.9–21.8	17.1–21.6	22.1–27.4	24.9	26.3	19.2	15.5–17.0	17.8
Preoral length	24.5	21.5	25.1–28.2	24.8–27.1	27.9–33.7	28.9	32.2	23.7	20.9–21.9	22.8
Prebranchial length	35.0		37.7–39.4		39.9–44.9	40.6	43.1	36.5	33.3–34.8	34.4
Head length	49.5		49.7–53.5		49.7–59.0	52.0	54.1	50.4	48.9–49.4	48.3
Prepelvic length	83.5		84.8–90.1		82.1–96.2	90.6	87.5	89.5	82.8–83.1	81.7
Snout-tip to vent	84.5	78.5	84.8–89.0	81.4–87.2	85.3–97.2	89.2	88.2	90.2	82.5–85.8	82.8
Pectoral inner margin	13.5		11.5–12.9		11.3–14.7	14.0		10.2	11.1–12.2	11.4
Pelvic anterior margin	18.0	18.0–20.8	18.3–21.5	13.2–22.2	19.8–25.0	22.2	24.3	19.2	16.0–17.3	18.3
Pelvic posterior margin			14.1–16.1		20.0–22.8	22.2		15.0	19.0–23.1	18.3
Pelvic fin base	13.5		10.6–14.4		10.9–15.0	12.9	15.3	8.6	12.6–16.2	12.8
Pelvic fin span			47.5–47.6		51.8–52.4	49.7		45.1	45.8–48.1	41.6
Tail base width	8.0	8.5–10.2	8.4–9.4	7.0–11.1	7.1–10.3	8.5	7.8	6.8	6.7–7.4	6.9
Tail base depth	5.5	6.9	5.0–5.8	4.4–6.4	4.5–6.4	5.3	4.3		5.8–6.5	6.1
Counts:										
Oral papillae	5		5		5(2)	5		4	5	5
Spiral valve turns	14	12–13	13–14		10(2)	11		20	20	19
Upper tooth rows	29	26–30	36–43	35–43	32–33(2)	40		46	38–44	38
Lower tooth rows	31	31–34	42–49	38–50	37–40(2)	45		43	38–48	41
Total pectoral radials	135	133–134	117–121	116–127	122–124	125	124	146	142–149	144

Table 1. Continued

	D. margarita		*D. margaritella*		*D. garouaensis*			*D. ukpam*		
	Lectotype 200 mm	Non-types 5:130–315 mm	Types 3:170–191 mm	Non-types 27:109–262 mm	Benue R. 8:68–340 mm	Cross R. 342 mm	Lagos 255 mm	Old Calabar 266 mm	Ogooué R. 3:499–650 mm	Zaire R. 360 mm
Propterygial radials	58	55–56	50–51	49–50	53–56	56	55	65	65–70	64
Mesopterygial radials	18	17–21	16–19	15–22	16–20	18	17	20	17–19	22
Metapterygial radials	59	59–60	50–54	51–56	49–52	51	52	61	59–64	58
Pelvic radials male			22–24	20			23	23		
Pelvic radials female	28		27		29	29			28–34	25+
Total vertebral segments	162			139–151	157–162	149	162	155(1)		
Total separate centra	130		116–124	119–128	128–131	120	126	122	108–120	
1st synarcual segments	34			25–28	33–35	31	40	38		
1st synarcual free centra	2		2–4	5	3–7	2	4	5	2–5	0
Intersynarcual centra	0		0	0	0–2	0	0	0	0	0
2nd synarcual centra					20–26	18	13			
2nd synarcual + monosp.	45		42–44	40–42	37–42	40	41	45	44–50	39
Diplospondylous	77		63–66	61–77	83–88	78	81	72	57–65	
Post-sting centra	6		9–13	6–11	11–17	5	9	0	0	0

spine; specimen *b* apparently is BMNH 1852.8.30:23, a 116-mm fetal or newborn male with two relatively small oval pearl spines. Günther's description clearly is based mainly on specimen *a*, which we therefore designate as lectotype. Specimen *b* belongs to *D. margaritella*.

Diagnosis.—A large marine and estuarine *Dasyatis*, 65 cm or more, most closely related to the much smaller marine and estuarine species *D. margaritella* and to the extremely flat freshwater species *D. garouaensis*. Pearl spines always present and very large (much smaller in *D. margaritella* and absent or represented by 2–3 low denticles in *D. garouaensis*). Denticles on dorsal surface of disc smooth, restricted to middle portion.

Disc oval, moderately flat, its medial lobe broad-based and moderately exserted, its anterolateral margin somewhat concave; disc depth 13.0–14.5% of disc width, disc width 0.9–1.1 times disc length; snout moderately long, preoral length 22–24% of disc width; dorsal surface of disc naked in young (except for pearl spine), but in older individuals (larger than about 200 mm) middle third of disc covered with small, circular, flat denticles and tail covered with small prickles; no enlarged thorns on disc or tail; a massive, usually circular, button-shaped pearl spine on back, 4.8–5.5 mm long; usually a single large slender sting on tail, its length 22% of disc width in newborn; eyes moderately large and somewhat elevated, eyeball length 1.4–2.3 times in interorbital space, interorbital space 1.5–2.0 in preorbital length; spiracles moderately large and flattened; floor of mouth with 5 elongate papillae; total tooth rows 26–30/31–34; pelvic fins short, anterior margins 18–21% of disc width; tail evenly tapering to a slender whiplash behind sting, but broad opposite and in front of it, its length when intact about 1.8–2.5 times disc width; base of tail horizontally oval and depressed in section; ventral tailfold moderately high, dorsal tailfold reduced to a low keel behind sting; disc and pelvic fins gray-brown above, without spots or prominent markings, uniformly pale or whitish below; intestinal valve turns 12–14; total pectoral radials 133–135; total vertebral centra 130, and total vertebral segments 162; vertebral centra extending behind origin of sting; a moderately large stingray, exceeding 65 cm.

Proportional measurements (as percent of disc width) and counts are given in Table 1. Preoral length 2.5–3.0 times internarial width and about 1.0 times width between first gill slits. Snout fairly broad, angle in front of eyes 123°. Spiracle length 1.0–1.3 times eyeball length, 0.8–0.9 times internarial width, and 1.8–2.0 times in distance between fifth gill slits. Nasal curtain with a fringed, weakly trilobate posterior margin. Mouth weakly arched, midline of lower jaw with a prominent indentation; a shallow to deep, curved groove extending posteriorly from posterior nasal flap around corners of mouth. Floor of mouth with 5 papillae, including a transverse row of one small medial and two large elongate paramedial papillae, and two smaller lateral papillae near ends of dental bands.

Teeth in quincunx pavement, with crowns closely adjacent to one another. Teeth similar in upper and lower jaws, upper and lower jaw teeth about equally large at symphysis, varying continuously lateral to synphysis, largest and most elongate at or near symphysis and smallest and least elongate at mouth corners. Upper dental band with a prominent knob of considerably enlarged teeth at symphysis, separated from similar, very large knobs at either side by depressions with smaller teeth; lower dental band with a well-marked symphyseal depression into which symphyseal knob of upper jaw fits, and a pair of prominent lateral knobs fitting into depressions in upper dental band.

Dorsal surface naked except for pearl spine in young below about 200 mm, but in larger specimens moderately large, heart-shaped or circular denticles form a middorsal belt of denticles on disc; lateral parts of disc naked. Larger individuals with small conical prickles on dorsal surface of tail behind sting.

Neurocranium, observed in radiographs, similar to that of *Himantura signifer* as described by Compagno and Roberts (1982) but with longer, more ovate nasal capsules.

Pelvic girdle (Fig. 10e) broadly arched, semicircular, and relatively narrow, with a medial angle but without a medial prepubic process. Lateral prepubic processes low, rounded, lobate, and not greatly expanded; iliac processes well developed; ischial processes short. Four obturator foramina present.

Claspers not studied in detail, but morphologically similar to those of *D. garouaensis.*

Dasyatis margaritella, new species

(Figures 2b, 3)

Trygon margarita Günther, 1870:479 (in part).
Dasyatis margarita Blache et al., 1970:53, fig. 116.

Holotype.—CAS-SU 68915, 190-mm male, Mbode, Cameroun, A. I. Good, 7 December 1940.

Paratypes.—CAS-SU 68916, 169-mm male and 180-mm female, same collection data as holotype.

Additional Material Examined But Not Included in Type-Series.—BMNH 1852.8.30.23, 116-mm immature male, West Africa, apparent syntype of *Trygon margarita* Günther, 1870; USNM 222590, 4 immature males, 109–139 mm, 2 females, 132–164 mm, and USNM 222593, 3 immature males, 129–141 mm, 146 mm female, both lots from Guinea-Bissau; ISH 141–142/62, 3 immature males, 135–196 mm, 201-mm adolescent male, 228-mm adult male, 3 females, 149–222 mm, Guinea; ISH 183/63, 226-mm adult male and 248-mm female, Conakry, Guinea; ISH 295/59, 167-mm immature male, Dubreka, Guinea; USNM 222591, 145-mm female, Liberia; BMNH 1920.8.12.1, 262-mm female, Sierra Leone; USNM 222591, 149-mm female, Liberia; BMNH 1914.11.2.75, 133-mm female, Lagos, Nigeria; BMNH 1937.4.19.4, 208-mm adult male, Lagos Lagoon, Nigeria; AMNH 41515, 204-mm female, Congo River mouth.

Derivation of Name.—*margaritella,* diminutive of Latin *margarita,* f. "pearl"; for the smaller size of this stingray and of its pearl spine, as compared to *D. margarita.*

Diagnosis.—*D. margaritella* is a marine species and the smallest dasyatid in West Africa. Males sexually mature at 208 mm or less; largest known specimen a 262-mm female. Most similar to the marine species *D. margarita,* which attains over 600 mm, has a larger pearl spine, and more numerous pectoral radials (133–135 vs. 116–127). It is also similar to *D. garouaensis,* a freshwater species with a much flatter disc and a longer snout.

Disc oval, moderately flat. Medial lobe broad-based and exserted, its anterior margin concave. Disc depth 11.0–15.5% of disc width, disc width 0.9–1.1 times disc length; snout moderately long, preoral length 25–27% of disc width; dorsal surface of disc naked in young (except for pearl spine), but above about 130–140 mm middle third of disc covered with small heart-shaped or circular flat denticles and tail posterior to sting with small prickles; no enlarged thorns on disc or tail; a moderately large, usually longitudinally oval pearl spine on back, 2.4–4.1 mm long; usually a single large slender sting on tail, 24–32% of disc width; eyes moderately large and somewhat elevated, eyeball length 1.2–1.9 times in interorbital space, interorbital space 1.7–2.4 in preorbital length; spiracles moderately large and flattened; floor of mouth with 5 elongated papillae; total tooth rows 35–43/38–50; pelvic fins short, anterior margins 13–22% of disc width; tail evenly tapering to a slender whiplash behind sting, but broad oppo-

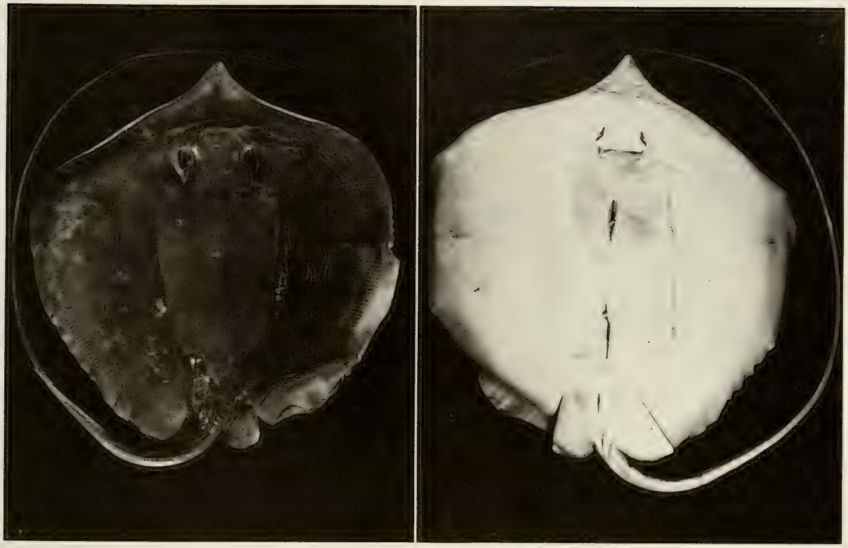


FIGURE 3. *Dasyatis margaritella,* holotype, 190-mm immature male, Mbode, Cameroun (CAS-SU 68915).

site and in front of it, its length from vent to tip when intact about 2.5–3.4 times disc width; base of tail horizontally oval and depressed in section; a moderately high ventral tailfold present but with only a low keel on the dorsal surface of the tail behind the sting; disc and pelvic fins gray-brown above, without spots or prominent markings, white below and without a marginal dark band; intestinal valve turns 13–14; total pectoral radials 116–127; total vertebral centra 116–128, and total vertebral segments 139–151; vertebral centra extending behind origin of sting. A small stingray, probably not exceeding 30 cm.

Proportional measurements (as percent of disc width) and counts are given in Table 1. Preoral length 2.5–3.3 times internarial width and 1.1–1.3 times width between first gill openings. Snout fairly narrow, angle in front of eyes 113–119°. Spiracle length 0.7–1.1 times eyeball length, 0.6–0.9 times internarial width, and 1.8–2.5 times in distance between fifth gill openings. Nasal curtain with a fringed, nearly straight or weakly trilobate posterior margin. Mouth weakly arched, midline of lower jaw with a prominent indentation; a shallow-to-deep, curved groove extending posteriorly from posterior nasal flap around corners of mouth. Skin on ventral surface of lower jaw more or less corrugated and papillate. Palate behind fringed maxillary valve with three strong, short ridges, a medial longitudinal ridge and a pair of diagonal lateral ridges. Floor of mouth with 5 oral papillae, including a transverse row of one smaller medial and two larger elongated paramedial papillae at midline of mouth, and two smaller lateral papillae near ends of dental bands.

Upper jaw with about 6, lower jaw with about 8 functional series of teeth. Teeth in quincunx pavement, close-set, with crowns closely adjacent to one another. Teeth similar in upper and lower jaws; uppers about as large as lowers at symphysis, varying continuously lateral to symphysis; teeth largest and longest relative to width at or near symphysis and smallest and shortest at mouth corners. Upper dental band with a prominent knob of slightly enlarged teeth at symphysis, separated from similar knobs at either side by depressions with smaller teeth; lower dental band with a well-marked symphyseal depression into which symphyseal knob of upper jaw fits, and a pair of prominent lateral knobs that fit into depressions in upper dental band.

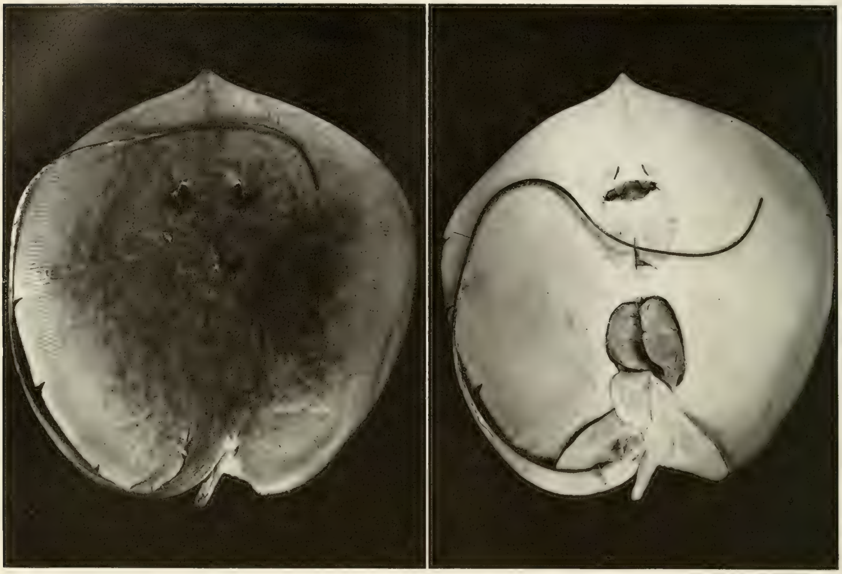


FIGURE 4. *Dasyatis garouaensis,* 340-mm mature male, Benue River at Makurdi, Nigeria.

Teeth of both jaws with low, broad-tipped, cuspless, rhomboidal crowns that have a transverse blunt keel or carina, reticulating ridges on their labial sides, a strong basal ledge, and concave, inset basal groove separating crown and root. Roots moderately large, fairly low, pedicellate, bilobed basally, with a transverse groove and nutrient foramen. Teeth of adult males somewhat longer than in females, but without elongated cusps.

Dorsal surface naked in young below about 130–140 mm, except for pearl spine, but in larger specimens moderately large, heart-shaped or circular denticles form a middorsal belt of denticles on disc; lateral parts of disc naked. Also, small conical prickles on dorsal surface of tail behind sting in larger individuals.

Neurocranium, observed on radiographs, similar to that of *Himantura signifer* as described in Compagno and Roberts (1982), but with longer, more ovate nasal capsules.

Pelvic girdle (Fig. 10f) broadly arched, semicircular, relatively narrow, with a medial angle but without a medial prepubic process. Lateral prepubic processes low, rounded, lobate, not greatly expanded; iliac processes well developed; ischial processes short. Four obturator foramina present.

Claspers not studied in detail, but similar morphologically to those of *Dasyatis garouaensis.*

Dasyatis garouaensis (Stauch and Blanc, 1962)

(Figures 4–5)

Potamotrygon garouaensis STAUCH AND BLANC, 1962:166, fig. 1–4 (type-locality Benue River at Malape, Cameroun); DAGET AND STAUCH, 1963:85–107 (reference); CASTEX, 1967: 167–176 (discussion).

Dasyatis sp. KREFFT, 1968:70, pl. 6 ("Rafin Kunama, Nebenfluss des Nigers etwa 300 Meilen oberhalb der Mündung").

Dasyatis garouaensis CASTELLO, 1973:67 (placed in *Dasyatis*); THORSON AND WATSON, 1975:701–712 (placed in *Dasyatis,* size, range, physiology, additional specimens reported from Niger and Benue rivers of Nigeria and Cameroun); REID AND SYDENHAM, 1979:46, 54–55 (possibly synonymy with *D. margarita,* range in Benue River system); COMPAGNO AND ROBERTS, 1982:321 (reference).

MATERIAL EXAMINED.—MNHN 1962-303, holotype, 202-mm female; MNHN 1962-304, 68-mm male and 78-mm female fetuses; MNHN 1967-441, 263-mm female; MNHN 1967-440, 300-mm adult male; MNHN 1967-439, 340-mm adult male; all from upper Benue River, Cameroun; CAS 49147, 342-mm adult female, Cross River, 5–10 km downstream from Mamfe, Cameroun; CAS 53108, 311-mm female, 340-mm adult male; Thorson collection, uncat., 238-mm female (radiograph only); Benue River at Makurdi, Nigeria; BMNH 1949.10.24.1, 255-mm adult male, Lagos, Nigeria.

DIAGNOSIS.—A moderately large and thin-bodied freshwater dasyatid. Largest known specimen a 342-mm adult female. Disc flatter than in any other West African dasyatid, its depth only 8.7–11.0% of disc width (vs. 11.0% or more in other species). Denticles on dorsal surface of disc highly variable, sometimes absent, always restricted to central portion. Pearl spine absent or represented by 2–3 low denticles. Most similar to the small marine species *D. margaritella* and the larger marine species *D. margarita,* both of which have well-developed pearl spines and shorter snouts.

Disc oval, very flat. Medial lobe fairly broad-based and elongated, its anterior margin straight or concave; disc width 0.9–1.0 times disc length; snout moderately long, preoral length 29–32% of disc width; dorsal surface of disc either entirely naked or with scattered, small, heart-shaped or circular flat denticles on its middle, no pearl spines (a few slightly enlarged, flattened, heart-shaped denticles occasionally present in midscapular area), and no enlarged conical denticles on disc and tail; a single, large, slender sting present on tail; sting 22.6–26.3% of disc width in adults; eyes small and hardly elevated, eyeball lengths 1.3–2.0 times in interorbital space; interorbital space, 2.4–3.2 times in preorbital length; spiracles moderately large and flattened; floor of mouth with 5 elongated papillae; total tooth rows 32–40/37–45; pelvic fins short, their anterior margins 20–25% of disc width; tail rapidly tapering to a slender whiplash behind sting but broad opposite and in front of it, its length from vent 2.5–3.5 times disc width when intact; base of tail horizontally oval and depressed in section; a moderately high ventral tailfold present but with only a low keel on dorsal surface of tail behind sting; disc and pelvic fins medium gray or gray-brown above, without spots or prominent markings, white below and without dark margins; tail darker or blackish, mottled, lighter below, underside of base white; intestinal valve turns 10; total pectoral radials 122–125; total vertebral centra 120–131 and total segments about 149–162; vertebral centra extending posterior to sting origin.

Proportional measurements (as percent of disc width) and counts are given in Table 1. Preoral length 4.0–6.0 times internarial width and 1.2–1.9 times width between first gill slits. Snout moderately broad, angle in front of eyes 110–116°. Spiracle length 0.9–1.2 times eyeball length, 0.8–1.2 times internarial width and 1.8–2.1 times in distance between fifth gill slits. Internal gill openings with close-set transverse ridges on gill arches, apparently serving as gill rakers. Nasal curtain with a fringed, concave posterior margin. Mouth nearly straight, midline of lower jaw slightly concave. A groove extending posteriorly from posterior nasal flap around mouth corner. Skin on anteroventral surface of lower jaw corrugated and papillate. Palate behind heavily fringed maxillary valve with three strong short ridges, a medial longitudinal ridge and a pair of diagonal lateral ridges; two short ridges also present behind the three palatine ridges. Floor of mouth with a transverse row of three elongated oral papillae, a larger medial papilla and a smaller lateral one behind each end of dental band; a pair of additional large papillae just behind and lateral to medial papilla. Upper jaw with 5–7 and lower jaw with 7–9 functional tooth series. Teeth in quincunx pavement, close-set, with crowns adjacent to one another. Teeth similar in upper and lower jaws, uppers slightly larger than lowers; teeth varying continuously lateral to symphysis, largest and longest relative to width at or near symphysis, smallest and shortest near mouth corners. Upper dental band with a small knob of slightly enlarged teeth at symphysis, separated from similar weak knobs on either side by depressions with smaller teeth; lower dental band with a corresponding symphyseal depression into which upper symphyseal knob fits, and a pair of very low lateral knobs which fit into upper parasymphyseal depressions. Teeth of both jaws with moderately high (females) to very high (males), peaked, broad-tipped (females) or acutely pointed, cuspidate (males) crowns shaped like mushroom caps, with a strong, sharp cutting edge (males) or a broad, blunt carina or transverse keel (females), a strong basal ledge, and a concave, inset basal groove separating crown from root. Root small, moderately high, pedicellate, bilobed basally, with a transverse groove and nutrient foramen. Dentition sexually dimorphic; teeth of males with triangular, concave, cuspidate crowns; females with low, rhomboidal, truncated, cuspless crowns.

Dorsal surface of disc either completely naked, without denticles (2 fetuses, the holotype, and a

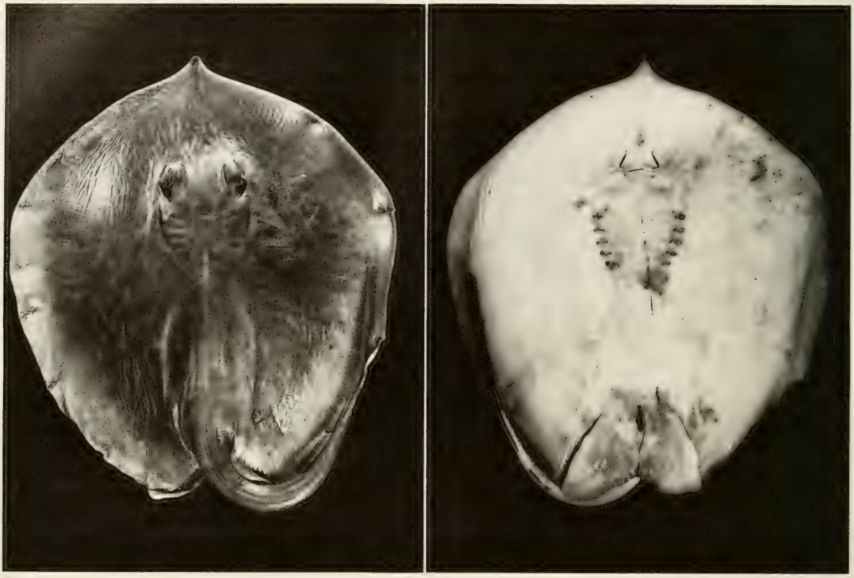


Figure 5. *Dasyatis garouaensis,* 342-mm mature female, Cross River near Mamfe, Cameroun (CAS 49147).

340-mm adult male), or with a variable number of small, heart-shaped or circular denticles buried in skin on middorsal area (remainder of specimens examined). Two large specimens (including 342-mm male from Mamfe) have a few scattered denticles along midline of back; two others have a small rectangular area of flat denticles centered on midscapular region but not extending outwards to cover middle third of disc as in *D. ukpam, D. margarita,* and *D. margaritella.* Five large specimens had 3 or 4 large, flattened, wedge-shaped denticles in midscapular region, but these not formed as domed, rounded pearl spines (although probably homologous to pearl spines).

Neurocranium, examined from radiographs, generally similar to that of *Himantura signifer* as described in Compagno and Roberts (1982), except frontoparietal fontanelle shorter and broader, and posterior margin of nasal capsules more transverse; width of nasal capsules about 75% of nasobasal cranial length.

Pelvic girdle (Fig. 10c–d) less arched than that of *D. ukpam,* convex anteriorly and without a medial prepubic process or a median angle. Pelvic girdle of *D. garouaensis* differs from that of *D. ukpam* as well as *D. margarita* and *D. margaritella* in having large, laterally expanded lateral prepelvic processes; these were prominent on all *D. garouaensis* radiographed, including specimens from Mamfe, Lagos, and Benue River in Nigeria and Cameroun. Pelvic girdle also with short ischial processes, long, slender iliac processes, and 4 obturator foramina.

Claspers of adult male short and stout, length of outer margin 10.2–11.6% of disc width, oval in cross section and somewhat depressed; height about $\frac{3}{5}$ of width at midlength. Dorsal surface of clasper slightly flattened, ventral surface broadly convex, lateral edge convexly arched, medial edge undulated, and tip bluntly pointed. Apopyle on anterodorsal surface, connected to hypopyle by an open, posteriorly curved clasper groove. Clasper glans simple, dorsal lobe supported by dorsal marginal and terminal cartilages, ventral lobe supported by ventral marginal and terminal cartilages as well as ventral covering piece. No structures inside hypopyle. A large pseudopera laterally situated on ventral lobe below hypopyle; a small pseudosiphon on dorsomedial surface of dorsal lobe, its cavity lying entirely below flange of dorsal marginal cartilage. Ventral lobe without clasper spur or associated terminal (T_3 cartilage). Clasper skeleton simple, with two cylindrical basal segments connecting pelvic basipterygium to axial cartilage. Axial cartilage cylindrical, nearly straight, with rodlike tip reaching ends of terminal cartilages. Beta cartilage present, a long, slender, separate, flattened plate running along lateral surface of clasper skeleton from posterior end of basipterygium to anterior end of dorsal marginal cartilage. Dorsal marginal cartilage broad and subquadratetriangular, with a diagonally truncate posterior edge, broad medial flange, and narrow lateral flange that forms roof of clasper groove. Ventral marginal cartilage a narrow, laterally expanded plate on axial cartilage, with a straight lateral margin forming floor of clasper groove. Dorsal terminal cartilage large, broad, wedge-shaped, and axially convex, with a broad anterior base articulating with posteroventral edge of dorsal terminal, a narrow posterior tip opposite tip of axial cartilage, and medial edge articulating with axial cartilage. Ventral terminal cartilage large, complex, oval, and scoop-shaped, with a broad, arched, lateral flange forming roof of pseudopera and a recurved, expanded posteroventral tip forming a partial floor for it along with ventral covering piece. Ventral covering piece large, elongate-oval, broadly convex ventrally, and scoop-shaped, enclosing terminal cartilages and rear tips of marginals ventrally.

Dasyatis ukpam (Smith, 1863)

(Figures 6–9)

Hemitrygon ukpam Smith, 1863:69 (type-locality Old Calabar River, Nigeria); Fowler, 1936:126 (placed in synonymy of *D. centroura*); Fowler, 1969:186 (in synonymy of *D. centroura*).

Trygon ukpam Günther, 1870:480 (description after Smith, 1863, placed in *Trygon* = *Dasyatis*).

Dasyatis margarita Loubens, 1964:11 (freshwater lakes south of Lambarene district, Ogooué basin; presumably no specimens preserved).

Dasyatis ukpam Stehmann, 1981:4 (in key to marine *Dasyatis* of West Africa); Compagno and Roberts, 1982:321 (reference).

Material Examined.—BMNH 1874.5.23.1, syntype, 266-mm late fetal male, Old Calabar River, Nigeria; USNM 219780, 520-mm immature female, Lake Ezanga, Ogooué River system, Gabon; CAS 42761, 650-mm immature female, Lake Ezanga near Nzame-Akesile village, Ogooué River system, Gabon; MNHN 1979-244, 499-mm immature female, Booué, Ogooué River, Gabon; MRAC 55778, 361-mm immature female, Binda, Congo (Zaire) River, Zaire.

Diagnosis.—*D. ukpam* is a very large and thick-bodied freshwater dasyatid, probably growing much bigger than our largest specimen, a 650-mm immature female. Newborn young, 266 mm, are as large as the largest known *D. margaritella* and far larger than newborn young of *D. margarita* and *D. garouaensis.* Entire dorsal surface of disc covered with stout-spined denticles (smooth in newborn) (peripheral portions of disc without denticles in all other West African dasyatids except the very large marine species *D. centroura,* with a diamond-shaped disc, and *Urogymnus,* with an extremely thick disc). Sting greatly reduced in size or absent (sting invariably absent in *Urogymnus* but normally present and relatively large in all other West African dasyatids).

Disc oval, very thick. Medial lobe narrow-based and short, its anterior margin broadly convex; disc depth 13.3–15.7% of disc width, disc width 0.9–1.0 times disc length; dorsal surface of disc entirely covered with denticles at all free-living stages except possibly newborn; small, heart-shaped or circular denticles covering middle of disc, small prickles on sides of disc, with scattered large, conical, stellate, sharp denticles (absent in newborn and fewer in small immatures than large) and usually 1–3 small to moderate-sized midscapular pearl spines on disc; no sting, or a single small, possibly vestigial one, only 6.5% of disc width in 520-mm specimen; eyes small and strongly elevated, eyeball lengths 2.1–3.3 times in interorbital space; interorbital space 1.5–1.9 times in preorbital length; spiracles large and high; floor of mouth with 4 or 5 elongated papillae; total tooth rows 38–46/38–48; pelvic fins short, anterior margins 16–19% of disc width; tail uniformly tapering to a slender whiplash, its length from vent when intact 2.0–2.9 times disc width; base of tail circular in section; a very low ventral tailfold but no dorsal fold or keel; disc and pelvic fins dark brown or gray-brown above, without spots or prominent markings, white below except for broad dark margins; tail blackish except for underside of its base; intestinal valve turns 19–20; total pectoral radials 142–148, total vertebral centra 108–122 and total segments 155 (in one specimen), vertebral centra ending in front of sting or extending to its origin.

Proportional measurements (as percent of disc width) and counts are given in Table 1. Preoral length 2.3–2.6 times internarial width and 0.9–1.0 times width between first gill openings. Snout broad, angle in front of eyes 123–132°. Spiracle

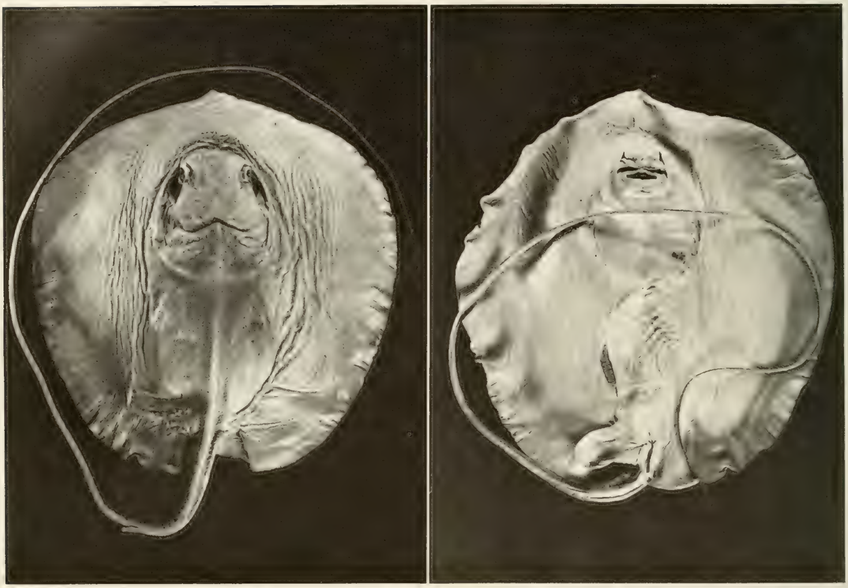


FIGURE 6. *Dasyatis ukpam,* 266-mm fetal male syntype, Old Calabar, Nigeria (BMNH 1874.5.23:1).

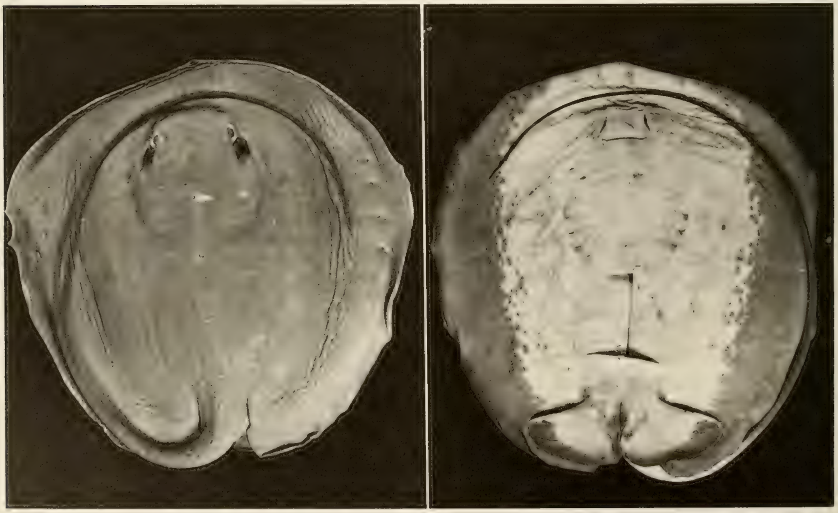


FIGURE 7. *Dasyatis ukpam,* 650-mm immature female, Lake Ezanga, Ogooué basin, Gabon (CAS 42761).

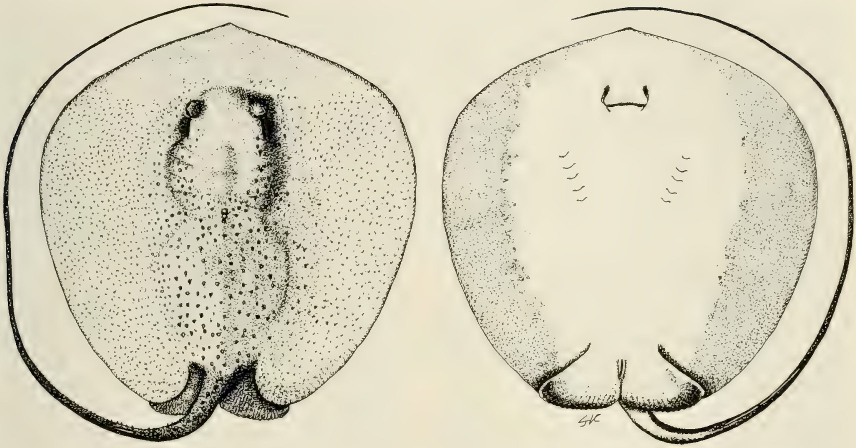


FIGURE 8. *Dasyatis ukpam,* 520-mm immature female, Lake Ezanga, Ogooué basin, Gabon (USNM 219780).

length 1.5–2.0 times eyeball length, 0.8–1.0 times internarial width, and 1.8–2.2 times in distance between fifth gill openings. Internal gill openings with close-set transverse ridges on gill arches. Nasal curtain with a fringed, slightly concave or trilobate posterior margin. Mouth weakly arched, midline of lower jaw slightly indented; a shallow to deep, curved groove extending posteriorly from posterior nasal flap around corners of mouth. Skin on ventral surface of lower jaw more or less

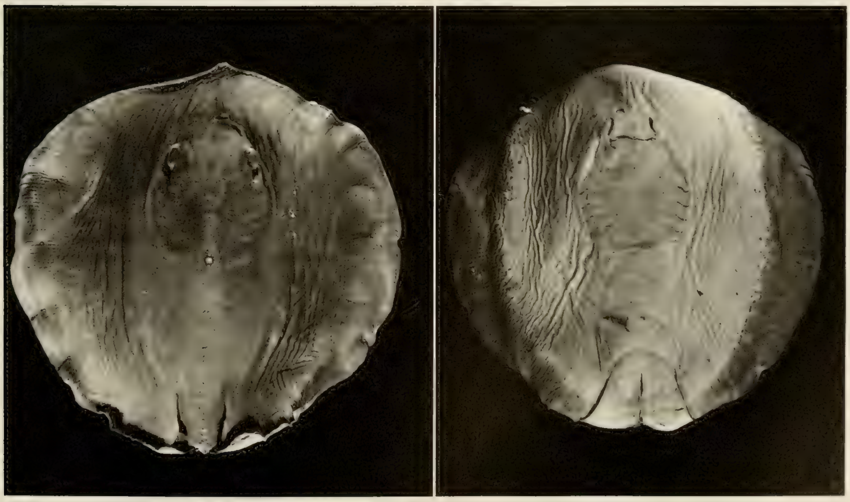


FIGURE 9. *Dasyatis ukpam,* 361-mm immature female, lower Zaire River at Binda, Zaire (MRAC 55778).

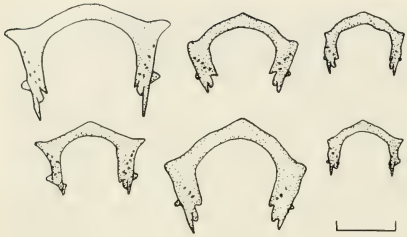


FIGURE 10. Pelvic girdle (dorsal view) in West African *Dasyatis*: (a) *D. ukpam*, 266-mm fetal male; (b) *D. ukpam*, 361-mm immature female; (c) *D. garouaensis*, 342-mm mature female; (d) *D. garouaensis*, 255-mm adult male; (e) *D. margarita*, 200-mm immature female; (f) *D. margaritella*, 190-mm mature male. Note prominent lateral prepelvic processes in *D. garouaensis*. Scale bar = 2 cm.

corrugated and papillate. Palate behind fringed maxillary valve with three strong, short ridges, a medial longitudinal ridge and a pair of diagonal lateral ridges. Two pairs of long, low ridges behind the three palatine ridges. Floor of mouth with a transverse row of usually three moderately large, elongated oral papillae, a medial papilla (absent in syntype) and a lateral papilla behind each end of dental band; a pair of large papillae just behind and lateral to medial papilla.

Upper jaw with about 4 and lower jaw with 6 functional tooth series. Teeth in quincunx pavement, close-set, with crowns closely adjacent to one another. Teeth similar in upper and lower jaws, uppers slightly larger than lowers at symphysis, varying continuously lateral to symphysis, teeth largest and longest relative to width at or near symphysis and smallest and shortest at mouth corners. Upper dental band with a low knob of slightly enlarged teeth at symphysis, separated from similar knobs on either side by depressions with smaller teeth; lower dental band with a weak symphyseal depression into which symphyseal knob of upper jaw fits; a pair of low lateral knobs fit into depressions in upper dental band. Teeth of both jaws in females with moderately high, broad-tipped, cuspless crowns shaped like mushroom caps, with a transverse, blunt keel or carina, strong transverse ridges on both labial and lingual sides, and a strong basal ledge and concave, inset basal groove separating crown and root. Roots moderately large, high, pedicellate, bilobed basally, with a transverse groove and nutrient foramen. Teeth of adult males unknown, but probably differ from those of females.

Dorsal surface of 266-mm late fetus covered with small flat denticles on middle third of disc and base of tail to its abbreviated sting, including dorsal surface of cranium, branchial region, scapular region, and abdominal area; in addition, specimen has two small, slightly elevated, enlarged rounded denticles or pearl spines in mediscapular area. The larger, free-living specimens examined have outer two-thirds of disc, snout, and tail posterior to sting region with small to moderately large, conical, prickle-like denticles in addition to flattened denticles covering midbelt; they also have massive, conical, erect, fluted, sharp denticles or thorns over much of dorsal surface of disc and tail base. Large thorns fewest on smallest (361-mm) specimen, most numerous on largest (650-mm), suggesting that they become more numerous with growth. These thorns make dorsal surfaces of large *D. ukpam* extremely rough, and, as noted by Smith (1863), difficult to handle. Free-living specimens examined have one or two round, enlarged pearl spines on mediscapular region.

Neurocranium observed on radiographs but it and other skeletal parts obscured by thickness of disc and heavy covering of denticles in this species. Cranium apparently similar to that of *Himantura signifer* as described in Compagno and Roberts (1982), but with a straighter anterior margin to its nasal capsules.

Pelvic girdle (Fig. 10a–b) broadly arched, semicircular, relatively thick, with a medial anterior angle but no medial prepubic process. Lateral prepubic processes low, rounded, and lobate; iliac processes well-developed; ischial processes short. Five obturator foramina present on one specimen.

Claspers of mature male not available.

DISCUSSION

It has been known for some time that stingrays identified as *Dasyatis margarita* represent two species (Daget and Iltis 1965; Blache et al. 1970; Stehmann 1981). It appears that the first ichthyologist to become aware of this was the late J. Cadenat; he recognized that the two species differ greatly in weight, the one not exceeding 1 kg while the other attains easily 15–20 kg and perhaps much more (quoted in Daget and Iltis 1965: 15). The small species is *D. margaritella*, the large one *D. margarita.* Both are common and widely distributed in shallow water along the coast of West Africa. Most accounts of *D. margarita* are based on *D. margaritella* or on both *D. margaritella* and *D. margarita. D. margaritella* is more common than *D. margarita* in museum collections and perhaps also in nature. We are unaware of any difference in habitat preference.

It is remarkable that such notable animals as freshwater stingrays remain so poorly known. We believe that they will be found in additional river basins in West Africa and that possibly additional freshwater species are present. We have heard that stingrays occur in the Sanaga basin in Cameroun, particularly in Lac Ossa, but have no material evidence for this. It is curious that no Dasyatidae have been reported from rivers west of Nigeria. This might be due to insufficient collecting.

A stingray was reported from the Cross River at Mamfe Pool by Sanderson (1937), but the specimen was not preserved, and the account is so extraordinary that we hardly know what to make of it. According to Sanderson, the ray was "diamond-shaped, like all fish of this class, and measured from the tip of one lateral point to the tip of the other, four feet eight inches; from the snout to the base of the tail, five feet eleven inches; and from the base to the tip of the tail, which had no fin, five feet two inches. Emerging from the upper edge of the tapering whip-like tail near its base was a long, straight, sharp spine or sting, one foot seven inches in length." He went on to say that the arrival of this monster altogether unhinged his sense of logic, so perhaps it also affected his ability to observe and record accurately. "That it was still alive and therefore undoubtedly caught in Mamfe Pool, as the natives stated, was almost incredible, because this bit of water was nearly three hundred miles from the sea. I therefore had to adjust myself to the idea that such things are true fresh-water animals indigenous to the great rivers of Africa. Why do not natural history books depict these fish instead of the everlasting crocodile?" Why not, indeed? Sanderson provides as good an answer as any: "We didn't want the brute because we were not collecting fish, but we photographed him alongside sundry natives and inanimate objects and purchased the sting." Unfortunately the photograph was not published and the sting had to be discarded: "When this sting got really dry it split longitudinally and opened like a star, revealing a clear crystalline plug within. This substance gradually broke up under the damp atmospheric conditions; some of it dropped in water fizzed furiously. I could not find anything that would preserve it among our selection of travelling drugs and chemicals."

We have seen dried stings of various rays without observing anything like the disintegration reported by Sanderson, and suspect he had a few chuckles and perhaps something else while concocting this giant sting. The fishermen at Mamfe, who regularly catch *D. garouaensis,* maintained that it is the only species of ray in the Cross River from Mamfe to the Nigerian border and that the example caught and preserved during the junior author's visit was nearly as large as the largest they had ever caught. When shown a photographic print of *D. ukpam* they indicated that this species was unknown to them. Concerning sting size, the largest sting we have observed on a West African freshwater ray is under four inches. In *Dasyatis centroura,* which probably has the largest sting of any marine species in West Africa, the sting of a specimen with a disc width of four feet eight inches would be only about six or seven inches. We conclude that *D. garouaensis* is the only species of stingray in the Cross River in the vicinity of Mamfe.

Identification of a specimen of *D. garouaensis* from Lagos may indicate that the species occurs in Lagos Lagoon and in the rivers flowing into it. Unfortunately the specimen is not accompanied by information on habitat, and we cannot rule out the possibility that it was caught in the Niger River and transported to Lagos.

Although the title of the paper in which *D. ukpam* was described states that it lives in the Old Calabar River, and the text indicates that it lives as much as 150 miles upriver (Smith 1863), this is based on hearsay. It should be noted that the vernacular name "ukpam" or "okpam" is a generical term for stingrays. At Mamfe this name is employed by present-day speakers of the Manyu and Ejagam languages for *D. garouaensis.*

The occurrence of an unidentified stingray in the Ogooué basin was first brought to our attention by an ichthyological colleague, Dr. Jaques Géry, who related to the junior author that he had observed two rays in the Ivindo near Makokou while collecting characins and other small fishes in 1964. The Ivindo flows into the Ogooué near Booué, where one of our specimens of *D. ukpam* was collected, but there are some formidable waterfalls on the Ivindo below Makokou and the species there might be different. The Zaire locality for *D. ukpam,* Binda, is on a relatively narrow and swift-flowing portion of the lower Zaire (Congo) River about 100 km upriver from the mouth of the river at Banana and 35 km downriver from the end of the mainstream rapids of the lower Zaire River near Matadi. No stingrays are known from the interior of the Zaire or Congo basin. So far as we have been able to determine *D. garouaensis* and *D. ukpam* are the only living freshwater stingrays known from Africa.

Acknowledgments

For providing information and facilitating examination of specimens we wish to thank Alwyne Wheeler, Mandy Holloway, and Oliver Crimmen, British Museum (Natural History); D. F. Thys van den Audenaerde, Musée Royale de l'Afrique Centrale, Tervuren, Belgium; and Thomas B. Thorson, School of Life Sciences, University of Nebraska. Fieldwork in Gabon was facilitated by the Centre National pour la Recherche Technique et Scientifique and particularly M. le Commissaire Nzoghe-Ngueme. We thank Jeanne Byloghe and Joseph Mebiaghe of Tame and Nzame-Akesile villages for catching *Dasyatis ukpam,* and Pierre Ville of Geri Consult, who also obtained a specimen of this species for us. Permission for fieldwork in Cameroun was kindly granted by the Office National pour la Recherche Scientifique et Technique. At Mamfe the junior author was assisted by S. T. Mbianyor of the Forestry Department, John Corrao and Alan Ferguson of the Peace Corps, and a number of excellent local fishermen.

Literature Cited

Bigelow, H. B., and W. C. Schroeder. 1953. Fishes of the western North Atlantic. Sears Found. Mar. Res., Mem. No. 1(2).

Blache, J., J. Cadenat, and A. Stauch. 1970. Clés de détermination des poissons de mer signalés dans l'Atlantique oriental. Faune Trop. (ORSTOM, Paris), No. 18.

Castello, H. 1973. Sobre la correcta posicion sistematica de la raya de agua dulce africana (Chondrichthyes, Dasyatidae) (Republic Federal del Camerun). Trab. V Congr. Latinoamer., Zool. 1:67–71.

Castex, M. 1967. Fresh water venomous rays. Pages 167–176 *in* Animal toxins. Pergamon Press, Oxford and New York.

Compagno, L. J. V., and T. R. Roberts. 1982. Freshwater stingrays (Dasyatidae) of Southeast Asia and New Guinea, with description of a new species of *Himantura* and reports of unidentified species. Environ. Biol. Fishes 7(4):321–339, 12 figs.

Daget, J., and A. Iltis. 1965. Poissons de Côte d'Ivoire (eaux douces et saumâtres). Mém. Inst. franc. Afr. noire no. 74.

Daget, J., and A. Stauch. 1963. Poissons de la partie Camerounaise du bassin de la Benoué. Mém. Inst. franc. Afrique noire 68:85–107.

Fowler, H. W. 1936. The marine fishes of West Africa. Bull. Amer. Mus. Nat. Hist. 70(1):1–606.

———. 1969. A catalog of world fishes (XI). Quart. J. Taiwan Mus. 22(3–4):125–190.

Günther, A. W. 1870. Catalogue of the fishes in the British Museum. 8.

Krefft, G. 1968. Knorpelfische (Chondrichthyes) aus dem tropischen Ostatlantik. Atlantide Rep. 10:33–76, pls. 3–6.

Loubens, G. 1964. Travaux en vue de développement de la pêche dans le bassin inferieur de l'Ogooué. Publ. Cent. Tech. Forest. Trop., Nogent-sur-Marne (Seine) 27:1–51.

Rafinesque, C. S. 1810. Caratteri di alcuni nuovi generi e nuove specie di animali (principalmente di pesci) e piante della Sicilia, con varie osservazioni sopra i medisimi. Palermo, 105 pp, 20 pls.

Reid, G. M., and H. Sydenham. 1979. A checklist of lower Benue River fishes and an ichthyogeographical review of the Benue River (West Africa).

Sanderson, I. 1937. Animal treasure. Viking Press, New York, 325 pp.

Smith, J. A. 1863. Notice of the ukpam, a large species (probably new) of sting ray (*Trygon,* Cuvier), found in the Old Calabar River, Africa. Proc. Roy. Phys. Soc. Edinburgh 1859–62, 2:64–69.

Stauch, A., and M. Blanc. 1962. Description d'un sélacien rajiforme des eaux douces du Nord-Cameroun, *Potamotrygon garouaensis* n. sp. Bull. Mus. Nat. Hist. Natr. (Paris) 34(2):166–171.

Stehmann, M. 1981. Dasyatidae. In Fischer, W., G. Bianchi, and W. B. Scott (eds.). FAO species identification sheets for fishery purposes. Eastern Central Atlantic. Fishing Area 34, 47(5):1–5.

Thorson, T. B., and D. E. Watson. 1975. Reassignment of the African freshwater stingray, *Potamotrygon garouaensis,* to the genus *Dasyatis,* on physiologic and morphologic grounds. Copeia 1975(4):701–712, figs. 1–3.

CALIFORNIA ACADEMY OF SCIENCES
Golden Gate Park
San Francisco, California 94118

PROCEEDINGS
OF THE
CALIFORNIA ACADEMY OF SCIENCES

Vol. 43, No. 19, pp. 301-315, 12 figs., 1 table. December 11, 1984

REVISION OF EASTERN PACIFIC CATALUFAS (PISCES: PRIACANTHIDAE) WITH DESCRIPTION OF A NEW GENUS AND DISCUSSION OF THE FOSSIL RECORD

By

John E. Fitch

Research Associate, California Academy of Sciences,
San Francisco, California 94118

and

Stephen J. Crooke

California Department of Fish and Game,
Long Beach, California 90802

Abstract: Four species of catalufas inhabit eastern Pacific waters: ***Cookeolus boops*** (Schneider, 1801), ***Heteropriacanthus cruentatus*** (Lacépède, 1801), ***Pseudopriacanthus serrula*** (Gilbert, 1891), and ***Priacanthus alalaua*** Jordan and Evermann, 1904. Each of these species is illustrated, and diagnostic characters, meristic data, morphometric measurements, maximum size, geographic range, depth distribution and other information also are presented. ***Heteropriacanthus*** is a new generic name for ***Priacanthus cruentatus,*** a cosmopolitan species that differs in numerous salient features from the species assignable to ***Priacanthus*** (i.e., ***alalaua, arenatus, hamrur, macracanthus, meeki*** and ***tayenus***). An identification key is presented. Otoliths (sagittae) and scales of the four eastern Pacific species also are illustrated. The only reported priacanthid fossils are from the Eocene of Europe. Of the six species, ***Pristigenys substriata*** is known from skeletal remains and is unquestionably a priacanthid. Only two of the five species described from otoliths, ***Pristigenys bella*** and ***P. dentifer,*** appear to be priacanthids, but there is no assurance they can be assigned to ***Pristigenys,*** since none of the skeletal "imprints" of ***P. substriata*** contained otoliths, nor do all of the otoliths assigned to these two species appear to be correctly identified.

Introduction

For years, fishermen aboard long-range sportfishing boats that operated out of San Diego sought only such large game species as yellowfin and bigeye tuna (*Thunnus albacares* and *T. obesus*), wahoo (*Acanthocybium solanderi*), yellowtail (*Seriola lalandi*), giant sea bass (*Stereolepis gigas*) and several kinds of large serranids (*Epinephelus* spp. and *Mycteroperca* spp.). During 1978, however, at the urging of California Department of Fish and Game (DFG) biologists, skippers and crew members of these vessels commenced fishing for and saving miscellaneous small fishes caught at the Revillagigedo Islands, Alijos Rocks, and other fishing spots off southern Baja California.

Among the first of these incidentally caught species turned over to DFG personnel were a half-dozen catalufas that appeared to represent three species of *Priacanthus*. A literature search

FIGURE 1. Type specimen of *Anthias macrophthalmus* Bloch, 1792 (ZMB 8156). Photo courtesy of Hans-J. Paepke, Museum für Naturkunde der Humboldt–Universität zu Berlin.

and examination of all the priacanthids in the fish collections at Scripps Institution of Oceanography (SIO), Natural History Museum of Los Angeles County (LACM), University of California, Los Angeles (UCLA) and California Academy of Sciences (CAS) revealed that, until then (Dec. 1978), any priacanthid collected in the eastern Pacific that was not judged to be either *Pseudopriacanthus* or *Cookeolus,* automatically had been relegated to *Priacanthus cruentatus* (see also Fitch and Schultz 1978).

Once it became obvious that we were dealing with several species, the differences in scale counts, pelvic fin pigmentation, eye diameter, otoliths, and gas bladder morphology became equally obvious. During the succeeding four years, in an effort to determine exactly what species we were observing, we examined several hundred priacanthids from throughout the world. As a result, we arrived at the conclusion that there were four species of catalufas in the eastern Pacific: *Cookeolus boops, Priacanthus alalaua, Priacanthus cruentatus* and *Pseudopriacanthus serrula.*

In the course of our investigation, we found that otoliths (sagittae) and gas bladders of *Priacanthus alalaua* were so radically different from otoliths and gas bladders of *P. cruentatus* that a new generic name was needed for one of the two. This necessitated determining the condition of the otoliths and gas bladder of Bloch's (1792) *Anthias macrophthalmus,* since it was the type-species for *Priacanthus* Oken, 1817. Fortunately, Bloch's type specimen, a skin from the right side of the fish, still exists in the Museum für Naturkunde der Humboldt-Universität zu Berlin (ZMB8156), and Hans-J. Paepke, Curator of Fishes, sent us an excellent photograph of this specimen (Fig. 1). Wayne Starnes (pers. comm.), to whom we sent a copy of the photograph, has confirmed that Bloch's *Anthias macrophthalmus* is conspecific with *Sciaena hamrur* Forsskål, 1775.

Key to Eastern Pacific Priacanthidae

1a. Pored scales in lateral line 35 to 40; dorsal soft rays 11 (rarely 10 or 12); anal rays 10; dorsal profile turns abruptly downward under base of soft portion of second dorsal fin; ventral profile turns abruptly upward

FIGURE 2. *Pseudopriacanthus serrula.* Photo by Jack W. Schott.

under anal fin base; ctenii on scales in parallel species, presenting a corrugated or waffled appearance .... *Pseudopriacanthus serrula*

1b. More than 50 pored scales in lateral line; 12 (rarely) or more dorsal soft rays; 12 or more anal rays; dorsal and ventral profiles tapering gradually to caudal peduncle; ctenii on scales not as above 2

2a. Eighteen to 20 scale rows between 8th dorsal spine and lateral line; more than 20 rows on dorsum of caudal peduncle; anal rays 13; peduncle depth about equal to horizontal eye diameter; dorsal, anal and caudal fins yellow, edged with black; ctenii thick and bristlelike, in rows .... *Cookeolus boops*

2b. Eight to 10 scale rows between 8th dorsal spine and lateral line; fewer than 15 scale rows on dorsum of caudal peduncle; anal rays 14; peduncle depth fits about 1¼ times into horizontal eye diameter; dorsal, anal and caudal fins never with yellow or tipped with black; ctenii thin and filamentous 3

3a. Second dorsal, anal and caudal fin membranes red, without spotting; pelvic fin membranes jet black; gas bladder with anteriorly projecting "ears" that extend to the otic bullae, and posteriorly projecting horns that reach to above end of anal fin; otoliths (sagittae) with a ventral keellike blade and centrally positioned pronglike rostrum; ctenii filamentous, in rows; preopercle completely scaled .... *Priacanthus alalaua*

3b. Second dorsal, anal and caudal fin membranes with rust-colored spotting (dusky in formalin-preserved specimens); pelvic fin membranes lightly pigmented to clear; gas bladder contained entirely within body cavity, without ears and no anterior or posterior projections; otoliths (sagittae) lack keellike blades, oval in outline, with normal, anteroventral rostrum; ctenii filamentous, only on scale margin, sparse; posterior margin of preopercle without scales .... *Heteropriacanthus cruentatus* new genus

SPECIES ACCOUNTS

Pseudopriacanthus serrula (Gilbert, 1891)

(Figure 2)

DIAGNOSTIC CHARACTERS.—35 to 40 pored scales in lateral line; 10 to 12 (typically 11) dorsal soft rays; 10 anal rays; ctenii on scales in a parallel series (Fig. 3d) presenting a corrugated or waffled appearance; dorsal profile turns abruptly downward, becoming nearly vertical, under second dorsal fin base; ventral profile becomes nearly vertical under anal fin base.

MERISTIC DATA.—D. X,10–12; A. III,10; P. 17; GR 6–7 + 15–18 = 21–25; pored lateral line scales 35–40; vertebrae 10 + 13 = 23. Twenty-three of the 25 specimens we examined for meristic data had 11 dorsal soft rays, one had 10, and one had 12.

MAXIMUM SIZE.—The largest individual we observed was a female 274 mm SL (353 mm TL) that weighed 1300 g. This was one of 24 individuals caught in gill nets in "30–40 fm" (55–73 m) off Magadalena Bay, Baja California, during March 1976.

RANGE.—Monterey Bay, California, to Talara, Peru (Fitch and Lavenberg 1975) and at most offshore islands from the Coronados to the Galapagos in 3.6 to more than 100 m (DFG, unpublished data).

REMARKS.—Morphometric data were taken on only 13 of the more than 60 individuals we examined (Table 1). The smallest of these (34 mm SL, LACM 22796) had a relatively short pelvic fin (41% of SL) as compared with the Eocene fossil *Pristigenys substriata* (Fig. 11) and pelagic stages of the extant *Cookeolus boops* (Fig. 5, Table 1). Fritzsche and Johnson (1981) considered *Pseudopriacanthus* a junior synonym of *Pristigenys,* but for reasons given later, we believe both genera are distinct and valid.

Of perhaps 20 individuals that have been caught or observed in Californian waters, one each was from Monterey Bay and off San Luis Obispo, the rest have been from south of Pt. Dume. Scuba divers report that *P. serrula* is unafraid and can be picked up by hand when encountered in its natural surroundings.

Cookeolus boops (Schneider, 1801)

(Figure 4)

DIAGNOSTIC CHARACTERS.—18 to 20 scale rows between eighth dorsal spine and lateral line; more than 20 rows of scales on dorsum of caudal peduncle; ctenii on scales thick and bristlelike (Fig. 3a), in rows; anal rays 12–13; dorsal, anal and caudal fins yellow, edged with black; peduncle depth about equal to horizontal eye diameter; pelvic fins of pelagic juveniles comprise 50–70% of SL or more.

MERISTIC DATA.—D. X,13; A. III,12–13; P. 18–19; GR 6–8 + 17–18 = 23–26; pored lateral line scales 53–61; vertebrae 10 + 13 = 23. One of the 35 specimens we examined for meristic data had 12 anal rays, the rest had 13.

MAXIMUM SIZE.—The largest individual we observed was a female 397 mm SL (507 mm TL) that weighed 2725 g. It was caught by a sportfisherman at Alijos Rocks, Baja California, Mexico, in 1974 in "18 fm" (33 m) of water. This fish (LACM 34253) was erroneously identified by Fitch and Schultz (1978) as *Priacanthus cruentatus.* In the western North Atlantic, a *C. boops* has been reported that was 507 mm SL and weighed 5.2 kg (Anderson et al. 1972).

RANGE.—Worldwide in tropical and subtropical seas; in the eastern Pacific from Alijos Rocks, Mexico (24°57′N, 115°45′W) to 10°N 98′W (LACM 30506-1). Although adults have been caught in water as shallow as 30 m in the eastern Pacific, they are most commonly hooked at depths "exceeding 40 fm" (73 m) and have been taken as deep as "75 fm" (137 m). Pelagic juveniles have been captured at the surface at scattered offshore localities between the Tres Marias Islands and the Gulf of Tehuantepec. In the western North Atlantic, *C. boops* has been taken at depths exceeding 365 m (Anderson et al. 1972).

REMARKS.—Although *Cookeolus* was not recognized from the eastern Pacific until Fritzsche (1978) reported upon six pelagic juveniles ranging from 148 to 226 mm SL, adults had been taken at Alijos Rocks as early as 1970, but were erroneously identified as *Priacanthus cruentatus* (Fitch and Schultz 1978). Not until 1978, when long-range sportfishing boats started bringing in fair numbers of adult *C. boops* from Alijos Rocks, the Revillagigedo Islands and Hurricane Bank (16°52′N, 117°28′W) were they recognized for what they were. Most of the confusion in identification had resulted from the relatively shorter

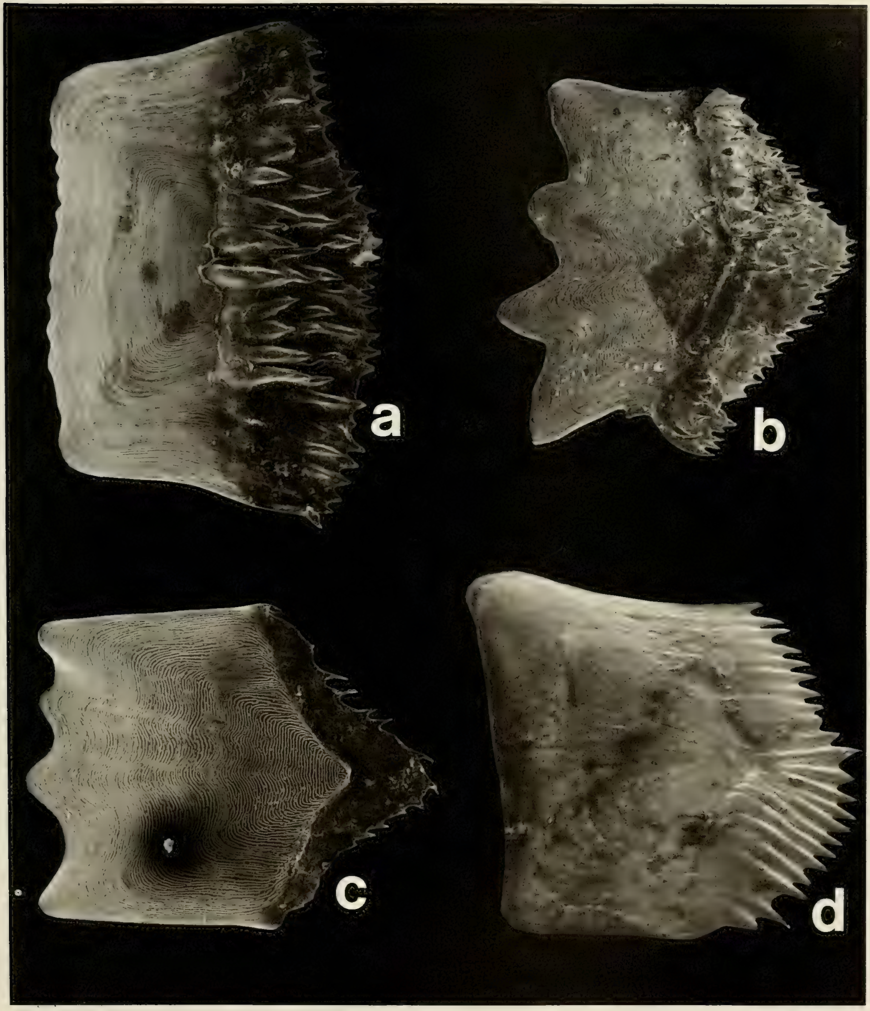


FIGURE 3. Scales of eastern Pacific Priacanthidae (scale height and length, in mm, in parens): a) *Cookeolus boops* (4.6 by 3.5); b) *Priacanthus alalaua* (3.1 by 3.1); c) *Heteropriacanthus cruentatus* (1.9 by 2.4); d) *Pseudopriacanthus serrula* (3.6 by 4.0). SEM photos by Richard Huddleston.

pelvic fins of the bottom-dwelling adults and the lack of spots and blotches which are so typical of the pelagic juveniles (Fritzsche 1978).

Although pelvic fin length commences to shorten when *Cookeolus* takes up a bottom-dwelling existence, six of the specimens we used in obtaining morphometric data (Table 1) still had pelvic fins that exceeded 40% of SL. All six of these fish, ranging from 197 to 267 mm SL (Fig. 5), had been hooked on the bottom. On the other hand, two bottom-dwelling specimens (222 and 257 mm SL) had pelvic fins that had short-

FIGURE 4. *Cookeolus boops.* Photo by Lee Stockland.

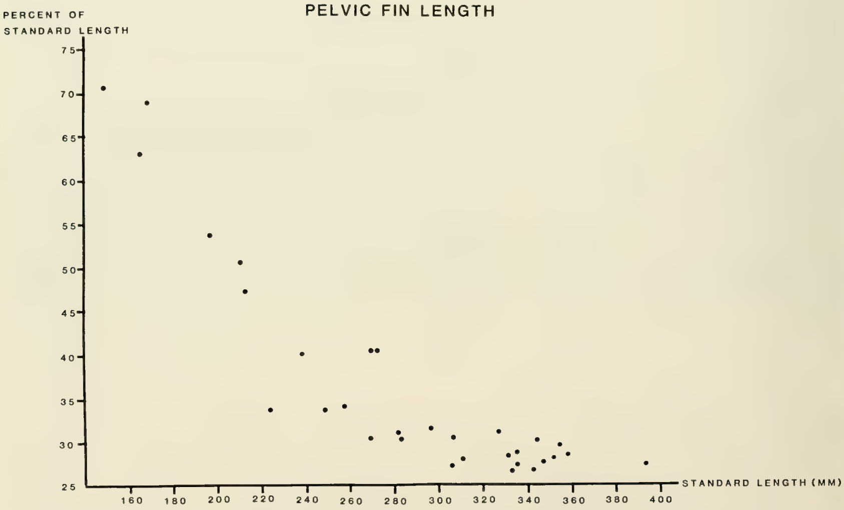


FIGURE 5. Pelvic fin length (as percent of SL) plotted against SL for 32 specimens of *Cookeolus boops.*

FIGURE 6. Juvenile *Cookeolus boops,* 211 mm SL, taken on hook and line in "15 fms" at Alijos Rocks. Photo by Paul Gregory.

TABLE 1. COMPARATIVE MEASUREMENTS FOR THE FOUR EASTERN PACIFIC PRIACANTHIDS (in percent standard length).

	Species and number of specimens measured			
Measurement	*Pseudopriacanthus serrula*	*Cookeolus boops*	*Priacanthus alalaua*	*Heteropriacanthus cruentatus*
Number of specimens	13	32	14	50
Standard length (mm)	34–261	151–392	215–261	81.5–245
Head length	36.1–41.2	31.2–37.4	29.4–33.3	28.6–36.4
Horizontal eye diameter	14.3–18.0	9.6–13.9	12.5–14.1	10.2–15.2
Snout length	9.0–11.4	9.8–11.7	9.5–10.5	9.0–10.1
Maxillary length	20.0–21.6	16.6–19.2	14.7–16.1	15.5–17.1
Bony interorbital width	7.9–10.2	8.2–10.5	8.0–9.1	8.4–10.1
Snout to 1st dorsal fin insertion	33.7–36.4	28.0–33.3	30.0–32.3	29.7–32.3
Snout to pectoral fin insertion	37.6–40.8	31.7–37.9	30.9–34.8	30.1–32.9
Snout to pelvic fin insertion	44.8–46.8	34.0–44.0	33.3–38.8	35.4–38.3
Snout to anal fin insertion	70.9–75.6	58.1–67.9	55.3–60.9	51.3–59.0
Dorsal fin insertion to pelvic insert	48.4–53.6	37.7–48.8	36.4–39.1	35.0–40.3
Depth perpendicular to AS_1	48.8–54.2	37.1–49.2	35.6–38.6	34.3–39.8
Caudal peduncle depth	12.8–14.0	9.6–12.3	7.7–8.2	8.3–10.5
Pectoral fin length	19.3–23.2	18.9–24.8	20.8–23.2	17.0–21.0
Pelvic fin length	25.6–35.4[1]	27.0–70.2[2]	25.3–31.4	19.7–26.7
Longest gill raker	5.9–8.8	5.0–7.2	4.1–5.4	4.4–5.2

[1] Pelvic fin length of 34 mm specimen (41.2%) not included, remaining specimens 172 to 261 mm SL.

[2] See Figure 5.

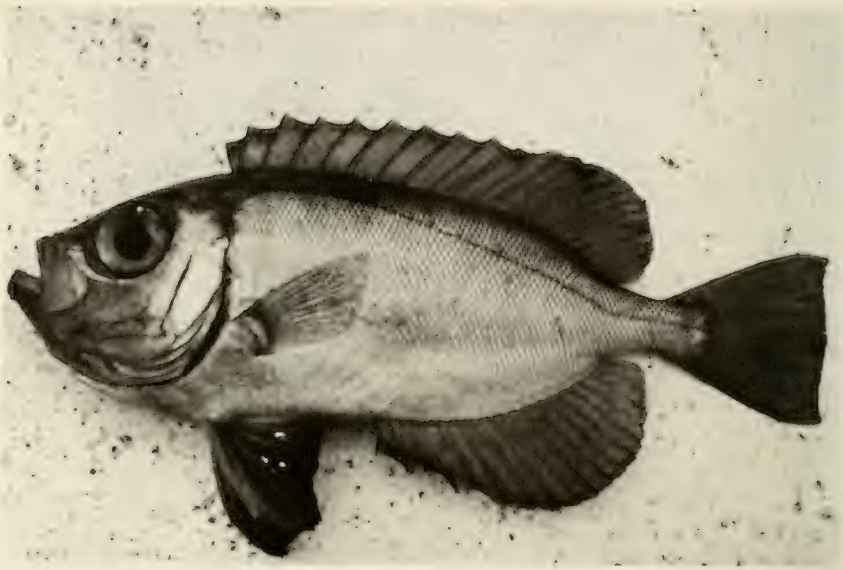


FIGURE 7. *Priacanthus alalaua.* Photo by Lee Stockland.

ened to 34% of SL (Figs. 5 and 6). The largest pelagic juvenile reported by Fritzsche (1978) was 226 mm SL. Based upon these lengths, in the eastern Pacific, *Cookeolus* remains in the pelagic environment until it reaches a size of approximately 200–250 mm SL.

Interestingly, the otoliths (sagittae) of *Cookeolus* also change with adulthood (Fig. 8c, d). Those of pelagic juveniles are almost perfectly oval in outline with a ratio of height into length of about 1:1.25. In adults, the otolith becomes more elongate (height into length ratio 1:1.6) and the posteroventral border becomes slightly concave as the marginal ornamentation (lobules) spreads and the notches deepen. We do not know of any other perciform in which such differences in otolith morphology occur with age.

Priacanthus alalaua Jordan and Evermann, 1904
(Figure 7)

DIAGNOSTIC CHARACTERS.—Second dorsal, anal and caudal fin membranes red; pelvic fin membranes jet black; gas bladder with anteriorly projecting "ears" that extend beyond the body cavity to the otic bullae, and posteriorly projecting horns that reach to above the end of the anal fin (Fig. 9); otoliths (sagittae) with a ventral keellike blade and centrally positioned pronglike rostrum (Fig. 8e); preopercle completely scaled; ctenii filamentous, in rows (Fig. 3b).

MERISTIC DATA.—D. X,13; A. III,14; P. 18–19; GR 4–6 + 14–17 = 19–23; pored lateral line scales 61–66; vertebrae 10 + 13 = 23. Only one of the 20 specimens we examined for meristic data had 19 elements in the pectoral fin; the rest had 18.

MAXIMUM SIZE.—The longest individual we observed was a female 261 mm SL (335 mm TL) from San Benedicto Island, Revillagigedos. The heaviest individual was a 257 mm SL female from Socorro Island, Revillagigedos, which weighed 574 g. Gosline and Brock (1960) report that in Hawaiian waters *P. alalaua* "reaches 14 inches in length" (357 mm), but they apparently did not examine any specimens of this species.

RANGE.—Hawaiian Islands and eastern north Pacific. In the eastern North Pacific, *P. alalaua* has been taken at Alijos Rocks and all of the Revillagigedo Islands (San Benedicto, Socorro, Roca Partida and Clarion). In the Revillagigedos, where sportfishermen catch fair numbers on oc-

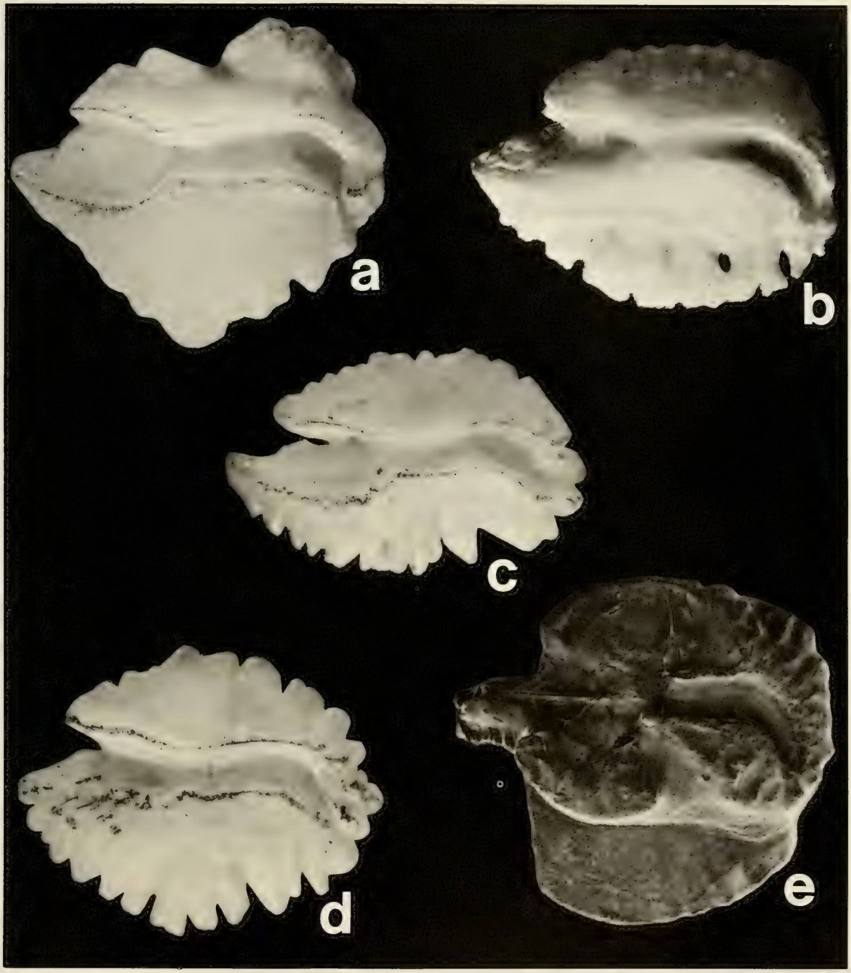


FIGURE 8. Otoliths (sagittae) of eastern Pacific Priacanthidae (otolith length and fish SL, in mm, in parens): a) *Pseudopriacanthus serrula* (7.2 and 2.9); b) *Heteropriacanthus cruentatus* (5.3 and 195); c and d) *Cookeolus boops* (7.6 and 257; 5.5 and 180); e) *Priacanthus alalaua* (3.6 and 221). Photos a through d by Jack W. Schott; SEM photo e by Brian White.

casion, it has been taken mostly at night in depths of "5 to 25 fm or more" (9–46 m).

REMARKS.—Although three individuals of *P. alalaua* were taken in gill nets set overnight just upcoast from Braithwaite Bay, Socorro Island, in April 1955, they were misidentified as *P. cruentatus,* and meristic data from them (e.g., "A. III,13") were reported by Fitch and Schultz (1978) along with data from seven *cruentatus* taken at the same time and place. Fortunately, their unique otoliths had been removed and saved, and counts and measurements were made before they were skeletonized, so subsequent identification as *P. alalaua* was easily verified.

FIGURE 9. Gas bladder (124 mm total length) from *Priacanthus alalaua* 220 mm SL. Drawing by Mary Butler.

We examined the entire collection (worldwide) of priacanthids at Los Angeles County Museum of Natural History and found that *arenatus, hamrur, macracanthus, meeki,* and *tayenus* possessed similar peculiar gas bladders and otoliths. Therefore, we believe these species should be assigned to *Priacanthus.*

Heteropriacanthus new genus

TYPE-SPECIES.—*Priacanthus cruentatus* (Lacépède, 1801).

DIAGNOSIS.—Second dorsal, anal and caudal fins with rust-colored spotting (dusky in formalin-preserved specimens); pelvic fin membranes lightly pigmented to clear; gas bladder thin-walled, contained entirely within the body cavity; otoliths (sagittae) oval in outline with normal anteroventral rostrum (Fig. 8b); ctenii filamentous, sparse, and only on scale margin (Fig. 3c); posterior margin of preopercle scaleless.

ETYMOLOGY.—From Greek *heteros* (different), alluding to its being different from other *Priacanthus.*

Heteropriacanthus cruentatus (Lacépède, 1801)

(Figure 10)

DIAGNOSTIC CHARACTERS.—As for the genus.

MERISTIC DATA.—D. X,12–13; A. III,14–15; P. 17–19; GR 5–6 + 17–20 = 22–25; pored lateral line scales 57–65; vertebrae 10 + 13 = 23. Only two of the 61 specimens we examined for meristic data had 12 dorsal soft rays; the rest had 13. One specimen had an anal count of V,13 (LACM 32283), obviously a freak, so it was not included. Of the remaining 60 specimens, two had counts of III,15 and the rest III,14. All but eight specimens had 18 total elements in their pectoral fins; three had 17 and five had 19.

MAXIMUM SIZE.—The largest individual we observed (sex undetermined) from the eastern Pacific was 247 mm SL (315 mm TL). This fish (SIO 70-136) was from the Gulf of Chiriqui, Panama. We did not obtain a weight for it or for any other large *H. cruentatus.*

RANGE.—Worldwide in tropical and subtropical seas. In the eastern Pacific, *H. cruentatus* ranges from Guadalupe Island, Baja California (SIO 60-18) to the Galapagos Islands, Ecuador (numerous West Coast collections) in depths of "2 to 15 fm" (3.6–27 m) at least. Within this range, it has been collected at all of the Revillagigedo Islands, Hurricane Bank, the Tres Marias Islands (Mexico), Cocos Island (Costa Rica), and many islands off Panama. Its mainland distribution is not so extensive, ranging from Cape San Lucas, Baja California (UCLA-W52-259) to Panama (SIO 70-140).

REMARKS.—Typically an overall reddish or crimson when alive, *H. cruentatus* often will develop silvery marbling or blotching on the sides and back. Thomson et al. (1979) suggest that this color pattern results from stress.

Although we examined specimens of *H. cruentatus* from several localities far removed from the eastern Pacific, we were unable to find any differences that could be considered of specific, or even subspecific, magnitude.

FOSSIL RECORD

Fossil priacanthids have been reported only from Europe and only from Eocene deposits. These fossil remains have consisted of skeletal bones and impressions from Italy (*Pristigenys substriata*: see Fritzsche and Johnson 1981), otoliths from Belgium and France (*Pristigenys rutoti* and *P. caduca*: Stinton and Nolf 1970; Nolf 1973), and otoliths and dorsal fin spines from England (*P. bella, P. spectabilis,* and *P. dentifer*: Stinton 1980).

In identifying fossil fishes, an ideal situation would be to have a three-dimensional specimen with all bony elements and conventional characters present (e.g., viscera, gas bladder, scales, otoliths, etc.). Unfortunately, this does not happen. Soft parts can only be inferred. Rarely are three-dimensional fossil fishes found, and even two-dimensional skeletal impressions are not all that common compared with isolated teeth, scales, otoliths, and bones (Schafer 1972). Obviously, the more complete the fossil specimen or specimens, the greater the likelihood of making a correct identification.

The skeletal impressions of *P. substriata* from Italy generally have been in excellent condition and have permitted direct comparison of many salient features with the same features on extant priacanthids. None of these two-dimensional skeletal impressions has contained otoliths, how-

FIGURE 10. *Heteropriacanthus cruentatus.* Photo by Paul Gregory.

ever; to associate isolated otoliths with the genus *Pristigenys* is pure speculation.

In using otoliths (sagittae) as a taxonomic character, the most important feature for determining family and/or generic relationships (including ancestry) is the sulcus or groove on the inner face: its position, configuration, proportions, angle of curvature, and other features. If features of the sulcus do not match exactly, the otolith cannot belong to the same genus as the one to which it is being compared. Overall otolith shape, ratio of height into length, marginal ornamentation and similar surface features are important primarily at species level.

FOSSIL ACCOUNTS

Pristigenys substriata (Blainville, 1818)

(Figure 11)

White (1936) presents an excellent account of the taxonomy of this species as follows:

> Among the numerous fossil fishes described by Volta (1796 . . .) from the lower Lutetian of 'Monte Bolca' was a small imperfect specimen which he identified with the living species *Chaetodon striatus*, . . . illustrating his description with a figure that is unusually obscure; this specimen was later referred by de Blainville (1818 . . .) to a new species *C. substriatus.* Agassiz (1835 . . .) recognizing that the fossil was not a *Chaetodon,* renamed it completely, *Pristigenys macrophthalmus,* and sketched a few of its more obvious characters, which led him to suppose that this was 'un genre voisin de *Beryx*'; and under Agassiz' name it was listed among the Berycidae by A. S. Woodward (1901 . . .); finally, Eastman (1905 . . .) added details omitted by previous authors, and re-figured the unique original specimen. Eastman rightly named the species *Pristigenys substriatus* (for while Agassiz' genus is good, so is de Blainville's species), and retained it in the Berycidae.

White went on to report that the fossil was not a berycoid but a priacanthid, which, in his opinion, was identical with the extant *Pseudopriacanthus* Bleeker, 1869, and that this generic name, by reason of its later publication date, must be replaced by *Pristigenys.*

White's report appears to have been overlooked by subsequent authors until Myers (1958) called it to the attention of contemporary ichthyologists. Subsequently, as discussed by Fritzsche and Johnson (1981), there has been considerable controversy as to the validity of placing *Pseudopriacanthus* in the synonymy of *Pristigenys.* In concurring with such synonymy, Fritzsche and Johnson point out that a "predorsal bone" is a character shared only by *Pristigenys* and *Pseudopriacanthus* among all priacanthid genera. Interestingly, they support their contention of close relationship by presenting four

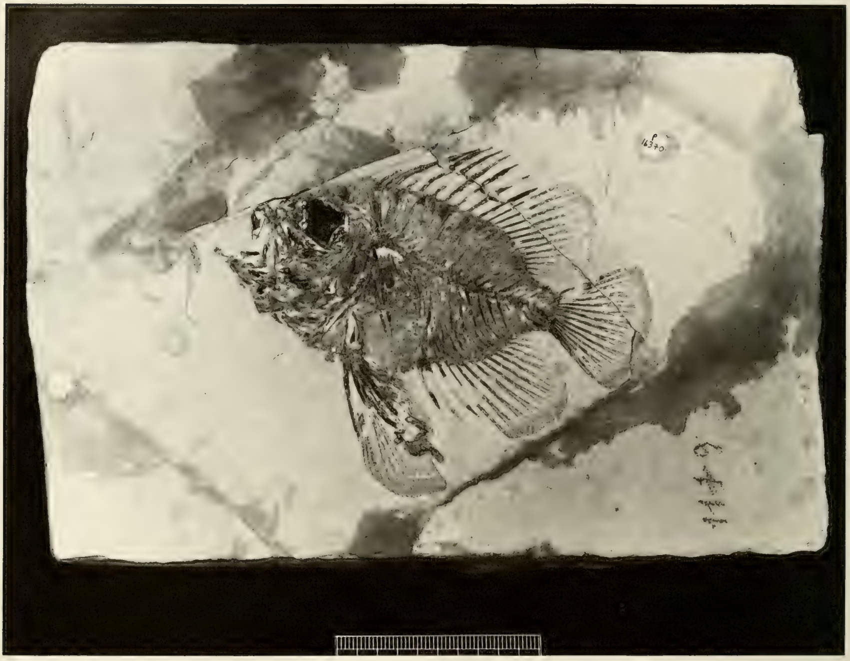


FIGURE 11. *Pristigenys substriata* (BMNH P.16370) 155 mm SL. Photo courtesy of Colin Patterson, British Museum (Natural History).

sets of morphometric data and two sets of meristic characters (from *Pristigenys substriata* and *Pseudopriacanthus altus*), while one paragraph later they state that "morphometric characters are not generally considered to be valid indicators of relationship" within the perciforms.

After carefully examining all available characters for the fossil *Pristigenys substriata* and for three species of the extant *Pseudopriacanthus* (i.e., *altus, niphonius,* and *serrula*), it is our contention that both *Pristigenys* and *Pseudopriacanthus* are valid genera. While we agree that these two genera share at least one character that appears to be of generic magnitude (i.e., the "predorsal bone" of Fritzsche and Johnson), there are other salient characters of equal magnitude that are shared with other priacanthid genera or are distinctive within their own genus.

Based upon the associated Monte Bolca fish fauna, *Pristigenys substriata* was living in a pelagic environment. The pelagic environment and extremely long pelvic fins (Fig. 5) are shared with juvenile *Cookeolus,* and apparently all known specimens of *P. substriata* represent juveniles as none exceeds 155 mm SL. The scales of *Pseudopriacanthus* (Fig. 3d) are unique among priacanthids for the shape and arrangement of ctenii; scales of *Pristigenys* appear to resemble those of *Priacanthus* or *Heteropriacanthus* (Colin Patterson, pers. comm.). Other features of *Pristigenys* (e.g., scale size, body shape, dorsal fin spine, and ray lengths) are intermediate to the same features as found on *Cookeolus* and *Pseudopriacanthus.* There is other less salient evidence to support retention of both *Pristigenys* and *Pseudopriacanthus* as valid genera.

Pristigenys rutoti (Leriche, 1905)

(Figure 12b)

Otoliths of this species were described and figured from Belgium by Leriche as "*Sparidarum rutoti.*" Subsequently, Schubert (1916) reported their occurrence in England (refuted by Stinton 1980) and mentioned their similarity to "*Otolithus* (*Sparidarum*) *rutoti Leriche* [sic]," but then erroneously referred them to Koken's (1891) *Otolithus* (*Sparidarum*) *gregarius* using the combination "*Otolithus* (*Pagellus*?) *gregarius.*" Additional errors in their taxonomy appeared in later years by other authors, climaxed by their being placed in "family Pseudopriacanthidae" (genus *Pseudopriacanthus*) by Stinton and Nolf (1970). Because Leriche used the genitive plural in giving these a generic name, he cannot be considered the authority for the species, nor can the 1905 publication date be considered valid. Schubert might possibly qualify as the author, but depending upon interpretation of the International Rules of Zoological Nomenclature, this also is questionable. It is entirely possible that Stinton and Nolf are the authorities for "*Pristigenys rutoti,*" with a publication date of 1970, but the matter is irrelevant to priacanthid taxonomy because features of the sulcus of this fossil otolith do not permit its placement in family Priacanthidae. In sagittae of extant priacanthids (except *Priacanthus*) the upper and lower rims of the ostium (anterior part of the sulcus) converge posteriorly to appear slightly ovoid and funnel-shaped (Fig. 7a–d).

In the fossil otolith, the dorsal rim of the sulcus sweeps posteriorly in a continuous, gentle sigmoid curve, making it difficult to distinguish ostium from cauda without reference to the ventral rim, which sweeps abruptly dorsad at its juncture with the cauda. The ostium comprises less than 37% of total otolith length in three species of *Pseudopriacanthus,* whereas in *Pristigenys rutoti,* ostium length exceeds 41% of otolith length. Finally, when priacanthid otoliths (except *Priacanthus*) are placed with the outer face down on a flat surface, the sulcal side is highly arched (convex). Sagittae of *P. rutoti* lie almost flat when placed in this position.

Pristigenys caduca Nolf, 1973
(Figure 12c)

Features of the sulcus of this otolith do not permit a placement in the family Priacanthidae.

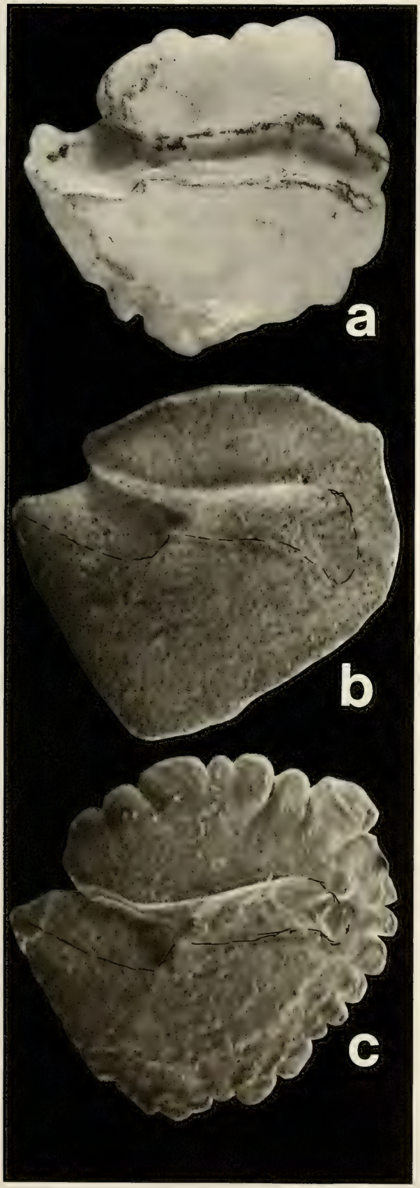


FIGURE 12. Otoliths (sagittae) of: a) *Pseudopriacanthus niphonius* (type species of *Pseudopriacanthus*) 6.5 mm long; b)

←

Pristigenys rutoti 2.7 mm long; and c) *Pristigenys caduca* 2.7 mm long. Photo of *Pseudopriancanthus* by Jack W. Schott; SEM photos of *Pristigenys* by Brian White. Sulcus of fossils highlighted with broken inked line to show configuration.

Again, the dorsal rim of the sulcus forms a continuous, gentle sigmoid curve, while the lower rim of the ostium sweeps abruptly upward at its posterior terminus—a beryciformlike ostial character, but also found in such unrelated fishes as *Lactarius, Epigonus, Ambassis, Glaucosoma,* some pempherids, and others.

Pristigenys bella Stinton, 1980

We have not handled otoliths from this species, but from Stinton's excellent photographs, it appears that the holotype and paratype shown in his text figure 34 are valid priacanthid sagittae. We cannot vouch for their generic placement, however, as otoliths do not accompany the skeletal impressions of *Pristigenys substriata,* the type of the genus. Again, because of ostial configuration, we question the assignment of the otoliths (presumably *P. bella*) shown in Stinton's Plate 13 (figs. 27 and 28) to family Priacanthidae. Stinton states that these otoliths "are from immature fish and demonstrate the ontogenetic changes [found in otoliths of these fishes]." Except for *Cookeolus,* which goes from a pelagic existence as juveniles to a benthic existence as adults, we have not observed ontogenetic changes in priacanthid sagittae, and the changes in *Cookeolus* otoliths are not the same as those attributed by Stinton to his fossil *P. bella.*

Pristigenys spectabilis Stinton, 1980

We have examined a dozen otoliths from this species, and judged by sulcal characters, it should not be assigned to family Priacanthidae. Stinton's excellent photographs of type material also show the non-priacanthid ostial configuration that precludes their being priacanthids.

Pristigenys dentifer Stinton, 1980

Based upon Stinton's photographs of the otoliths of *P. dentifer,* we believe that more than one species is involved. Some of his illustrated sagittae are very similar to priacanthid otoliths in sulcal characters, while others do not appear to be. One of his paratypes was found associated with "a few bones and spines" inside the cavity of a gastropod, *Clavilithes macrospira.* According to Stinton "some [of the] peculiarly prickly fin spines . . . were independently identified as a species of *Pristigenys.*"

We were loaned one of these fin spines by Colin Patterson (BMNH), who informed us (pers. comm.) that these prickly spines "are certainly different from those of *Pristigenys substriata,* which are smooth apart from longitudinal ribs." We compared the fossil spine with fin spines of all extant genera of priacanthids and could find no agreement with any of them. Camm Swift (LACM) examined the spine and suggested it bore resemblance to some beryciform fin spines, but was unable to suggest a family or generic affiliation.

Otoliths (especially sagittae) generally are excellent taxonomic tools, but when working with fossils, factors other than those observed on the otoliths themselves must be considered. Zoogeography, environment and habitat preferences are especially important. If zoogeography had been considered, it is doubtful that embiotocid perch (presently restricted entirely to the North Pacific Ocean) and *Leuresthes, Atherinops,* and other New World atherinids would have been reported from the tropical and subtropical Eocene of Europe.

Except for the early pelagic stage of *Cookeolus boops,* all extant priacanthids inhabit areas of high relief. Fishes living in these kinds of habitats frequently fossilize, but their remains rarely contain otoliths. Fossil deposits that contain otoliths almost invariably represent faunas that inhabit flat relief, or pelagic and mesopelagic realism. The occasional otolith from an inhabitant of rocky, high-relief habitat found in a fossil deposit generally represents a prey item or a straggler into the flat-relief area, a not uncommon phenomenon today. Such otoliths are rare, however, so the abundance of Eocene sagittae assigned to family Priacanthidae (*Pristigenys* spp.) by European paleontologists indicates that habitat preference was not a consideration. As already pointed out, features of the sulcus also were overlooked when making such assignments. Regardless, otoliths are excellent taxonomic tools, extremely abundant in the fossil record, and if properly used, can furnish an insight into the past that can not be gained any other way.

ACKNOWLEDGMENTS

As with any such project, our investigation could not have been completed without our borrowing or making use of specimens, library materials, work space, ideas, and the special talents of others. Our sincere thanks are extended to Lillian J. Dempster and W. I. Follett (CAS); Paul

A. Gregory, Jack W. Schott and Donald L. Schultze (DFG); Mary Butler, Robert J. Lavenberg, Camm C. Swift and Brian N. White (LACM); Richard H. Rosenblatt (SIO); Boyd W. Walker (UCLA); William A. Bussing (Univ. Costa Rica); John E. Randall (Bishop Museum, Hawaii); Wayne J. Baldwin (Hawaii Institute of Marine Biology); Bruce B. Collette (National Marine Fisheries Service, Washington, D.C.); Frederick H. Berry (NMFS, Miami); Richard W. Huddleston (Chevron Oil Field Research Co.); James B. Shaklee (now CSIRO, Australia); Peter Forey and Colin Patterson (British Museum Natural History); Hans-J. Paepke (East Germany); Christine Karrer (West Germany); Dirk Nolf (Belgium); F. C. Stinton (England); George Coates (Australia); and Lee Stockland (Tustin, Calif.).

Wayne C. Starnes (USNM) and Ronald A. Fritzsche (Humboldt State Univ.), who also are conducting research on priacanthids, were extremely helpful.

Finally we wish to thank the skippers and crews of the *Qualifier* 105, *Red Rooster* and *Royal Polaris* and in particular George Cargal and Norman Kagawa.

Literature Cited

Agassiz, J. L. R. 1835. Revue critique des poissons fossiles figurés dans l'Ittiolitologia Veronese. Neues Jahrb. Miner., p. 290–316. (Not seen, ref. in White 1936.)

Anderson, W. D., Jr., D. K. Caldwell, J. F. McKinney, and C. H. Farmer. 1972. Morphological and ecological data on the priacanthid fish *Cookeolus boops* in the western north Atlantic. Copeia 1972(4):884–885.

Blainville, H. M. D. 1818. Poissons fossiles (*In* Nouveau Dictionnaire d'Histoire Naturelle . . . Nouvelle édition, vol. 27, Paris). (Not seen, ref. in White 1936.)

Bleeker, P. 1869. Neuvième notice sur la faune ichthyologique du Japon. Versl. Akad. Amsterdam (2), 3:237–259.

Bloch, M. E. 1792. Naturgeschichte der ausländischen Fische. Berlin Vol. 6, iv + 126 p.

Eastman, R. 1905. Les types des Poissons fossiles du Monte Bolca au Muséum d'Histoire naturelle de Paris. Mém. Soc. géol. France 13:1–31.

Fitch, J. E., and R. J. Lavenberg. 1975. Tidepool and nearshore fishes of California. Univ. Calif. Press, Berkeley. 156 p.

Fitch, J. E., and S. A. Schultz. 1978. Some rare and unusual occurrences of fishes off California and Baja California. Calif. Fish Game 64(2):74–92.

Forsskål, P. 1775. Descriptiones animalium avium, amphibiorum, piscium, insectorum, vermium; quae in itinere oriental observavit. Post mortem auctoris edidt Carsten Niebuhr. Copenhagen. 20 + XXXIV + 164 p.

Fritzsche, R. A. 1978. The first eastern Pacific records of bulleye, *Cookeolus boops* (Bloch and Schneider, 1801), (Pisces, Priacanthidae). Calif. Fish Game 64(3):219–221.

Fritzsche, R. A., and G. D. Johnson. 1981. *Pseudopriacanthus* Bleeker, a synonym of the priacanthid genus *Pristigenys* Agassiz. Copeia 1981(2):490–492.

Gilbert, C. H. 1891. A supplementary list of fishes collected at the Galápagos Islands and Panama, with description of one new genus and three new species. U.S. Natl. Mus., Proc. 13:449–455.

Gosline, W. A., and V. E. Brock. 1960. Handbook of Hawaiian fishes. Univ. Hawaii Press, Honolulu. ix + 372 p.

Jordan, D. S., and B. W. Evermann. 1904. Descriptions of new genera and species of fishes from the Hawaiian Islands. U.S. Fish. Comm., Bull. 22:161–208.

Koken, E. 1891. Neue Untersuchungen an tertiären Fisch-Otolithen II. Deutsch. Geol. Ges., Zeitsch. 43:77–170.

Lacépède. 1801. Histoire naturelle des poissons, Paris. Vol. 3. 558 p.

Leriche, M. 1905. Les Poissons éocènes de la Belgique. Musée Royal Hist. Nat. Belg., Mém. 3:49–228.

Myers, G. S. 1958. The priacanthid fish genus *Pristigenys*. Stanford Icthyol. Bull. 7:40–42.

Nolf, D. 1973. Deuxième note sur les téléostéens des sables de Lede (Éocène Belge). Bull. Soc. belge Géol., Paléont., Hydrol. 81(1–2):95–109.

Oken, L. 1817. Cuviers und Okens Zoologien neben einander gestellt. Isis oder Encyclopaedische Zeitung 8(148):1181–1183.

Schafer, W. 1972. Ecology and palaeoecology of marine environments. Univ. Chicago Press. xiii + 568 p.

Schneider, J. G. 1801. M. E. Blochii. Systema ichthyologiae . . . post obitum auctoris correxit, interpolavit J. G. Schneider. Berlin, 1x + 584 p.

Schubert, R. J. 1916. Obereocäne Otolithen vom Barton Cliff bei Christchurch (Hampshire). Kaiserlich-königlichen Geologischen Reichsanstalt, Jahrb. 65(3–4):277–289.

Stinton, F. C. 1980. Fish otoliths from the English Eocene. Part IV. Palacontographical Soc. Monogr., p. 191–258.

Stinton, F. C., and D. Nolf. 1970. A teleost otolith fauna from the Sands of Lede, Belgium. Bull. Soc. belge Géol., Paléont., Hydrol. 78(3–4):219–234.

Thomson, D. A., L. T. Findley, and A. N. Kerstitch. 1979. Reef fishes of the Sea of Cortez. John Wiley & Sons, New York. XV + 302 p.

Volta, G. S. 1796. Ittiolitologia veronese del museo Bozziano ora annesso . . . 2 vols. Verona. (Not seen, ref. in White 1936.)

White, E. I. 1936. On certain Eocene percoid fishes. Ann. Mag. Nat. Hist., ser 10, 18(103):43–54.

Woodward, A. S. 1901. Catalogue of fossil fishes in the British Museum Natural History. Part IV, London. 636 p. (Not seen, ref. in White 1936.)

CALIFORNIA ACADEMY OF SCIENCES
Golden Gate Park
San Francisco, CA 94118

PROCEEDINGS
OF THE
CALIFORNIA ACADEMY OF SCIENCES

Vol. 43, No. 20, pp. 317-321, 3 figs. December 11, 1984

AMAZONSPRATTUS SCINTILLA, NEW GENUS AND SPECIES FROM THE RIO NEGRO, BRAZIL, THE SMALLEST KNOWN CLUPEOMORPH FISH

By

Tyson R. Roberts

California Academy of Sciences, Golden Gate Park, San Francisco, California 94118

Abstract: *Amazonsprattus scintilla* new genus and species, inhabiting the Rio Negro and its tributaries in the Amazon basin of Brazil and feeding on minute aquatic Diptera and planktonic Cladocera, is the smallest known clupeomorph fish. The largest specimen is 19.5 mm standard length, but males and females are sexually ripe as small as 14-16 mm. Superficially it looks very much like a herring and particularly resembles the tropical western Atlantic genus *Jenkinsia* (Clupeidae). On the other hand, further investigation might indicate that it is closely related to some small and poorly known Amazonian anchovies currently placed in *Anchoviella* (Engraulididae).

Introduction

Among the secondary freshwater fishes sharing the Amazon basin with 1500 or so species of primary freshwater Ostariophysi are somewhat more than a dozen species of the clupeomorph families Clupeidae and Engraulididae. Amazonian Clupeidae, or herrings, include several species of *Ilisha* or *Pellona,* some piscivorous and attaining nearly one meter; *Pristigaster cayana* Cuvier, 1829, with its greatly expanded thorax, attaining perhaps 250 mm; and *Rhinosardinia amazonica* (Steindachner, 1880), typically 40–60 mm long. The Engraulididae, or anchovies, include *Cetengraulis juruensis* Boulenger, 1898, attaining perhaps 200 mm, and a number of species currently placed in *Anchoviella,* some as small as 30–40 mm. Recently, while searching for comparative material of larvae, I was thus surprised to find some sexually ripe Amazonian fishes, which looked like clupeomorphs, less than 20 mm in standard length. Study of cleared and stained preparations confirmed that these specimens are not Ostariophysi and that they represent an undescribed genus and species of clupeomorph.

Amazonsprattus, new genus

Type-species.—*Amazonsprattus scintilla,* new species.

Diagnosis.—Minute, slender, scaleless clupeomorphs without pre- or post-pelvic abdominal scutes. Ventral myotomic progression incomplete. Premaxilla absent or minute and toothless. Maxilla with 16–20 very small conical teeth. Two supramaxillae. Dentary and palate usually toothless (one tooth observed on dentary in one specimen). Branchiostegal rays 4–5. Dorsal fin with 12–13 rays, its origin in posterior half of body; anal fin with 14–16 rays, its origin below anterior third of dorsal fin. Pectoral fin rays 7–9. Pelvic fin rays 6.

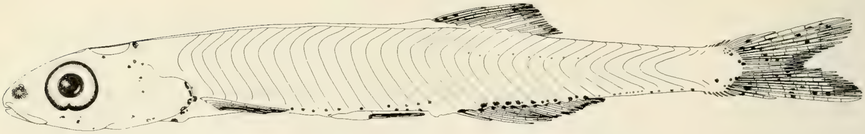


FIGURE 1. *Amazonsprattus scintilla,* 17.0 mm (holotype, CAS 52175).

Amazonsprattus scintilla, new species

(Figures 1–3)

HOLOTYPE.—CAS 52175, 17.0 mm (sex undetermined), Rio Jufari between Castanheiro Grande and Santa Fé, collected by Martin Brittan, 21 April 1964.

PARATYPES.—CAS 52176, 18: 14.3–19.0 mm (five males, eight females, six sex undetermined), collected with holotype (5: 16.5–19.0 mm cleared and stained with alcian and alizarin); CAS-SU 68891, 19.5 mm (sex undetermined), Rio Negro at Santa Isabel, collected by Carl Ternetz, 17 January 1925.

DESCRIPTION.—Head compressed and moderately elongate, its length almost four times in standard length. Eyes moderately large and strongly compressed or flattened laterally. Eye diameter about four times in head length. Entire medial surface of eyes closely approximate (so that forebrain is confined to a small space dorsal to eyes), and medial surface of eyes just as flat as lateral surface. Ventral surface of eyeball with a prominent choroid fissure. Hyaline eyelid well developed. Snout moderately elongate, its length about equal to eye diameter. Nasal organ moderately large, with rather small anterior and posterior nostrils. Mouth terminal. Lower jaw elongate, extending posteriorly to below posterior margin of eye, but gape much restricted and entirely anterior to eye. Maxilla slender and moderately elongate, extending posteriorly to below anterior margin of eye. Anterior and posterior portions of cranial fontanel open, posterior portion entirely bridged by a narrow, cartilaginous taenia medialis. Circumorbital bones apparently five (very fragile, hence easily broken, and staining very weakly with alcian). Hyosymplectic entirely cartilaginous, without large, axe-shaped anterodorsal process usually present in clupeids. Opercle with strongly concave dorsoanterior and dorsoposterior margins; dilatator process of opercle present but weakly developed. First gill arch with a total of 18–19 large, elongate gill rakers on its leading edge. Rakers on trailing edge of first gill arch and on successive arches slightly less numerous and considerably smaller. Upper and lower pharyngeal toothplates small, with 8–10 conical teeth (branchial and hyoid arches otherwise edentulous). Hyoid and branchial arches entirely cartilaginous except for branchiostegal rays, gill rakers, and pharyngeal toothplates.

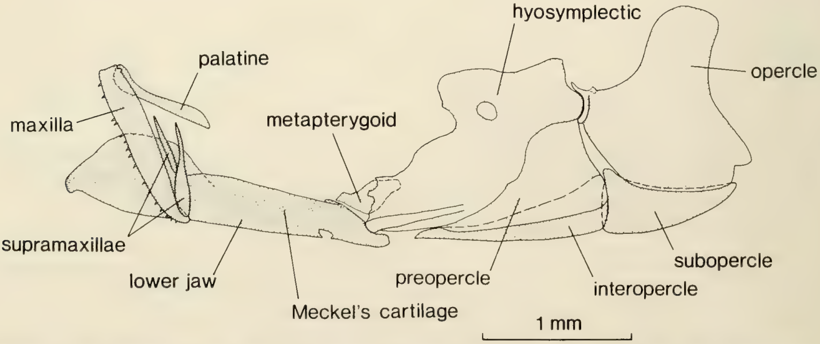


FIGURE 2. *Amazonsprattus scintilla,* 18.0 mm, CAS 52176. Lateral view of jaws, suspensorium, and opercular bones (hyosymplectic and palatine cartilaginous).

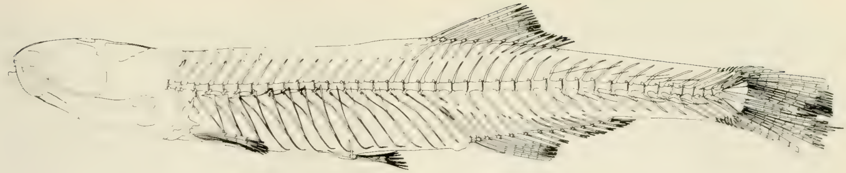


FIGURE 3. *Amazonsprattus scintilla,* 18.8 mm, CAS 52176. Axial skeleton. Total vertebrae 17 + 21 = 38; pectoral girdle abnormally incomplete; a series of 10–11 small, irregularly triradiate intermuscular bones lateral to vertebrae 2–13 has been omitted for clarity.

Body compressed, slender, its greatest depth about 6–8 in standard length. Abdomen rounded. Myotomes well defined, those fully formed 33–34, or about four fewer than total vertebrae. Dorsal and anal fin rays low set, with moderately falcate margins, dorsal fin rays about 1.5 times longer than anal. Pectoral and pelvic fins relatively small, pelvic smaller than pectoral. Pelvic scute variably developed, absent or failing to stain in some specimens, weakly to strongly stained with alcian or alizarin in others. In specimens with relatively well developed scutes there is an elongate anteromedian process and an elongate lateral ascending process on each side. Pectoral girdle with bony posttemporal, supracleithrum, and cleithrum (postcleithra absent), cartilaginous scapulocoracoid, and three rows of radials (proximal, medial, and distal, with five, five, and eight radials respectively). Caudal fin moderately deeply forked, upper and lower lobes about equal and with rounded margins. Upper and lower lobes overlapping slightly when adducted. Principal rays 4–5 of upper lobe and 3–4 of lower lobe with delicate alar flaps (not illustrated). In an 18.8-mm specimen the large alar flap on ray 5 consisted of four overlapping scalelike laminae (lightly stained with alcian) that may actually be modified scales. Caudal fin with 10 + 9 principal rays, 8–9 upper and 8 lower procurrent rays. Caudal fin skeleton with a parhypural, six separate hypurals, and a single epural. Hypural 2 fused to complex ural centrum (as in many clupeoids).

Total vertebrae 37(4) or 38(1), 16–17 abdominal plus 20–21 caudal. All vertebrae with a simple, slender neural spine. Supraneurals 6–8. Origin of pelvic fin below vertebrae 13–14, of dorsal fin above vertebra 18, and of anal fin below vertebrae 20–21. All abdominal vertebrae except first two with fully developed ribs. First two vertebrae usually without ribs, sometimes second vertebrae with incompletely developed ribs (Fig. 3). Distal ends of most abdominal ribs deflected posteriorly. First two caudal vertebrae with reduced ribs. Intermuscular bones well developed anteriorly and posteriorly. Anteriorly two dissimilar and morphologically complex sets of intermuscular bones. A series of about 13 epipleural intermuscular bones parallel to abdominal vertebrae 3–16. Anteriormost eight epipleurals with a well developed anteromedial process proximally; this process is absent from last five epipleurals, which become progressively smaller. Distal ends of epipleurals, except reduced posteriormost one, closely approximated to distal half of ribs (Fig. 3). In addition to epipleurals, a series of 10–11 small, irregularly triradiate intermuscular bones lies just dorsal to epipleurals and directly lateral to centra of abdominal vertebrae 2–12 or 13 (not illustrated). Posterior two processes of these triradiate elements lie quite near body surface, but anterior process lies much deeper. Posteriorly, two similar series of 8–10 simple dorsal and ventral intermuscular bones extend laterally just above and below caudal vertebrae 9–19 (Fig. 3).

Alimentary canal with a well-defined stomach. Pyloric caeca in two or three groups: a dorsal group with one or two elongate caeca; a ventral group with about four or five elongate caeca; and sometimes a second ventral group of about four short, poorly defined or only partially separate caeca. Intestine straight. Gut contents of four specimens were as follows: specimen 1) two dipteran pupae; specimen 2) a single dipteran pupa; specimen 3) numerous small Cladocera of two size classes, 270 × 150 μm and 72 × 55 μm; and specimen 4) a single dipteran pupa, several small dipteran larvae, and moderately numerous cladocerans of a single kind. My sketches of the cladocerans in this fourth specimen, 424 × 255 μm, with a pair of curved, divergent, strongly deflected horns 184 μm long projecting from the rostrum, were tentatively identified as *Bosminiopsis deitersi* Richard, 1895, by Thomas Zaret.

Gonads readily identifiable in most of the type-specimens. Eight, 15.9–18.2 mm, have creamy or pale orangish ovaries with eggs in more or less good condition observable through body wall with transmitted light. One of these, 17.3 mm, contained 20 eggs 0.2 mm in diameter. Five, 14.3–16.2 mm, have milk-white testes. In two of these the testes are particularly well developed and exhibit numerous "segments" or laminae, about five per myotome, comparable to laminae observed in testes of other minute teleosts (e.g., *Sundasalanx*; Roberts 1981, fig. 1a). In both sexes the gonads appear to be single and occupy only the posterior half of the body cavity, from about the origin of the pelvic fin to the vent. In seven specimens, 16.0–19.5 mm, gonads not observed and sex undetermined.

Judging from preserved material live *Amazonsprattus* probably are translucent or even transparent. Only a few melanophores on head, largest and most obvious a group of about six superficial to cleithrum and clearly visible through gill cover, and two large ones on either side of dorsoposterior margin of hindbrain (Fig. 1). A number of large, deep-lying melanophores associated with posteroventral portion of cranium (not illustrated). Dorsal surface of cranium otherwise usually devoid of pigment. Tip of snout and lower jaw, and side of head just below eye and midway between eye and end of gill cover sometimes with a few small melanophores. Body with relatively few melanophores, mostly on ventral half, including base of anal fin and caudal peduncle. A row of about 10 melanophores, one per segment, along each ventral myotomic border, and a midventral row of about five near pelvic fins. Two rows of segmental melanophores near anal fin base: one row at ventral end of myotomes and between pterygial muscles, another on bases of anal-fin rays. A row of small melanophores, more than one per segment, on ventral portion of caudal peduncle, and some small melanophores near base of caudal fin. A nearly straight row of small segmental melanophores on side of body just above midline (without evident anatomical relationship to any underlying structures). In holotype and most paratypes this row commences posterior to dorsal fin origin (Fig. 1), but in some paratypes it extends nearly entire length of body. Dorsal surface of body devoid of pigmentation. A few melanophores on basal portion of anterior dorsal fin rays, but dorsal fin without basal melanophores like those of anal fin. Caudal fin relatively densely pigmented, with large melanophores more or less regularly distributed on upper and lower lobes (Fig. 1); an area near middle of caudal fin devoid of melanophores. Sexual differences in pigmentation not observed.

Note on Type-Localities.—The Rio Jufari is a low-gradient, swampy tributary with an enormous mouth-bay at its confluence with the Rio Negro, about 20 km upriver from the relatively narrow mouth of the much more important Rio Branco. Maps I have seen do not show Castanheiro Grande or Santa Fé; according to the collector (pers. commun. M. Brittan, March 1983) several days of slow boat travel up the Jufari were required to reach the collecting sight. Santa Isabel is an old name for the modern town of Tapurucuará. This portion of the Amazon basin lies within equatorial rain forest; here the waters of the Rio Negro and its tributaries (excepting the Rio Branco) are generally darkly tinted, have a pH of 4–5, and are extremely low in mineral conduct.

Etymology.—Amazon; and sprattus (Latin, masc.), a herring or herringlike fish; scintilla (Latin, masc.) a spark, hence the smallest trace or particle (employed as a noun in apposition).

Discussion

Few collectors have preserved specimens of the smallest Amazonian fish species, and it may well be that the smallest species of various other groups have yet to be discovered. In the Amazon, where community structure of freshwater fishes may be more complex than anywhere else, minute body size seems to have arisen primarily in response to biotic factors. This, in my opinion, is the general reason why so many of the smallest Amazonian fishes belong to secondary freshwater fish groups which in terms of relative numbers of species represent an insignificant fraction of the fauna. *Amazonsprattus* provides an excellent example of the survival of a group of secondary fishes in the midst of the Amazonian ichthyofauna by evolution of minute body size and an entirely freshwater life history, possibly involving year-round continuous reproduction of minute young. Other particularly striking examples of the phenomenon include the two minute species of *Poecilia* (or *Pamphorichthys*) and the two or more minute species of *Microphilypnus*. These are the only members of the families Poeciliidae and Eleotrididae inhabiting the interior of the Amazon basin. For further discussion of these and other examples see Roberts (1972).

Relationships of *Amazonsprattus* are unclear, and for the moment it is perhaps best left unassigned to family. Having examined its skeletal anatomy and made comparisons with a number of herrings and anchovies, I was inclined to place the genus in Clupeidae, largely on account of its jaw structure, which is unlike anything I have observed in Engraulididae. But my colleague Gareth Nelson, who is studying Amazonian *Anchoviella* and has examined some small undescribed species I have not seen, is inclined to believe that it may belong to this group of Engraulididae.

ACKNOWLEDGMENTS

For information, comments, or other assistance I wish to thank Martin Brittan, Norma Chirichigno, Dusty Chivers, Lillian Dempster, William N. Eschmeyer, Karsten Hartel, Michael Hearne, Albertina Kameya, Vincent Lee, Sarah Ward, Thomas Zaret, and George Zorzi. The manuscript was reviewed by Gareth M. Nelson and Peter J. Whitehead.

LITERATURE CITED

ROBERTS, T. R. 1972. Ecology of fishes in the Amazon and Congo basins. Bull. Comp. Zool. 143(2):117–147.

———. 1981. Sundasalangidae, a new family of minute freshwater salmoniform fishes from Southeast Asia. Proc. California Acad. Sci. 42(9):295–302, 6 figs.

CALIFORNIA ACADEMY OF SCIENCES
Golden Gate Park
San Francisco, California 94118