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**REVIEW OF THE INDO-PACIFIC PIPEFISH GENUS
DORYRHAMPHUS KAUP (PISCES: SYNGNATHIDAE),
WITH DESCRIPTIONS OF A NEW SPECIES
AND A NEW SUBSPECIES**

by

C.E. DAWSON

Abstract

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Doryrhamphus, a genus of trunk-pouch pipefishes commonly associated with rock or coral habitats, is diagnosed and a key is provided to the five species and five subspecies recognized. The genus *Dentirostrum* Herald and Randall is synonymized with *Doryrhamphus*, treated species and subspecies are diagnosed and illustrated, distribution (based on material examined) is delineated and comprehensive synonymies are provided. The genus includes two species groups which (in subadults and adults) differ in having either one or two spines on principal ridges of the posterior predorsal rings. Species of the single-spine group are distinguished by differences in meristic values and preserved coloration, as well as by the presence of one or two ventrolateral projections on the snout of males, or the absence thereof. Species of the two-spine group are distinguished by differences in meristic values and preserved coloration, as well as by the presence of either one or two spines on principal ridges of tail rings.

The single-spine group includes the type-species, *D. excisus* (three subspecies), with one ventrolateral projection on snout in males, *D. japonicus* with no projection on snout, and *D. bicarinatus* n. sp. with two projections on snout. *Doryrhamphus e. excisus* (a senior synonym of *D. melanopleura*), with modally 17-18 trunk rings ranges from eastern Africa and Persian Gulf to the west coast of the Americas. This pipefish, the most widely distributed syngnathid, exhibits some west-east clinal increase in counts of total rings and dorsal-fin rays. *Doryrhamphus e. abbreviatus* n. ssp. is a Red Sea endemic characterized by modally 16 trunk rings as well as by 26-28 total rings and 18-20 dorsal-fin rays. *D. e. paulus* (Revillagigedo Is., Mexico) shares the modal count of 16 trunk rings, but has 30-32 total rings and 23-27 dorsal-fin rays. *D. japonicus* (19-20 trunk rings) is known only from the main islands of Japan, whereas *D. bicarinatus* (16 trunk rings) is known from Indian Ocean coasts of South Africa and Mozambique.

The two-spine group includes *D. negrosensis* (2 subspecies) with 2 spines on ridges of tail rings in subadults and adults and *D. janssi* (one spine on ridges of tail rings). *D. n. negrosensis* (modally 15 trunk and 29 total rings) is known from Borneo to the Ryukyu Is. and southeastward to the New Hebrides, excluding Australia. *D. n. malus* (modally, 16 trunk and 31 total rings) is an Australian Great Barrier Reef endemic. *D. janssi*, with more tail rings than *D. negrosensis* (21-23 versus 13-16), is known from the eastern Indian Ocean (off NW Australia) and from the Gulf of Thailand and Philippines southeastward to New Guinea and NE Australia in the western Pacific Ocean. Planktonic young of *D. excisus* and early juveniles of *D. negrosensis* are illustrated and briefly described.

Contents

Introduction	1
Methods and Materials	1
Genus <i>Doryrhamphus</i> Kaup	2
Key to species and subspecies of <i>Doryrhamphus</i>	3
<i>D. excisus</i>	4
<i>D. excisus excisus</i> Kaup	4
<i>D. excisus abbreviatus</i> n. ssp.	9
<i>D. excisus paulus</i> Fritzsche	10
<i>D. japonicus</i> Araga and Yoshino	10
<i>D. bicarinatus</i> n. sp.	13
<i>D. negrosensis</i>	15
<i>D. negrosensis negrosensis</i> Herre	15
<i>D. negrosensis malus</i> (Whitley)	19
<i>D. janssi</i> (Herald and Randall)	19
Acknowledgements	21
Tables	22
References	25
Index	27

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Introduction

Representatives of the trunk-pouch (gastrophorine) syngnathid genus *Doryrhamphus* are among the more common pipefishes associated with rock and coral habitats in temperate-tropical waters of the Indo-Pacific region. Duncker (1915) included the genus in his subfamily *Doryrhamphina* (= *Doryrhamphinae*), briefly treated three nominal species, and introduced fundamental nomenclatural errors which have persisted in subsequent literature. The genus was most recently treated by Herald (1953), but his study material was limited and his conclusions have not been accepted by most recent workers. Although specimens are rather common in collections and species of *Doryrhamphus* are frequently referenced in the literature, taxonomy and nomenclature are presently confused and available descriptions and keys do not permit ready identification of individuals or species. In an effort to resolve these problems, I here review the genus *Doryrhamphus* Kaup, and include herein one previously undescribed species and one species currently referred to the monotypic genus *Dentirostrum* Herald and Randall. This review is based on the examination of the majority of available museum material.

Methods and Materials

Measurements are in millimetres (mm) and some are referred to standard length (SL), total length (TL) or head length (HL). Counts of trunk rings begin with that bearing the pectoral fins and end with that bearing the anus (anal ring); colour descriptions are from specimens preserved in alcohol; as employed here, the term "venter" refers to the ventral body surface; other methods are those of Dawson (1977).

Synonymies are largely complete, but some references, particularly in the Japanese literature, have undoubtedly been overlooked.

Materials examined include only those lots from which data were taken and are listed by general localities from west to east and roughly north to south; depths are in metres (m). Distributions are based on materials examined; maps delineate general localities, each symbol represents one or more collections.

Abbreviations

Abbreviations for repositories of materials examined are: AMNH — American Museum of Natural History, New York. AMS — Australian Museum, Sydney. ANSP — Academy of Natural Sciences, Philadelphia. BMNH — British Museum (Natural History), London. BOC — Bingham Oceanographic Collection, Yale University, New Haven. BPBM — Bernice P. Bishop Museum, Honolulu. CAS — California Academy of Sciences, San Francisco. CAS-SU — Stanford University collections, now at CAS. FMNH — Field Museum of Natural History, Chicago. GCRL — Gulf Coast Research Laboratory Museum, Ocean Springs. IORD — Institute of Oceanic Research and Development, Tokai University, Shimizu. LACM — Los Angeles County Museum of Natural History. MCZ — Museum of Comparative Zoology, Harvard University, Boston. MNHN — Muséum National d'Histoire Naturelle, Paris. NMW — Naturhistorisches Museum, Vienna. QM — Queensland Museum, Brisbane. RMNH — Rijksmuseum van Natuurlijke Historie, Leiden. ROM — Royal Ontario Museum, Ottawa. RUSI — J.L.B. Smith Institute of Ichthyology, Grahamstown. SIO — Scripps Institution of Oceanography, La Jolla. SMLB — Seto Marine Biological Laboratory, Kyoto University, Sirahama. SMF — Natur-Museum und Forschungs-Institut Senckenberg, Frankfurt am Main. SMLVO — Subtropical Marine Laboratory, Tokai University, Yaeyama. UCLA — University of California, Los Angeles. UG — University of Guam, Agana. UMML — University of Miami, Marine Laboratory, Rosenstiel School of Marine and Atmospheric Sciences. USNM — National Museum of Natural History, Smithsonian Institution, Washington, D.C. WAM — Western Australian Museum Perth. YCM — Yokosuka City Museum. ZMA — Zöologisch Museum Amsterdam. ZMB — Zoologisches Museum, Museum für Naturkunde der Humboldt-Universität, Berlin. ZMUC — Zoologisk Museum, University of Copenhagen.

¹Gulf Coast Research Laboratory Museum, Ocean Springs, Miss. 39564; U.S.A.

Genus *Doryrhamphus* Kaup

Doryrhamphus Kaup, 1853:233 (*nomen nudum*); Kaup, 1856:54 (type-species: *Doryrhamphus excisus* Kaup 1856, by monotypy).

Pristidoryrhamphus Fowler, 1944:158 (type-species: *Pristidoryrhamphus jacksoni* Fowler 1944, by original designation).

Dentirostrum Herald and Randall, 1972:123 (type-species: *Dentirostrum janssi* Herald and Randall 1972, by original designation).

DIAGNOSIS.—Superior trunk and tail ridges discontinuous near rear of dorsal-fin base, not arched dorsad below dorsal-fin base in subadults and adults; inferior trunk ridge and lateral tail ridge end on or near anal ring; lateral trunk ridge confluent with inferior tail ridge; venter of trunk slightly V-shaped in females and juvenile males, the median ridge distinct but not enlarged or keel-like. Median dorsal snout ridge low to moderately elevated, entire, irregularly emarginate or spinulose, begins near rear of upper jaw, usually ends above nares, sometimes continued faintly on interorbital; snout essentially smooth dorsolaterally in young, with 1-5 irregular, bilateral, rows of spines or spinules in most subadults and adults ventrolateral margin of snout entire or with 1-2 bony projections on quadrate in subadult and adult males of some species (Fig. 1c-e). Supranarial (= supranasal of Herald and Randall, 1972) ridges prominent, often spiny, usually reach anterior third or more of interorbital; dorsal margin of orbit entire to spiny; interorbital somewhat depressed; posterior supraorbital ridges distinct, sometimes continued on interorbital; frontal, nuchal and prenuchal ridges low to somewhat elevated, the margins entire, irregularly emarginate or spiny; upper third of opercle with a complete longitudinal ridge; lower part of opercle finely striate, often with prominent supplemental ridges; pectoral-fin base not protruding strongly laterad, usually with two distinct ridges. Dorsum of body a little depressed between superior ridges; principal ridges prominent, indented to slightly notched between rings; superior and inferior ridges often angled a little laterad, especially on tail rings; principal ridges of each ring with 1-2 prominent spines in juveniles and adults, ridge margins otherwise entire; scutella without longitudinal keels; without dermal flaps; dorsal fin originates on trunk, its base not elevated; pectoral fins usually emarginate, the median rays shorter than those above and below; caudal fin moderately large, median rays the longest, membranes broad. Trunk rings 14-20, total rings 26-39, total subdorsal rings 3.5-8.25, dorsal-fin rays 16-29, pectoral-fin rays 17-23, anal-fin rays 4, caudal-fin rays typically 10. Head length 3.5-5.3 in SL, snout length 1.5-2.5 in HL, length of dorsal-fin base 1.3-3.3 in HL (data from late juveniles-adults). Brood pouch begins on 1st trunk ring, ends near anal ring; without protective plates; membranous pouch folds meet or nearly meet on midline of egg-filled pouch (semi-type closure of Herald, 1959), the free margins simple or edged with a narrow outfold of membrane; brood-pouch eggs deposited in 2-6 transverse rows and in 1-2 layers. Without odontoid processes in jaws (Dawson and Fritzsch, 1975) or bony inclusions in gill membranes (Dawson, 1978); all branchial elements, except 3rd basibranchial, present (Fritzsch, 1980).

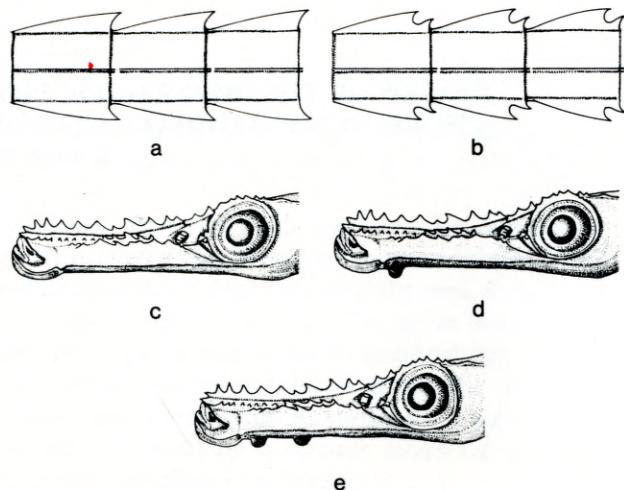


Figure 1. Lateral view of trunk rings (a & b) illustrating single (a) and double (b) spines on principal ridges; (c-e) subadult-adult males with plain snout (c) and snouts with one (d) or two (e) bony ventrolateral projections.

COMPARISONS.—Among gastrophorine (trunk pouch) pipefish genera, the principal ridge configuration of *Doryrhamphus* and combination of spiny rings, modally 10 caudal-fin rays and absence of brood-pouch plates is shared only with *Dunckerocampus* Whitley. These genera differ principally in morphology of the brood area of mature males but they also differ in some aspects of ridge development and in general coloration. In *Doryrhamphus*, eggs of brooding males are protected by bilateral membranous pouch-folds that enclose the eggs and meet or nearly meet on the ventral midline of the trunk. These membranes have free margins and are not “temporarily united” as reported by Weber and de Beaufort (1922) and others. Brooding males of species of *Dunckerocampus* lack pouch-folds and eggs are carried exposed in shallow membranous compartments on the venter of the trunk. Although these genera are characterized by the presence of well-developed spines on the principal ridges, there are material differences in sequence of spine development. In *Doryrhamphus*, rings of early juveniles (ca. 10-16 mm SL) have a single distal spine on each principal ridge and, in some species, a second spine may later develop on some ridges. In contrast, juveniles of *Dunckerocampus* have two spines on the principal ridges of each ring, the penultimate spine becomes vestigial or obsolete with increasing standard length, and subadults and adults typically have a single spine distally on the principal ridges of each ring. Furthermore, subadults and adults of species of *Doryrhamphus* have 1-5 dorsolateral rows of spines or spinules on either side of the median dorsal snout ridge (absent in *Dunckerocampus*) and these species usually have some indication of a striped color pattern, rather than the banded pattern common to most species of *Dunckerocampus*.

Juvenile representatives of other gastrophorine genera with the principal ridge configuration of *Doryrhamphus* (e.g. *Microphis*, *Oostethus*, etc.) may also have spiny ridges, but species of *Doryrhamphus* are distinguished by their lower number of total rings (26-39 versus 39-51) and higher number of caudal-fin rays (typically 10 versus 9).

RELATIONSHIPS.—Among genera of pipefishes wherein the brood area is located on the trunk of males (*Gastrophori* of Duncker, 1915), there are four which share a common suite of characters with *Doryrhamphus*. All have prominent ridges or sculpturing on the head, rings ending posteriad in one or two spines, 10 caudal-fin rays, 4 anal-fin rays and a relatively elongate 1st trunk ring (except *Choerichthys*). Duncker (1915) included *Dunckerocampus* Whitley (as *Acanthognathus* Duncker) in the subfamily Syngnathoidinae (as *Gastrotokineinae*) due to the absence of pouch-protective plates and membranous pouch-folds in brooding males. *Doryrhamphus* (with pouch-folds) and *Choeroichthys* Kaup (with both pouch-folds and plates) were referred to the Doryrhamphinae. Following Duncker's reasoning, two subsequently described genera (*Maroubra* Whitley, *Heraldia* Paxton) lacking lateral pouch-folds and plates would be included in the Syngnathoidinae.

I presently believe that these five genera, despite differences in pouch morphology, are related by the character combination noted above and that they must be placed in the same subfamily, the Doryrhamphinae. Dawson and Allen (1978) have shown that the anterior-pored brood pouch of *Apterygocampus* Weber crosses subfamilial lines between the Syngnathinae and Hippocampinae. Variation in pouch morphology of the doryrhamphine genera discussed here further suggests that subfamilial definitions of Duncker (1915) and Herald (1959) require reevaluation.

REMARKS.—*Pristidoryrhamphus* Fowler (1944), based on a misidentified specimen of *Doryrhamphus negrosensis* Herre, was synonymized with *Doryrhamphus* by Herald (1953).

The monotypic genus *Dentirostrum* Herald and Randall (1972) was originally distinguished from *Doryrhamphus* solely on the basis of the relatively long snout and large size of the type-species, *Dentirostrum janssi* Herald and Randall. This fish has more tail rings than usual for species of *Doryrhamphus* (20-23 versus 11-17) but differences in snout length, relative size, and numbers of tail rings are insufficient reasons for separate generic treatment. The type-species of *Dentirostrum* agrees with *Doryrhamphus* in having spiny rings, in the striped color pattern of adults, brood-pouch morphology, principal ridge configuration, development of snout spines and ridges and number of caudal-fin rays. In the apparent absence of substantial differentiating characters, I synonymize *Dentirostrum* with *Doryrhamphus*.

The median dorsal snout ridge is low and entire, and the dorsolateral ridges are absent or vestigial in early juveniles and occasional adults of species of *Doryrhamphus*. The median snout ridge may be a laterally compressed and dorsally notched or emarginate, plate-like, elevated process in some subadults and adults; whereas it may be represented, in others of the same species, by a linear series of peg-like spines. The dorsolateral snout ridges may consist of minute denticulations in some subadults and adults; whereas these ridges may be represented, in others, by enlarged, largely antrorse, spines. The dorsal and dorsolateral snout ridges are usually best developed and most complex in adult males of the several species. Subadult and adult males of some species have 1-2 bony ventrolateral projections on the snout (Figs. 1d and e). These bilaterally paired

processes originate from the quadrate, they usually angle a little mesiad and are present in small fish lacking evidence of brood-pouch development. The number of these projections, or absence thereof, is highly consistent within a species, and atypical conditions (usually unilateral) occur in less than 0.5 percent of specimens examined.

In subadults and adults, superior ridges usually have two distal spines on the anterior 4-5 trunk rings. The second spine may be well developed or vestigial, and it is usually present on one or more of these anterior rings, even in species which are otherwise characterized by single spines on the principal ridges. For this reason, determination of the single or double spined state, for species identification, is based on the condition of the posterior predorsal trunk rings.

In most species, trunk rings are more numerous than tail rings and the dorsal-fin base crosses more trunk rings than tail rings. However, numbers of tail rings equal or exceed trunk rings in *D. bicarinatus*, and subdorsal tail rings often equal or exceed subdorsal trunk rings in *D. negrosensis*.

Juveniles and adults have a dark stripe crossing the side of the snout and postorbital region to the postero-dorsal angle of opercle, and the caudal fin is usually dark brown or black with irregular blotches of pale or white.

Species of *Doryrhamphus* are marine, and they are most commonly associated with rock or coral substrates; planktonic young have been taken in the 0-35 m range over a depth of 4 960 m. The genus is represented throughout the Indo-Pacific region from the northern Red Sea to the west coast of the Americas and from the Xora River, South Africa (ca. 32°S) to Sagami Bay, Japan (ca. 35°N). One of the five species of *Doryrhamphus* is represented by three subspecies, another by two. These subordinate taxa represent allopatric populations that share unique morphological features, but differ in meristic values and coloration (in *negrosensis*). They could be considered as separate species, but a conservative treatment is adopted here.

Key to subadults and adults of species of *Doryrhamphus*

- 1a. Posterior 4-6 predorsal trunk rings with one well-developed spine on superior ridges (Fig. 1a) 2
- 1b. Posterior 4-6 predorsal trunk rings with two well-developed spines on superior ridges (Fig. 1b) 6
- 2a. Trunk rings modally 16-18; males with 1-2 bony ventrolateral projections on snout (Figs. 1d & 1e) 3
- 2b. Trunk rings modally 19; males without bony ventrolateral projections on snout (Fig. 1c) *japonicus*
- 3a. Subdorsal trunk rings 5.0-3.0; upper half of side of trunk plain or with a broad dark stripe; males with one ventrolateral projection on snout (Fig. 1d); *excisus* subspecies 4
- 3b. Subdorsal trunk rings 2.5-2.0; upper half of side of trunk with a narrow dark stripe; males with two ventrolateral projections on snout (Fig. 1e) *bicarinatus*

- 4a. Trunk rings 17-19 (modally 17-18) *e. excisus*
 4b. Trunk rings 15-17 (modally 16; 16 or fewer in 84% of specimens examined) 5
 5a. Total rings 26-28; dorsal-fin rays 18-20 *e. abbreviatus*
 5b. Total rings 30-32; dorsal-fin rays 23-27 *e. paulus*
 6a. Tail rings 13-16; most tail rings with two spines on principal ridges; (*negrosensis* subspecies) 7
 6b. Tail rings 21-23; tail rings with one spine on principal ridges *janssi*
 7a. Trunk rings modally 15; total rings 27-29 (modally 29); dorsum with narrow pale stripe from snout tip to caudal-fin base *n. negrosensis*
 7b. Trunk rings modally 16; total rings 30-32 (modally 31); pale stripe on dorsum ends on anterior third of trunk *n. malus*

Doryrhamphus excisus Kaup

SYNONYMY.—See subspecies.

DIAGNOSIS.—Principal ridges of posterior predorsal trunk rings with one distal spine; trunk rings 15-19 (18 or fewer in 96.5% of specimens examined); subdorsal trunk rings 5.0-3.0; subadult and adult males with one bony ventrolateral projection on snout; body plain brownish or with a broad dark stripe between superior and lateral trunk ridge.

COMPARISONS.—Compared to congeners sharing the single spine on principal ridges of the posterior predorsal rings, the single ventrolateral projection on the snout distinguishes subadult and adult males of *D. excisus* from those of *D. bicarinatus* (2 projections) and *D. japonicus* (0 projections). *Doryrhamphus excisus* has more subdorsal trunk rings than *D. bicarinatus* (5.0-3.0 versus 2.5-2.0) and usually has fewer trunk rings than *D. japonicus* (15-18 in 96.5% versus 19-20). Furthermore, *D. excisus* is brownish or, most commonly, has a broad dark stripe covering most of the area between the superior and lateral trunk ridges. In *D. bicarinatus* and *D. japonicus* this stripe is narrow, it closely follows the superior ridge and typically occupies less than half the space between the superior and lateral trunk ridges.

Compared to congeners with two spines on the

principal ridges of the posterior predorsal rings (*negrosensis*, *janssi*), *D. excisus* is further distinguished by higher numbers of subdorsal trunk rings (5.0-3.0 versus 3.0-0.75) and by the presence of a ventrolateral projection on the snout of subadult and adult males (absent in *negrosensis* and *janssi*).

REMARKS.—As interpreted here, *Doryrhamphus excisus* includes three subspecies: one in the Red Sea, one in the Revillagigedo Is. of Mexico, and one which ranges throughout much of the remaining subtropical-tropical Indo-Pacific region (Fig. 2). These subspecies are distinguished by differences in numbers of trunk rings, total rings and dorsal-fin rays (see key and diagnoses).

Doryrhamphus excisus excisus Kaup

Figs. 2-6

Doryrhamphus excisus Kaup, 1856:54, pl. 3, fig. 5 (orig. descr. from Paris Museum syntypes, type-locality not stated); Duméril, 1870:586 (synonymy, descr.); Günther, 1910:434 (close to *D. pleurotaenia*); Weber, 1913:117 (Indonesian records); Jordan, 1919:254 (orthotype of *Doryrhamphus*); Bertin and Estève, 1950:45 (syntypes listed); Baissac, 1976:198 (listed, Mauritius); Fritzsche, 1980:187 (nomenclatural note).

Syngnathus melanopleura Bleeker, 1858:458, 462, 464 [orig. descr.]; Novaselma, Kokos [Cocos] Is. [Indonesia]; Bleeker, 1859:161 (listed).

Doryrhamphus melanopleura: Bleeker, 1859a:188 (compiled); Duméril, 1870: 586 (jr. syn. of *D. excisus*); Duncker, 1915:61 (synon.; descr.; range, in part); Weber and de Beaufort, 1922:64, fig. 27 (synon.; descr.; range, in part); Duncker and Mohr, 1925:107 (notes on behavior and coloration; New Guinea); McCulloch and Whitley, 1925:137 (listed); Whitley, 1927:4 (listed); Fowler, 1928:111 (synon., in part; counts, range); McCulloch, 1929:91 (compiled); Fowler, 1931:323 (compiled); Whitley, 1932:275 (Low Is., Qld., Austr.); Herre, 1935:164 (compiled); Mukerji, 1935:275, fig. 2 (descr., notes on brood-pouch eggs, etc.; Andaman Is.); Abe, 1939:531 (listed); Herald, 1940:59, 63 (in key; Baja California and Galapagos Is.); Schultz, 1943:71, 73 (in key; Samoa); Tinker, 1944:142 (listed); Fowler, 1949:66 (compiled); Kählsbauer, 1950:271 (counts, Society Is.); Marshall, 1950:172 (listed); Herald, 1953:245 (in key); Smith, 1953:517, pl. 106, fig. 358a (characters, Mozambique); Matsubara, 1955:426 (in key; distribution); Baissac, 1956:326 (compiled); Fowler, 1956:198, fig. 107 (name only); Munro, 1958:89, fig. 617 (characters; Qld.); Munro, 1958a:141 (compiled); Whitley and Allan, 1958:60 (listed); Fowler, 1959:135 (characters; range, in part; cites type-locality as Cocos-Keeling Is.); Riker, 1959:6 (listed); Gosline and Brock, 1960:134, 319 (characters in key); Fourmanoir, 1961:104 (listed); Smith, 1963:530, pl. 79, fig. e (synon., in part; characters; comment on subspecies);

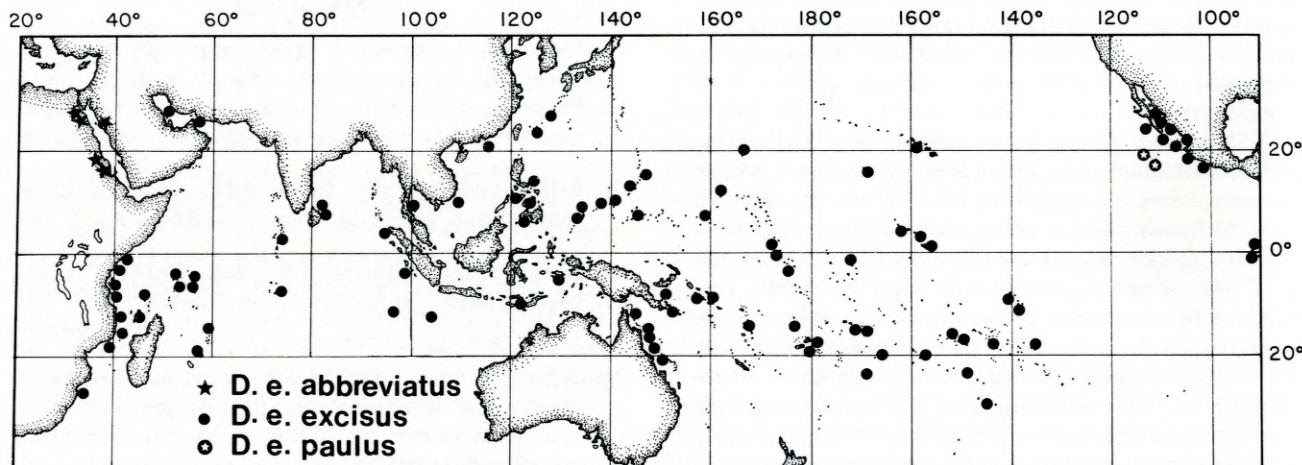


Figure 2. Distribution of subspecies of *Doryrhamphus excisus* based on material examined. West American records omitted south of 15° N latitude.

Smith and Smith, 1963:11, pl. 96, fig. i (Seychelles); Marshall, 1964: 113, pl. 26 (synon.; descr.; Qld., Austr.); Whitley, 1964:38 (listed); Gosline, 1965:824 (reef-protected zone, Hawaii); Smith, 1965:615 (distribution); Marshall 1966:176, pl. 26, fig. 120 (color note); Mauge, 1967:220 (*Acropora* zone, Madagascar); Munro, 1967:152, 155, pl. 17, fig. 253 (in key, characters, New Guinea); Jones, 1969:7 (listed); Kähnsbauer, 1970:153 (characters, New Guinea); Palmer, 1970:222 (listed); Hiyama and Yasuda, 1971:310, fig. 347 (color plate); Kami, 1971:226 (listed); Herald and Randall, 1972:130 (cleaner species); Randall and Helfman, 1972:130 (cleaner species on *Apogon*, *Brachinus*, *Gymnothorax*); Rosenblatt *et al.*, 1972:5, 14 (Panama); Shino, 1972:61 (compiled); Randall, 1973:182 (Tahitian name); Burgess and Axelrod, 1974a:325, fig. 71 (color plate); Kähnsbauer, 1974:279 (listed); Lindberg, 1974:127, fig. 482 (fig. only); Vivien, 1974:34 (Madagascar); Brusca and Thomson, 1975:48 (listed); Jhingram, 1975:26 (listed); Mayland, 1975:136 (*Artemia* nauplii, cyclops, etc., as aquarium food items); Paxton, 1975:444 (notes diurnal upside down swimming behavior); Smith, 1975:29 (compiled); Wheeler, 1975:179, pl. 230 (descr. notes; color plate); Baissac, 1976:197 (compiled); Shino, 1976:107 (compiled); Thomson and McKibbin, 1976:22, fig. (descr. notes); Carcasson, 1977:79, pl. 41, fig. 321 (characters, range); Tinker, 1978:157, fig. (characters); Allen and Steene, 1979: 19 (listed); Thomson *et al.*, 1979:61, fig. (characters,

ecol. and behavior notes); Fritzsche, 1980:188, fig. 4c (in key, descr., range); Jones and Kumaran, 1980:161, 164, fig. 140 (in key; descr., Laccadive Arch.).

Doryrhamphus melanopleura: Bleeker, 1860:72 (misspelling, compiled); Vivien, 1974:26, 33 (Madagascar).

Doryrhamphus californiensis Gill, 1862:284 (orig. descr., Cape St. Lucas); Duméril, 1870:586 (characters); Jordan and Gilbert, 1881:371 (type lost or destroyed); Jordan, 1885: 371 (compiled); Jordan, 1887:850 (characters, type lost); Duncker, 1915:62 (characters, doubtful species, perhaps = *D. melanopleura*); Ulrey, 1929:6 (Cape San Lucas); Jordan *et al.*, 1930:243 (compiled); Fowler, 1944:496 (compiled); Nichols and Murphy, 1944:239 (among coral, 9-11 m; Panama); Pfeiffer, 1963:137 (alarm substance cells absent); Pfeiffer, 1977:657 (compiled); Fritzsche, 1980:188 (holotype incorrectly shown as CAS specimen).

Doryichthys californiensis: Günther, 1870:186 (descr. compiled).

Doryichthys excisus: Günther, 1870:186 (descr. compiled); Peters, 1876:447 (listed); Bleeker, 1878:16 (listed); Sauvage, 1891:528 (listed).

Doryichthys melanopleura: Hubrecht, 1879:51 (listed).

Doryichthys pleurotaenia Günther, 1880:62, pl. 26, fig. d (orig. descr.; 18 fms off Honolulu); Snyder, 1904:523 (listed); Günther, 1910:434 (descr.; close to *D. excisus*, Rotuma I.).

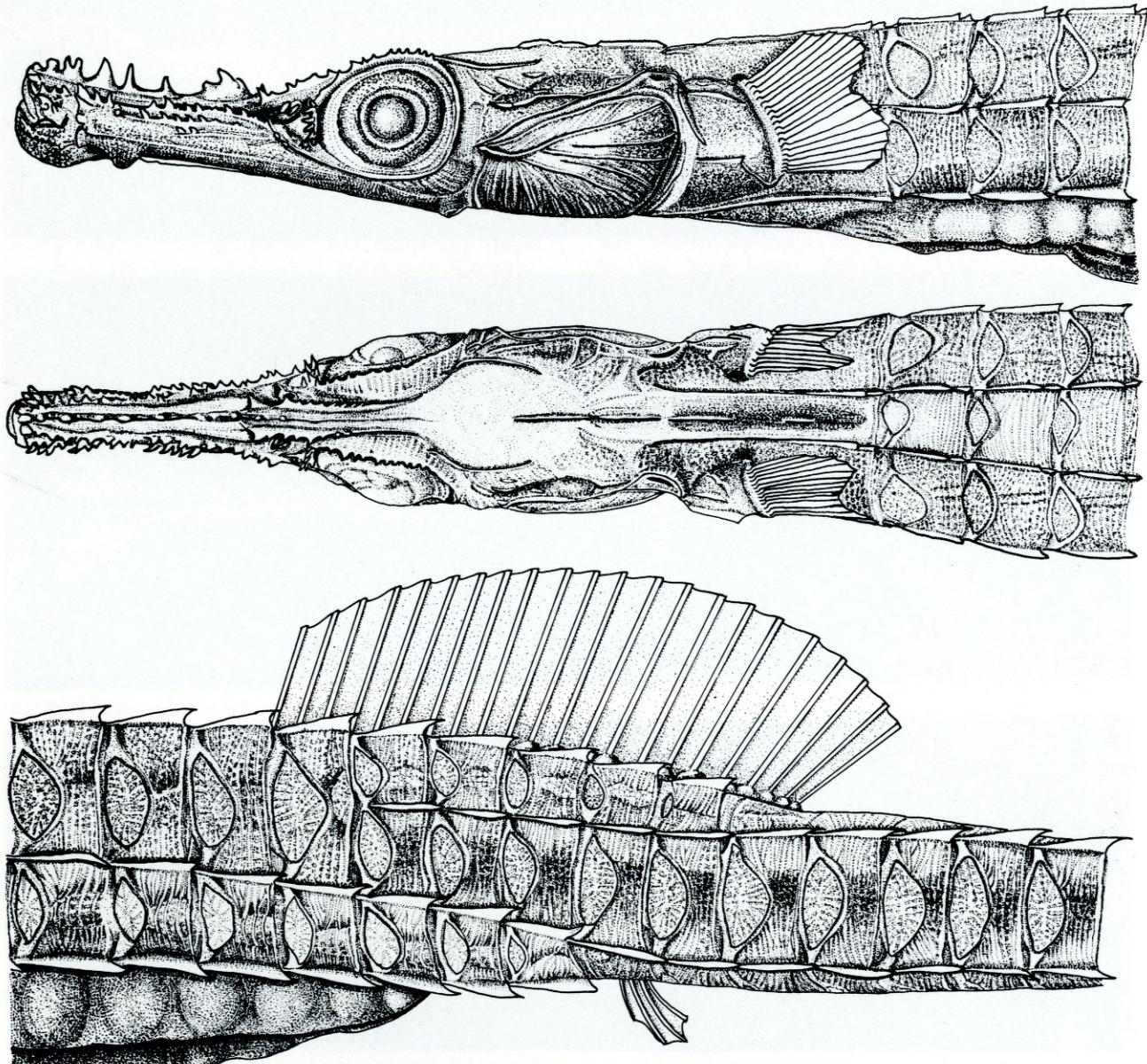


Figure 3. *Doryrhamphus excisus excisus*. Lateral (upper figure) and dorsal (middle figure) aspects of head and anterior trunk rings; note single ventrolateral projection on anterior part of snout. Lower figure, lateral aspect of body. Drawings from 41 mm SL brooding male, GCRL 17059.

Doryrhamphus (*Doryrhamphus*) *californiensis*: Jordan and Evermann, 1896:773 (descr. compiled, type lost); Jordan and Evermann, 1896a:328 (compiled).

Doryrhamphus pleurotaenia: Jordan and Evermann, 1905:121, fig. 37 (descr., Hawaii); Steindachner, 1906:1419 (Samoa).

Microphis pleurotaenia: Jordan and Seale, 1906:214 (Hawaii); McCulloch, 1910:432 (listed; Torres Strait and Cairns Reef, Austr.); Jordan and Jordan, 1922:28 (rare off Honolulu).

Microphis extensus Snyder, 1911:525 (orig. descr.; Naha, Okinawa); Snyder, 1912:495, pl. 62, fig. 2 (listed); Okada, 1938:158 (listed); Böhlke, 1953:61 (compiled).

Microphis melanopleura: Fowler, 1934:397 (compiled, New Hebrides); Fowler, 1944:189 (listed).

Doryrhamphus melanopleura melanopleura: Herald, 1953:254 (characters, comparisons); Briggs, 1961:553 (distribution); Masuda *et al.*, 1975: 183, pl. 25b (common, tidepools and reef flats, Ryukyu Is.; color plate).

Doryrhamphus melanopleura cooki Weed and Woods in Herald, 1953:254, 249 (orig. descr.; Aitutaki I., Cook Archipelago).

Doryrhamphus melanopleura pleurotaenia: Herald, 1953:254, 248 (except Socorro I. specimens, characters, comparisons); Briggs, 1961:553 (distribution, in part).

Microphis mayottae Fourmanoir, 1954:210 (orig. descr.; Dzaoudzi, Comoro Is.); Fourmanoir, 1957:21, pl. 2a (characters).

Doryrhamphus melanopleura: Yu and Chung, 1975:3 (misspelling; Liuchiu I., Taiwan).

DIAGNOSIS.—Trunk rings 17-19 (usually 17-18); total rings 30-35 (32 or more in 78% of specimens examined).

DESCRIPTION.—Rings 17-19 + 13-17, dorsal fin rays 21-29, pectoral-fin rays 19-23, subdorsal rings 5.0-3.0 + 1.75-4.5 = 5.75-8.25; see Tables 1-8 for additional counts. Proportional data based on 33 specimens

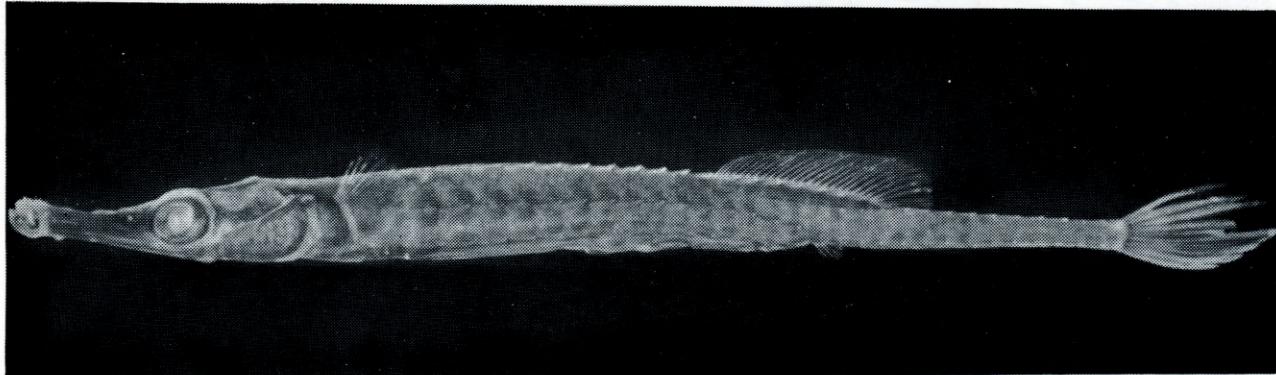
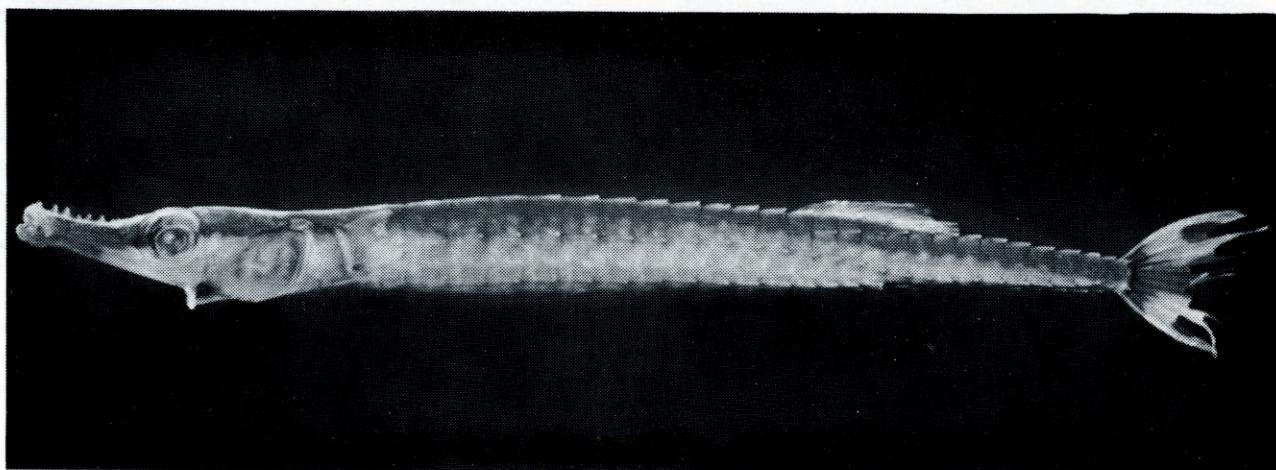
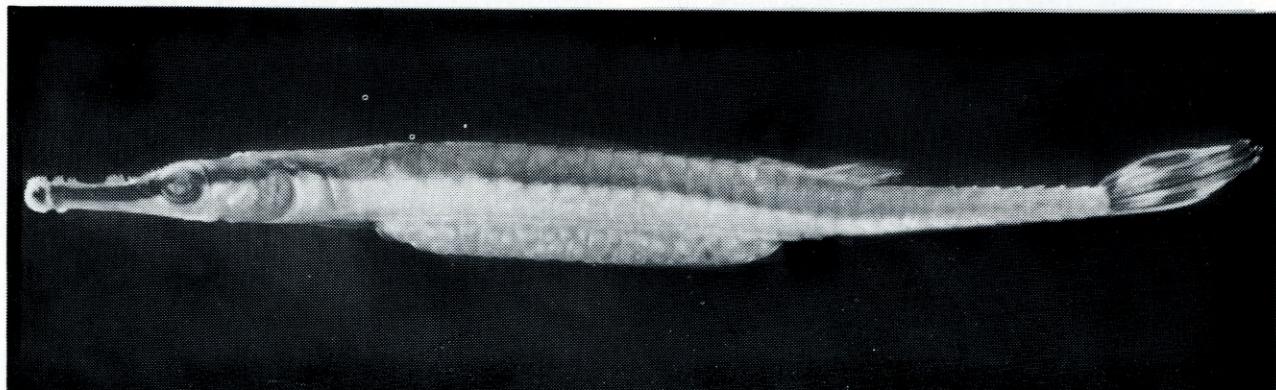


Figure 4. Top — *Doryrhamphus excisus excisus*, 45 mm SL brooding male, GCRL 17059. Middle — *D. e. abbreviatus*, 32 mm SL female paratype, SMF 8124. Bottom — *D. e. paulus*, 26.5 mm SL male paratype, SIO 72-67.

31.4-65.0 ($\bar{x} = 44.6$) mm SL follow: HL in SL 3.9-4.9 (4.4), snout length in HL 2.0-2.4 (2.2), snout depth in snout length 3.9-7.1 (5.4), length of dorsal-fin base in HL 1.3-2.0 (1.6), anal ring depth in HL 3.9-6.4 (4.6), trunk depth in HL 2.6-4.6 (3.5), pectoral-fin length in HL 3.9-6.4 (5.0), length of pectoral-fin base in pectoral-fin length 1.0-1.6 (1.3).

COMPARISONS. *Doryrhamphus e. excisus* differs from *D. e. abbreviatu*s and *D. e. paulus* in having higher numbers of trunk rings (modally, 17-18 versus 16). It further differs from *D. e. abbreviatu*s in having higher numbers of total rings (30-35 versus 26-28), dorsal-fin rays (21-29 versus 18-20) and pectoral-fin rays (usually, 20-21 versus 19). Additionally, southeastern Pacific (Line and Cook Is. to Marquesas Is.) and eastern Pacific mainland populations of *D. e. excisus* have higher numbers of total rings (usually, 33-35 versus 30-31) than *D. e. paulus* (Revillagigedo Is.).

TYPES.—Kaup's (1856) description of *Doryrhamphus excisus* was introduced by the following statement: "I am acquainted with a pair of examples of this species belonging to the Paris Museum, and five very young ones in the Berlin Museum, collected by Hemprich and Ehrenberg in the Red Sea." No further mention is made of the Berlin material and the description, including figure (Pl. III, fig. 5), is based entirely on the male and female specimens in the Paris collection. Although Kaup, probably due to lack of data, failed to indicate the origin of the Paris specimens, Duméril (1870) misinterpreted Kaup's opening remarks and incorrectly stated that these fish were collected at Massaua (= Massawa), the Red Sea locality of the Berlin material. Günther (1870) also reported the Red Sea as the type-locality and further misinterpreted Kaup's description by noting a count of 16 + 14, rather than 17 + 14, rings. Later, Duncker (1915), without examining the Paris material, deduced that the Paris and Berlin specimens represented separate taxa. He restricted the name *excisus* to the Red Sea population and designated the Berlin specimens as syntypes. At the same time, he also introduced Bleeker's (1858) *melanopleura* as the first available name for the population represented by Kaup's Paris Museum specimens of *Doryrhamphus*. Since Kaup's (1856) description was based solely on the two specimens of unknown origin in the Paris Museum, Duncker's (1915) restriction of *excisus* to the Red Sea population, represented by the Hemprich and Ehrenberg specimens, is invalid. This name must be based on the Paris syntypes of *D. excisus*, Bleeker's *melanopleura* is a junior synonym thereof, and the Red Sea population is innominate. The presence of 31 total rings clearly distinguishes the Paris syntypes of *D. excisus* from the Red Sea population (26-28 total rings), and these specimens probably came from Mauritius or other locality where the population of *D. excisus* has a modal count of 17 trunk rings. I select the male Paris syntype (54 mm SL) as the lectotype of *Doryrhamphus excisus* Kaup. This fish (MNHN 6211) has 17 + 14 rings, 22 dorsal-fin rays, 21 rays in each pectoral fin, 3.75 + 2.5 subdorsal rings and one ventrolateral projection on side of snout (see Kaup's pl. III, fig. 5). The specimen was originally described as having 16 rings "up to the anus" and "14 rings in the tail", but the anal ring was omitted from these values. I count one more pectoral- and 2 more dorsal-fin rays than originally described, but such

discrepancies are not unusual. The female Paris syntype (42 mm SL), now cataloged with the male, is the paralectotype. The Berlin specimens are referred to *D. e. abbreviatu*s.

The holotype of *Syngnathus melanopleura* Bleeker (RMNH 7251) is a male (55 mm SL) with a single ventrolateral projection on the snout, 19 + 14 rings, 25 dorsal-fin rays, 5 + 2.25 subdorsal rings and 21 rays in the right pectoral fin; left pectoral and caudal fins are damaged.

The holotype of *Doryichthys pleurotaenia* Günther (BMNH 1879.5.14.587) is an ink-marked female (42.5 mm SL) with 17 (rather than the originally described 18) trunk rings, 14 tail rings, 25 dorsal-fin rays, 21 pectoral-fin rays and 4.5 + 2.75 subdorsal rings.

Snyder's (1911) original material of *Microphis extensus* included five specimens. The holotype (USNM 68226) was described as a female (47 mm total length) with 19 + 15 rings and 22 dorsal-fin rays, and another specimen was noted as "cotype, No. 21418, Stanford University collection." The holotype, now 41 mm SL, is an immature male with 18 + 15 rings, 23 dorsal-fin rays and 4.0 + 2.75 subdorsal rings. There are now four specimens (USNM 74537, CAS-SU 21418) labeled "cotypes."

The holotype (FMNH 16220) and four paratypes (FMNH 16221, USNM 116089) of *Doryrhamphus melanopleura cooki* Weed and Woods are *D. e. excisus*.

The holotype of *Doryrhamphus californiensis* Gill was reported missing by Jordan and Gilbert (1882) and has not been found. Fritzshe's (1980) listing of this specimen as SU 19255 is erroneous. The holotype was evidently never cataloged in the Stanford collection, and SU 19255 is assigned to three specimens of *D. e. excisus* collected at Cape San Lucas, Mexico, in 1953.

I have not examined the holotype of *Microphis mayottae*, but Fourmanoir's (1957) illustration is that of *Doryrhamphus excisus*; the original count of 21 trunk rings (Fourmanoir, 1954) is evidently in error.

GEOGRAPHIC VARIATION.—Materials examined (Table 7) show the presence of a number of Indian Ocean populations wherein trunk rings are modally 17 or 18. This count is modally 17 in the western Pacific region bounded by the Gulf of Thailand, the Philippines, the New Hebrides and eastern Australia. Other examined Pacific populations have modal counts of 18 rings, except for Hawaii where trunk rings are modally 17. These differences are presently unexplained, but similar shifts in modal trunk-ring counts also occur in the gastrophorine pipefish *Choeroichthys brachysoma* (see Dawson, 1976). I find no features which justify separate taxonomic treatment of these 17 and 18 ring populations of *Doryrhamphus e. excisus*.

With the exception of a few populations (e.g. Fiji, Hawaii) with slightly reduced values, there is a tendency toward higher numbers of total rings in the central Pacific area (Table 7), with highest values occurring in the southeastern region (Cook Is. to Marquesas Is.). A similar but more consistent trend occurs in frequencies of dorsal-fin rays (Table 8) and total subdorsal rings, wherein highest values occur eastward of the Fiji Is.

Well-marked specimens of most populations have a prominent, broad, dark lateral stripe on trunk and tail; and the dorsum, lower half of side and venter of trunk are largely pale. Some fish, particularly those from the

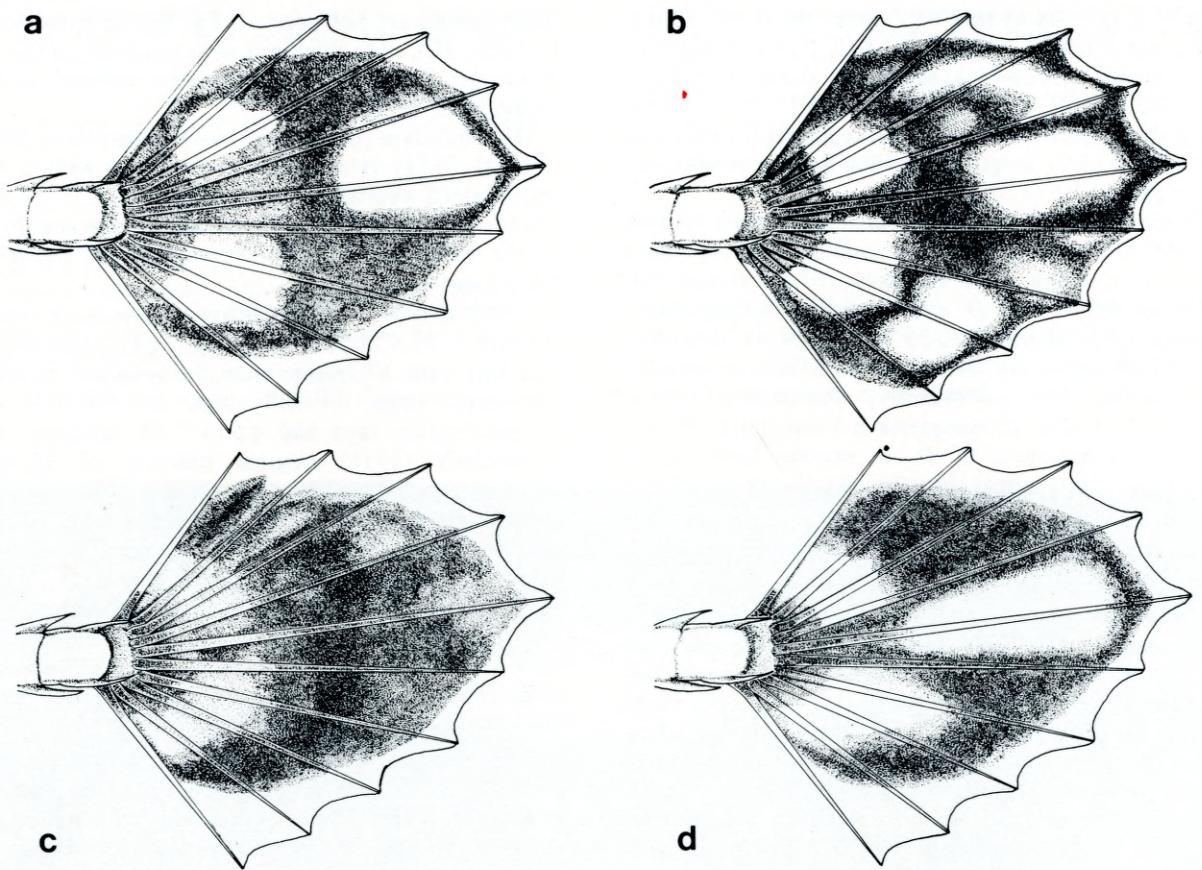


Figure 5. Markings on caudal fins of *Doryrhamphus excisus excisus*: (a) Mozambique, (b) Ryukyu Is., (c) Hawaii, (d) Panama.

southeastern central Pacific region (Austral Is., Tuamotus, etc.), may be largely brownish due to a rather dark ground colour which tends to obscure the lateral stripe. Markings on the caudal fin are highly variable (Fig. 5) but these seem to reflect individual rather than geographic variation.

Tendencies toward higher values for some meristic characters and darker coloration in the central and eastern Pacific appear to be clinal and I find no character combination which clearly differentiates specimens from these regions from other populations of *D. e. excisus*.

REMARKS.—Males develop the ventrolateral projection on the snout at lengths of 23-29 mm, some have evidence of pouch development at 32 mm and the smallest brooding male examined is 33 mm SL. The pouch of a 41 mm SL male contains a total of 88 eggs with a maximum diameter of ca. 1.0 mm. A 39.5 mm SL fish has pouch eggs in a single layer of three transverse rows, with 16 eggs in the outer left row. A 47.5 mm SL specimen has two layers of pouch eggs in four transverse rows with 25 eggs in the left ventrolateral row.

Planktonic postlarvae (5.5 mm TL) have a short, deep, snout, incompletely differentiated rings; and a median membranous finfold that almost encircles the body (Fig. 6). Other planktonic young (8-13 mm SL) have lost the finfold, have a longer, more slender snout; and rings and fin-rays are well developed.

Several small specimens (17-18.5 mm SL) have the striped body coloration of adults, but I have not seen banded juveniles similar to those reported by Fritzsche (1980).

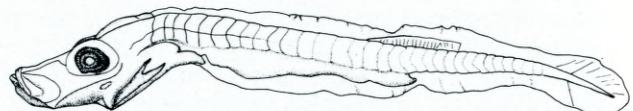


Figure 6. *Doryrhamphus excisus excisus*. Semi-diagrammatic delineation of planktonic larva (5.5 mm TL, GCRL 16393); note dorsal and ventral membranous median fin-fold.

DISTRIBUTION.—Throughout the Indo-Pacific region (Fig. 2) from the Persian Gulf and east coast of Africa (to 32°S) to the west coast of the Americas, from ca. 26°38'N to the Galapagos Is., Ecuador (ca. 01°S). The southernmost record from eastern Africa is based on a single specimen taken off the mouth of the Xora R. Among other material examined from this coast, the southernmost locality is Inhambane, Mozambique (ca. 24°S). This species is common in the Ryukyu Is., but I am uncertain as to whether it reaches the main islands of Japan. Some examined collections are from tidepools, but most are from open waters over rock or coral substrates. Among 93 samples with useful data, 55 are from depths of 0-5 m, 14 from 5-10 m, 18 from 10-20 m, 5 from 20-40 m and one SCUBA collection is from 45-49 m.

Doryrhamphus e. excisus has the widest geographical distribution of any syngnathid, and is the only pipefish known to have crossed the East Pacific Barrier (Briggs, 1961). In view of demonstrated accommodation to a variety of habitats, there appears little doubt that *D. e. excisus* could successfully transit the proposed Panamanian sea-level canal and become established in Caribbean-Atlantic waters.

MATERIAL EXAMINED.—564 specimens, ca 4.4-66 mm SL.

LECTOTYPE.—MNHN 6211 (54.0 mm SL, brooding male), locality unknown.

PARALECTOTYPE.—MNHN 6211 (42.0 mm SL, adult female), locality unknown.

OTHER MATERIAL.—PERSIAN (ARABIAN) GULF, Bahrain I.: BMNH 1975.4.5.8-9 (2, 48.5-62). INDIAN OCEAN, Kenya: LACM 31617-12 (1, 47.5), LACM 31619-20 (1, 62.5), RUSI 2470 (3, 37.5-53), RUSI 2481 (1, 49.5), RUSI 2483 (1, 49.5). Tanzania: ANSP 122495 (2, 42.42.5), BPBM 17592 (1, 52), RUSI 2468 (1, 18), RUSI 2477 (2, 58-65). Mozambique: CAS 15158 (2, 43-48), RUSI 2466 (1, 32), RUSI 2467 (1, 57), RUSI 2469 (1, 47.5), RUSI 2471 (1, 30), RUSI 2472 (2, 48.5-55), RUSI 2473 (1, 46.5), RUSI 2476 (1, 40), RUSI 2479 (1, 46), RUSI 3984 (2, 44-49.5). South Africa: RUSI 2474 (1, 26). Aldabra Is.: USNM 226317 (1, 46). Comoro Is.: CAS 33389 (1, 47), CAS 33735 (1, 51.5), CAS 35035 (1, 48), USNM 214136 (1, 54). Gulf of Oman, Khor Fakkan: WAM P.25998-013 (2, 42.5-49). Seychelles Is.: ANSP 108983 (1, 41), ANSP 108987 (1, 30.5), ANSP 108988 (2, 33-45.5), ANSP 108991 (2, 38-44), ANSP 110018 (1, 46), ANSP 110020 (3, 42.5-60), ANSP 110021 (1, 31.5), ANSP 110026 (1, 56.5), ANSP 110027 (2, 39-41), ANSP 110029 (1, 48.5), ANSP 110034 (1, 47), ANSP 110044 (2, 29-44), ANSP 110049 (2, 36-47), ANSP 110055 (1, 35), ANSP 110060 (10, 27.5-50.5), RUSI 2475 (1, 48), RUSI 2480 (1, 47). Amirante Is.: ANSP 110048 (1, 38), ANSP 110051 (1, 62.5), GCRL 13777 (1, 61), USNM 214135 (1, 49). Mauritius: BPBM 21798 (2, 46-48.5), RUSI 74-95 (2, 34-60), RUSI 74-96 (6, 39.5-57), RUSI 74-100 (2, 46-48), RUSI 74-310 (1, 46). Cargados Carajos (St. Brandon) Shoals: USNM 216174 (1, 52.5), USNM 216175 (9, 34-56), USNM 216176 (1, 48), USNM 216177 (7, 37.5-54), USNM 216178 (1, 45.5), USNM 216179 (1, 42), USNM 216194 (3, 29-42). Maldives Is.: BOC 7778 (1, 36). Chagos Arch., Diego Garcia: GCRL 17059 (2, 41.5-45), ROM 4298 (2, 44-49), USNM 226323 (1, 35.5), USNM 226324 (3, 39.5-47.5). Sri Lanka: BOC 6830 (1, 36), USNM 226315 (1, 30.5), USNM 226318 (3, 21-25), USNM 226319 (1, 48.5), USNM 226320 (2, 21-23.5), USNM 226321 (1, 29.5), USNM 226322 (1, 29.5), USNM 226325 (3, 31-37), USNM 226331 (4, 15.5-18), USNM 226332 (1, 30). Kokos (Cocos) Is.: RMNH 7251 (55, holotype of *Syngnathus melanopleura*). Cocos-Keeling Is.: ANSP 128426 (3, 42-49), ANSP 128429 (2, 46-55), ANSP 128430 (1, 47), ANSP 128431 (1, 51). Off Sumatra: ZMUC P.39577 (1, 8.3). Christmas I.: WAM P.26102-16 (2, 19-38), WAM P.26103-021 (1, 57). PACIFIC OCEAN, Gulf of Thailand and S China Sea: CAS 15839 (1, 48), CAS 15840 (1, 25), CAS 15841 (1, 44). Philippine Is.: GCRL 16954 (1, 33), GCRL 17014 (3, 30.5-36.5), USNM 219157 (1, 19.5), USNM 220633 (1, 42.5), USNM 220634 (1, 33.5), USNM 226309 (2, 31.5-39), USNM 226311 (2, 27.5-29), USNM 226312 (1, 39.5), USNM 226313 (1, 31.5), USNM 226314 (1, 27.5). Celebes Is.: USNM 209588 (1, 41), USNM 209751 (1, 33.5), ZMA 109.188 (2, 23-32). Ryukyu Is.: CAS-SU 21418 (2, 28-37, "cotypes" of *Microphis extensus*), GCRL 16981 (1, 41), IORD uncat. (5, 33-47.5), SMLVO uncat. (1, 46), USNM 68226 (41, holotype of *M. extensus*), USNM 74537 (2, 23.5-43, "cotypes" of *M. extensus*), USNM 226310 (1, 51), USNM 226327 (1, 32), USNM 226328 (1, 34), USNM 226329 (2, 40.5-51). Caroline Is.: CAS 15817 (2, 41), CAS 15818 (1, 18.5), CAS 15819 (1, 47), CAS 15820 (1, 50), CAS 15821 (1, 52), CAS 15822 (1, 39.5), CAS 15823 (3, 40-44), CAS 15824 (1, 54), CAS 15825 (1, 16), CAS 15826 (1, 36), CAS 15827 (2, 38.5-49.5), CAS 15828 (2, 28.5-47), CAS 15829 (5, 29.5-39), USNM 223231 (1, 28.5). New Guinea: GCRL 16956 (2, 39-47), USNM 226330 (1, 31), USNM 226333 (3, 34-48). Australia (Qld.): AMNH 35913 (1, 34), AMNH 36476 (12, 24.5-38.5), AMS I.10740 (2, 31.5-32), AMS I.11755 (3, 36.5-40), AMS I.14008 (2, 34.5-35.5), AMS I.18121-001 (1, 38), AMS I.19473-048 (1, 28.5), AMS I.20755-057 (3, 16-33), AMS I.20756-002 (1, 20.5), AMS I.20756-003 (1, 18.5), AMS I.20770-002 (2, 29-34), AMS IA.2373 (2, 44.5-46.5), AMS IA.2713 (2, 39), AMS IB.2522 (1, 31.5), QM I.10985 (1, 41), QM I.16090 (1, 33). Mariana Is.: ANSP 114313 (2, 33.5-37), ANSP 117191 (3, 36-38.5), ANSP 117214 (1, 40.5), CAS 15830 (3, 26-39.5), CAS 15831 (1, 43), CAS 15832 (1, 39.5), CAS 15833 (2, 46.5), CAS 15834 (1, 40), CAS 15835 (2, 44.5), CAS 15836 (2, 33-34.5), CAS 15837 (4, 31-44), CAS 15838 (7, 29.5-48.5), UG 4203 (9, 25-42), UG 4247 (4, 22.5-40), UG 4926 (1, 24.5). Solomon Is.: BPBM 16124 (2, 41), CAS 19957 (1, 39), CAS 19958 (2, 36-37). New Hebrides Is.: AMS IA.782 (1, 51). Marshall Is.: BPBM 8024 (1, 46), BPBM 8188 (1, 41), BPBM 8223 (3, 22.5-37.5), BPBM 8257 (1, 43), BPBM 10935 (1, 56), BPBM 18396 (1, 38), CAS 15807 (3, 50.5-56), CAS 15808 (6, 42.5-56.5), CAS 15809 (1, 54), CAS 42885 (3, 17-57.5), CAS 42956 (1, 39.5), CAS 42967 (2, 54-55), CAS 42979 (1, 46), CAS 43255 (1, 44),

CAS 43321 (6, 31.5-47), CAS 43416 (4, 29-49), CAS 43502 (1, 36.5), GCRL 4044 (1, 49). Gilbert Is.: AMS I.18046-028 (1, 41), AMS I.18052-058 (2, 23-29), BMNH 1969.8.26.136 (1, 48), USNM 167358 (1, 45). Fiji Is.: BMNH 1897.8.23.197 (1, 48), USNM 214133 (1, 40), USNM 214134 (1, 52). Johnston Atoll: AMS I.20589-001 (2, 44.5-46). Canton I.: CAS 40519 (1, 39.5). Samoa Is.: BPBM 11318 (1, 34.5), GCRL 16104 (1, 48), USNM 84164 (1, 35), USNM 116089 (3, 46-47, paratypes of *Doryrhamphus melanopleura cooki*), USNM 116090 (1, 51.5), USNM 214132 (1, 48). Hawaiian Is.: ANSP 80656 (1, 20), BMNH 1879.5.14.587 (42.5, holotype of *Doryichthys pleurotaenia*), BPBM 7911 (3, 23.5-37), BPBM 7932 (3, 29-52.5), CAS 15810 (3, 45-51), CAS 20402 (1, 54.5), CAS 20405 (2, 54-55), CAS 47129 (1, 50.5), GCRL 16385 (2, 13-18), GCRL 16386 (4, 36-40), GCRL 16393 (1, 4.5), GCRL 16394 (1, 11.5). Line Is.: BPBM 26391 (1, 44), CAS 15811 (1, 47), CAS 15812 (1, 46), USNM 214131 (1, 41). Cook Is.: AMS IA.5375 (2, 44-54), BPBM 5655 (3, 38.5), CAS 15816 (1, 49), FMNH 16220 (51.5, holotype of *D. m. cooki*), FMNH 16221 (48, paratype of *D. m. cooki*). Society Is.: BPBM 5882 (1, 38.5), CAS 15813 (1, 46), CAS 15814 (1, 50), CAS 15815 (1, 46.5), FMNH 75875 (1, 34), GCRL 14906 (3, 27.43) MNHN uncat. (1, 49), USNM 226316 (1, 37.5). Austral Is.: BPBM 12961 (2, 48.5-55.5), BPBM 13004 (2, 53.5-55), BPBM 17265 (1, 56.5), USNM 226326 (2, 46-49). Marquesas Is.: AMS I.21769-007 (1, 44), BPBM 11715 (2, 45.5-55), BPBM 12643 (2, 41.5-45), BPBM 12748 (1, 58.5). Tuamotu Arch.: BPBM 10271 (1, 50), BPBM 26392 (1, 50). Mexico: CAS 14020 (4, 34.5-39), CAS 24569 (1, 40.5), CAS 24589 (1, 39), CAS 24632 (9, 30.5-51), CAS 24649 (1, 49), CAS 24650 (4, 47-60), CAS 27941 (1, 45.5), CAS 47363 (2, 42-47.5), CAS 48187 (1, 35.5), CAS-SU 16336 (1, 47), CAS-SU 19081 (1, 43), CAS-SU 19255 (3, 41.5-46.5), SIO 57-291 (2, 47-48), SIO 59-228 (3, 41-42), SIO 61-269 (4, 44.5-50.5), SIO 61-277 (2, 46), SIO 62-20 (2, 29-46.5), SIO 62-29 (2, 28-44), SIO 62-49 (1, 27.5), SIO 62-55 (1, 49.5), SIO 62-56 (2, 33.5-50.5), SIO 62-58 (1, 49.5), SIO 62-63 (1, 41.5), SIO 64-54-57 (3, 55-61), SIO 70-155 (10, 33-53), SIO 74-90 (3, 31.5-45.5). Costa Rica: GCRL 6553 (1, 38), FMNH 91872 (1, 47.5), FMNH 91873 (1, 33), UCLA W64-45 (1, 48.5), UCLA W64-46 (1, 39). Panama: CAS 35544 (4, 42.5-54.5), GCRL 13089 (2, 52-54), MCZ 50750 (1, 56.5), MCZ 50752 (8, 33-39.5), MCZ 50755 (2, 47.5-51.5), MCZ 56891 (4, 26-46), MCZ 56893 (1, 31), MCZ 56894 (1, 26), SIO 67-35 (1, 40), SIO 67-36 (2, 38.5-40.5), SIO 67-37 (2, 40-44), SIO 67-38-57 (3, 39.5-53.5), SIO 67-39-57 (2, 42-47), SIO 70-135 (2, 48-52), SIO 70-136 (1, 44), SIO 70-139 (2, 30-36.5), SIO 70-359 (4, 31-39.5), UMML 33183 (7, 37-53). Colombia: UMML 33182 (3, 36-53). Ecuador (incl. Galapagos Is.): CAS 23727 (2, 59-66), CAS 39231 (3, 26-46.5), CAS 39255 (1, 16.5), CAS 39277 (5, 26-46.5), CAS 39305 (1, 33.5), CAS 39394 (1, 46), LACM 8013 (1, 51), LACM 8076 (4, 37-55), SIO 64-1015 (3, 53.5-62.5), UMML 33180 (1, 46), UMML 33181 (1, 38).

Doryrhamphus excisus abbreviatus n. ssp.

Figs. 2 & 4

Doryrhamphus excisus Kaup, 1853:233 (*nomen nudum*); Kaup, 1856:54 [in part, Berlin Mus. syntypes only; Red Sea (Massaua)]; Bamber, 1915:480 (listed); Duncker, 1915:62 (descr.; name incorrectly restricted to Red Sea population); Dollfus and Petit, 1938:497 (in part, Red Sea ref. only); Kählsbauer, 1950:271 (counts); Herald, 1953:245 (in key); Fowler, 1956:198 (synonymy, in part); Smith, 1963:530 (in key; descr.; possibly confined to Red Sea); Fritzsche, 1980:190 (compared with *D. paulus*).

Doriichthys excisus: Klunzinger, 1871:652 (ref.); Botros, 1971:239, 241, 341 (Red Sea endemic).

DIAGNOSIS.—Trunk rings 15-16; total rings 26-28 (modally 27); dorsal-fin rays 18-20.

DESCRIPTION.—Rings 15-16 + 11-12, dorsal-fin rays 18-20, pectoral-fin rays 18-20, subdorsal rings 4.5-3.0 + 1.0-2.25 = 5.0-6.0; see Tables 1-6 for additional counts. Proportional data based on 13 specimens 26.5-43.0 ($\bar{x} = 33.6$) mm SL follow: HL in SL 3.5-4.1 (3.9), snout length in HL 2.2-2.5 (2.4), snout depth in snout length 4.1-5.3 (4.7), length of dorsal-fin base in HL 1.8-2.4 (2.1), anal ring depth in HL 4.2-5.2 (4.5), trunk depth in HL 2.8-4.2 (3.5), pectoral-fin length in HL 4.3-6.5 (4.9), length of pectoral-fin base in pectoral-fin length 1.0-1.3 (1.2). Counts and measurements of the holotype (USNM 226446) are: rings 16 + 11, dorsal-fin rays 18, pectoral-fin rays 19 x 18, subdorsal rings 4 + 1,

SL 38.0, HL 9.3, snout length 3.9, snout depth 0.9, length of dorsal-fin base 4.5, anal ring depth 2.1, trunk depth 2.6, pectoral-fin length 2.1, length of pectoral-fin base 1.9.

ETYMOLOGY.—Named *abbreviatus*, shortened, in reference to the reduced number of tail rings.

COMPARISONS.—This subspecies shares the modal count of 16 trunk rings with *D. e. paulus*, but it is clearly distinguished from *D. e. excisus* and *D. e. paulus* by lower numbers of tail rings, total rings and dorsal-fin rays (Tables 1-6). Furthermore, *D. e. abbreviatus* has somewhat fewer pectoral-fin rays (modally, 19 versus 20-21) and subdorsal tail rings (1.0-2.25 versus 1.75-4.5) than related subspecies.

REMARKS.—The holotype (38 mm SL) is an immature male without fully developed brood-pouch folds. A 21 mm SL male (NMW 40278) has traces of developing pouch folds, and the only brooding male examined (BMNH 1915.10.25.3) is 43 mm SL.

Kaup's (1856) Red Sea syntypes of *D. excisus* (ZMB 4368/1-5) are now in poor condition, but they are clearly representatives of this subspecies. Two of the five specimens lack heads and most fins, and the remaining three, a male and two females (ca. 21-23 mm SL), have 16 + 12 rings. All Red Sea records of *D. excisus* evidently refer to *D. e. abbreviatus*.

DISTRIBUTION.—A Red Sea endemic known, in the west, from the Gulf of Suez (El Tûr, Sinai Peninsula) to Massawa and from Jiddah on the east coast (Fig. 2). The few available data indicate collections within the 0-9 m range.

MATERIAL EXAMINED.—23 specimens, 21-43 mm SL.

HOLOTYPE.—USNM 226446 (immature male, 38 mm SL), Red Sea, Strait of Jubal, 27°16'46"N, 33°46'25"E, 0-2.4 m, sta. HA-29, 1 Jan. 1965. L. Kornicker and H.A. Fehlmann.

PARATYPES.—RED SEA, El Tûr USNM 226447 (2, 30-31), 0-9.1 m, sta. VGS 69-29, 27 Sept. 1969, V. G. Springer, Strait of Jubal: GCRL 17061 (1, 42.5) and USNM 226448 (1, 36), taken with holotype. GCRL 17062 (1, 34.5) and USNM 226449 (1, 35), 0-7.6 m, sta. HA-32, 4 Jan. 1965, H. A. Fehlmann. USNM 226450 (1, 31), 0-4.6 m, sta. HA-38, 10 Jan. 1965, H. A. Fehlmann. USNM 226451 (1, 31), 0-2.4 m, sta. HA-31, 3 Jan. 1965. USNM 226452 (1, 32), 0-6.1 m, sta. HA-30, 2 Jan. 1965. Hurghada (Al Ghardaqa): SMF 8124 (1, 32), 9 Sept. 1964, D. Magnus. BMNH 1915.10.25.3 (1, 43), probable locality, Crossland, Jiddah: CAS 23510 (2, 26.5), NMW 40277 (1, 29.5) and NMW 40278 (1, 21), 1895-96, F. Steindachner. RMNH 18389 (1, 31.5), 1880, Kryut.

OTHER MATERIAL.—RED SEA, Sudan, Port Sudan: BPBM 20418 (1, 32). Ethiopia, Massawa: ZMB 4368/1-5 (5, incl. 3 (21-23) and 2 damaged), Hemprich and Ehrenberg (syntypes of *D. excisus*).

Doryrhamphus excisus paulus Fritzsche

Figs. 2 & 4

Doryrhamphus melanopleura pleurotaenia: Herald, 1953: Tab. 19, 248 (in part, Revillagigedo Is. (Socorro I.) only); Briggs, 1961: 553 (in part, Revillagigedo Is. only).

Doryrhamphus melanopleura: Ricker, 1959a: 5 (listed, Socorro I.).

Doryrhamphus paulus Fritzsche, 1980: 189, fig. 4b (orig. descr.; Isla Socorro, Islas Revillagigedos, México).

DIAGNOSIS.—Trunk rings 16-17 (modally 16); total rings 30-32 (modally 31); dorsal-fin rays 23-27.

DESCRIPTION.—Rings 16-17 + 14-15, dorsal-fin rays 23-27, pectoral-fin rays 19-23 (usually 21-22), subdorsal rings 4.75-4.0 + 1.75-2.5 = 5.75-6.75; see Tables 1-6 for additional counts. Proportional data based on 11 specimens 46.5-72.5 ($\bar{x} = 63.2$) mm SL follow: HL in SL 4.3-5.3 (4.7), snout length in HL 1.9-2.2 (2.1), snout depth in snout length 4.8-6.2 (5.5), length of dorsal-fin base in HL 1.6-2.0 (1.8), anal ring depth in HL 4.5-5.6 (5.0), trunk depth in HL 3.0-4.3 (3.9), pectoral-fin length in HL 4.5-5.8 (5.3), length of

counts. Proportional data based on 9 specimens 25.5-39.0 ($\bar{x} = 30.2$) mm SL follow: HL in SL 3.5-3.8 (3.6), snout length in HL 2.0-2.2 (2.1), snout depth in snout length 5.3-7.0 (6.2), length of dorsal-fin base in HL 1.7-2.1 (1.9), anal ring depth in HL 4.9-6.5 (5.9), trunk depth in HL 4.2-4.6 (4.4), pectoral-fin length in HL 4.6-5.5 (5.1), length of pectoral-fin base in pectoral-fin length 1.3-1.4 (1.2).

COMPARISONS.—This subspecies shares the modal trunk ring count of 16 with *D. e. abbreviatus*, but differs in having more tail rings (14-16 versus 11-12), dorsal-fin rays (23-27 versus 18-20) and subdorsal tail rings (2.5-4.25 versus 1.0-2.25). The modal count of 16 trunk rings distinguishes *D. e. paulus* from *D. e. excisus*, which has modally 17 or 18 throughout its range (Table 7) and 18 in eastern Pacific populations (Line Is. to W coast of Americas). Compared to these eastern Pacific populations, *D. e. paulus* further differs from *D. e. excisus* in having somewhat fewer total rings (30-32 versus 32-35).

REMARKS.—Among material examined, the ventrolateral projection on the snout is present on some males (19.5-21.5 mm SL) without brood-pouch folds. The pouch of a brooding male (24 mm SL) contains ca. 20 eggs in a single layer of two transverse rows.

This insular endemic shows less differentiation from *D. e. excisus* than does the Red Sea population (*D. e. abbreviatus*), but meristic differences, principally the lower number of trunk rings, are considered sufficient for its recognition as a subspecies.

DISTRIBUTION.—Known only from depths of 3-17 m at Socorro I. and Clarion I., Revillagigedo Is., Mexico (Fig. 2).

MATERIAL EXAMINED.—28 paratypes, 16-39 mm SL. For additional data, see Fritzsche (1980).

MEXICO, Revillagigedo Is., Socorro I.: CAS 13699 (9, 20-31), 1 CAS-SU 36442 (1, 30), CAS-SU 67255 (1, 24), GCRL 15753 (1, 26.5), LACM 31781-2 (3, 21.5-32), LACM 31782-12 (5, 25.5-32), SIO 72-67 (6, 16-26.5). Clarion I. SIO 74-155 (2, 28.5-39).

Doryrhamphus japonicus Araga and Yoshino

Figs. 7, 8, 11

? *Doryrhamphus extensus* (not of Snyder): Ogawa, 1961: 336, 339, 341 (note on aglomerular kidney).

? *Doryrhamphus melanopleura* (not of Bleeker): Shiogaki and Dotsu, 1973: 18, pl. 2, fig. 5 (listed); Burgess and Axelrod, 1974: 213, fig. 379 (colour fig. only).

Doryrhamphus melanopleura japonica Araga and Yoshino in Masuda et al., 1975: 183, pl. 25c (misspelling; orig. descr.; colour fig.): Tanabe Bay (Honshu I.), Japan.

? *Doryrhamphus extensus* (not of Snyder): Khalil, 1980: 32 (misspelling; ref. to Ogawa, 1961).

DIAGNOSIS.—Principal ridges of posterior predorsal trunk rings with one distal spine; trunk rings usually 19; subdorsal trunk rings 4.75-4.0; males without bony ventrolateral projection on snout; trunk with narrow dark stripe between superior and lateral ridges.

DESCRIPTION.—Rings 19-20 + 14-15, dorsal-fin rays 21-23, pectoral-fin rays 19-23 (usually 21-22), subdorsal rings 4.75-4.0 + 1.75-2.5 = 5.75-6.75; see Tables 1-6 for additional counts. Proportional data based on 11 specimens 46.5-72.5 ($\bar{x} = 63.2$) mm SL follow: HL in SL 4.3-5.3 (4.7), snout length in HL 1.9-2.2 (2.1), snout depth in snout length 4.8-6.2 (5.5), length of dorsal-fin base in HL 1.6-2.0 (1.8), anal ring depth in HL 4.5-5.6 (5.0), trunk depth in HL 3.0-4.3 (3.9), pectoral-fin length in HL 4.5-5.8 (5.3), length of

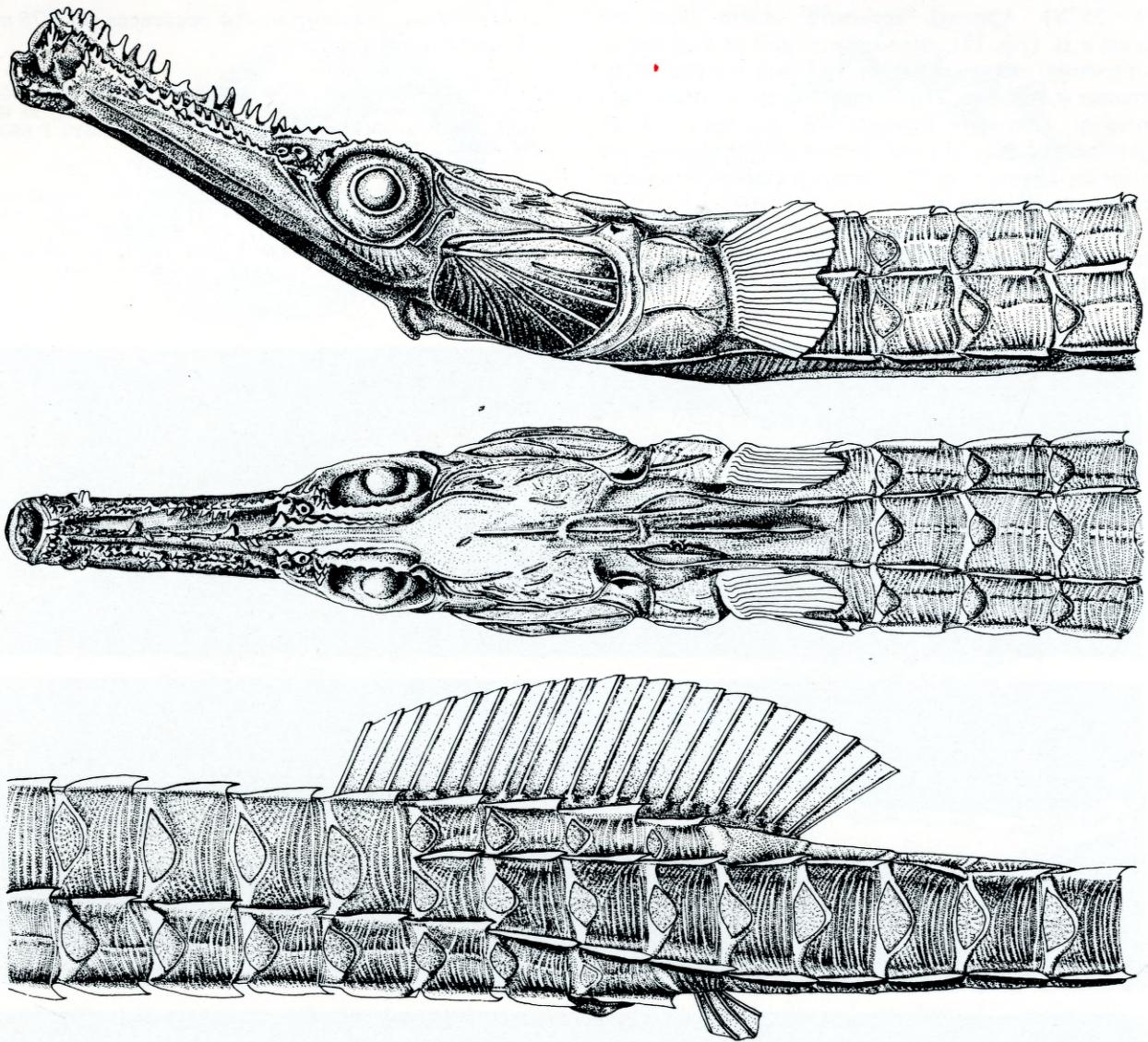


Figure 7. *Doryrhamphus japonicus*. Lateral (upper figure) and dorsal (middle figure) aspects of head and anterior trunk rings; lower figure, lateral aspect of body. Drawings from 70 mm SL adult male paratype, SMBL F.65030.

pectoral-fin base in pectoral-fin length 1.1-1.5 (1.3).

Dark stripe on trunk closely follows superior ridge (Fig. 8), typically covers less than half of space between superior and lateral ridges; see Fig. 9 for markings on caudal fin.

COMPARISONS. —Absence of ventrolateral projections on the snout of males distinguishes *D. japonicus* from congeners which share the presence of single spines on the principal ridges of the posterior predorsal rings. This species has more trunk rings than *D. bicarinatus* and *D. excisus* (modally, 19 versus 16-18) and shares the narrow lateral stripe on trunk with *D. bicarinatus* (stripe typically broad in *excisus*). *Doryrhamphus japonicus* has more subdorsal trunk rings (4.75-4.0 versus 2.5-2.0) and fewer subdorsal tail rings (1.75-2.5 versus 2.75-3.5) than *D. bicarinatus*, and reaches a greater length than *D. excisus* (at least, 75 versus 66 mm SL). Compared to *D. negrosensis* and *D. janssi*, characterized by the presence of two spines on principal ridges of the posterior predorsal rings, *D. japonicus* is further distinguished by higher numbers of trunk rings (19-20 versus 14-17).

REMARKS. —Although originally described (Araga and Yoshino, 1975) as a subspecies of *D. excisus* (as *melanopleura*), absence of ventrolateral projections on the snout of subadult and adult males (characteristic of *excisus*) clearly indicates separate intrageneric lineage and dictates species status for *D. japonicus*.

Recently preserved aquarium-hatched larvae (ca. 4.8 mm TL and 22 hrs. old), received from Ann G. Thresher, have the head and body shaded with brown microchromatophores. A faint dark bar, its width about 1/2-1/3 of pigmented eye diameter, crosses side just behind the nape. There are 8 diffuse brown blotches on the dorsal finfold: 4 predorsal, 2 above dorsal-fin base and 2 between rear of dorsal-fin base and caudal fin. Beginning below the 3rd blotch on the dorsal finfold, there are six similar, opposing, blotches on the ventral finfold. The caudal fin, shaded lightly with brown, has single small, pale, distal spots above and below.

DISTRIBUTION. —This species was originally described from Tanabe Bay, southern Honshu I., Japan and present material includes specimens from Sagami Bay

(ca. 35°N). Although apparently absent from the Ryukyu Is. (Fig. 11), the southern limit of distribution is presently unknown. Ogawa's (1961) material of *D. extensus* (68-82 mm TL) from Shirahama (Tanabe Bay) probably represents misidentified specimens of *D. japonicus* and Shiogaki and Dotsu's (1973) specimen of *D. melanopleura* from Nomokazi (Kyushu I.) may also prove to be *D. japonicus*.

The type material was collected from sublittoral rocky reefs. There is one sample from a tidepool (CAS 14512) and one from a depth of 10 m (GCRL 17433).

MATERIAL EXAMINED.—14 specimens, 46.5-75 mm SL, and 4 larvae.

PARATYPES.—Japan, Wakayama Pref., Tanabe Bay: SMBL F.65030 (70, male) and SMBL F.65031 (63.5, male), 30 May 1965, M. Ohta. SMBL F.68011 (65, male) and SMBL F.68012 (66, female), 16 Sept. 1968, C. Araga.

OTHER MATERIAL.—Japan, Kanagawa Pref., Sagami Bay: GCRL 17432 (1, 75), GCRL 17433 (2, 63-64.5), GCRL 17434 (4, ca. 4.8 TL), YCM P.5290 (1, 48), YCM P.5330 (1, 72.5), YCM P.5412 (1, 46.5), YCM P.5468 (1, 54.5). Wakayama Pref., Tanabe Bay: CAS 14512 (2, 69-70), YCM P.7261 (1, 72.5).

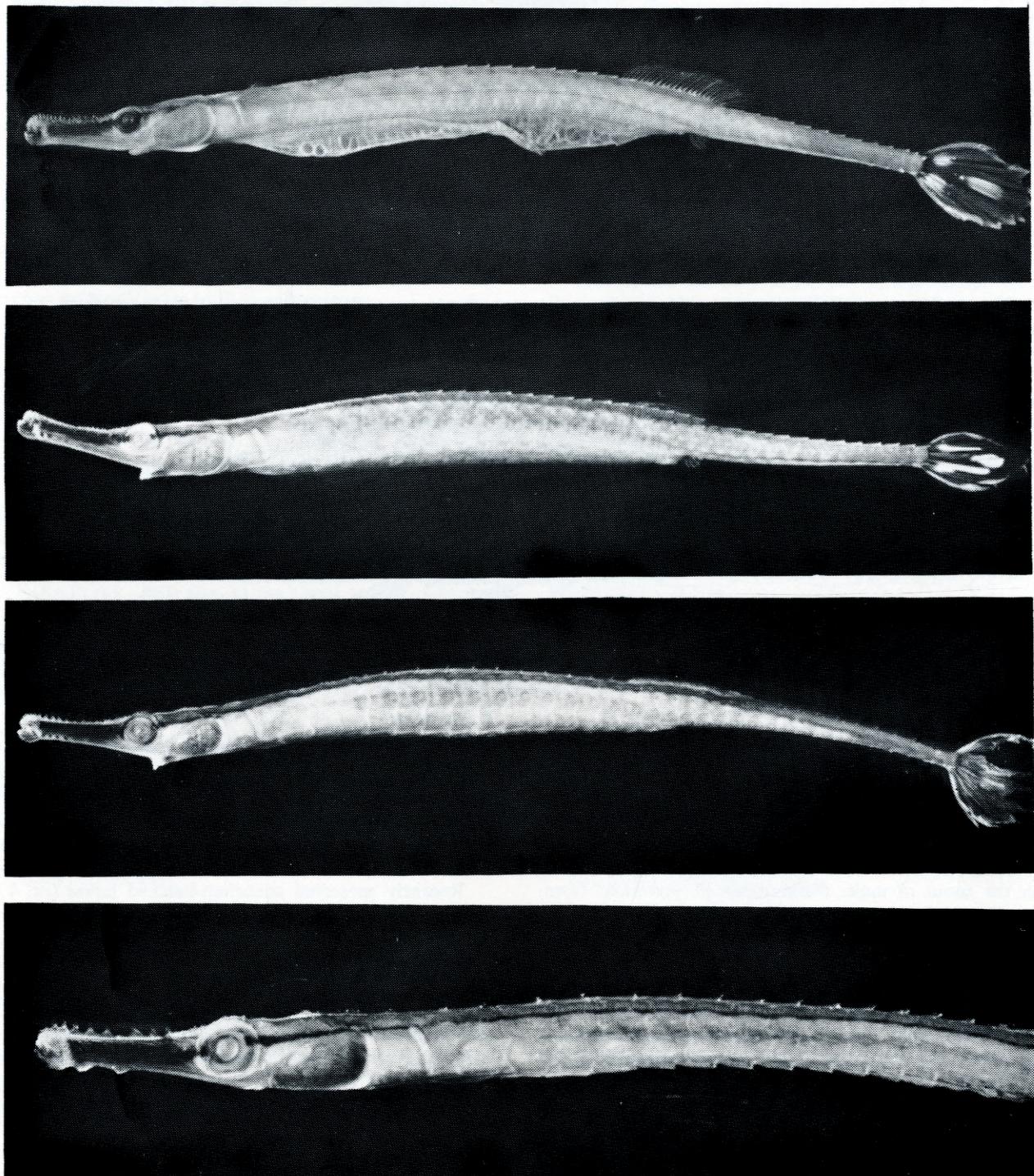


Figure 8. Upper pair. —*Doryrhamphus japonicus*: Above, 72.5 mm SL adult male, YCM P.5330; below, 72.5 mm SL adult female, YCM P.7261. Lower pair — *D. bicarinatus*: Above, 57 mm SL adult female paratype, GCRL 17063; below, 45 mm SL subadult male holotype, RUSI 10049.

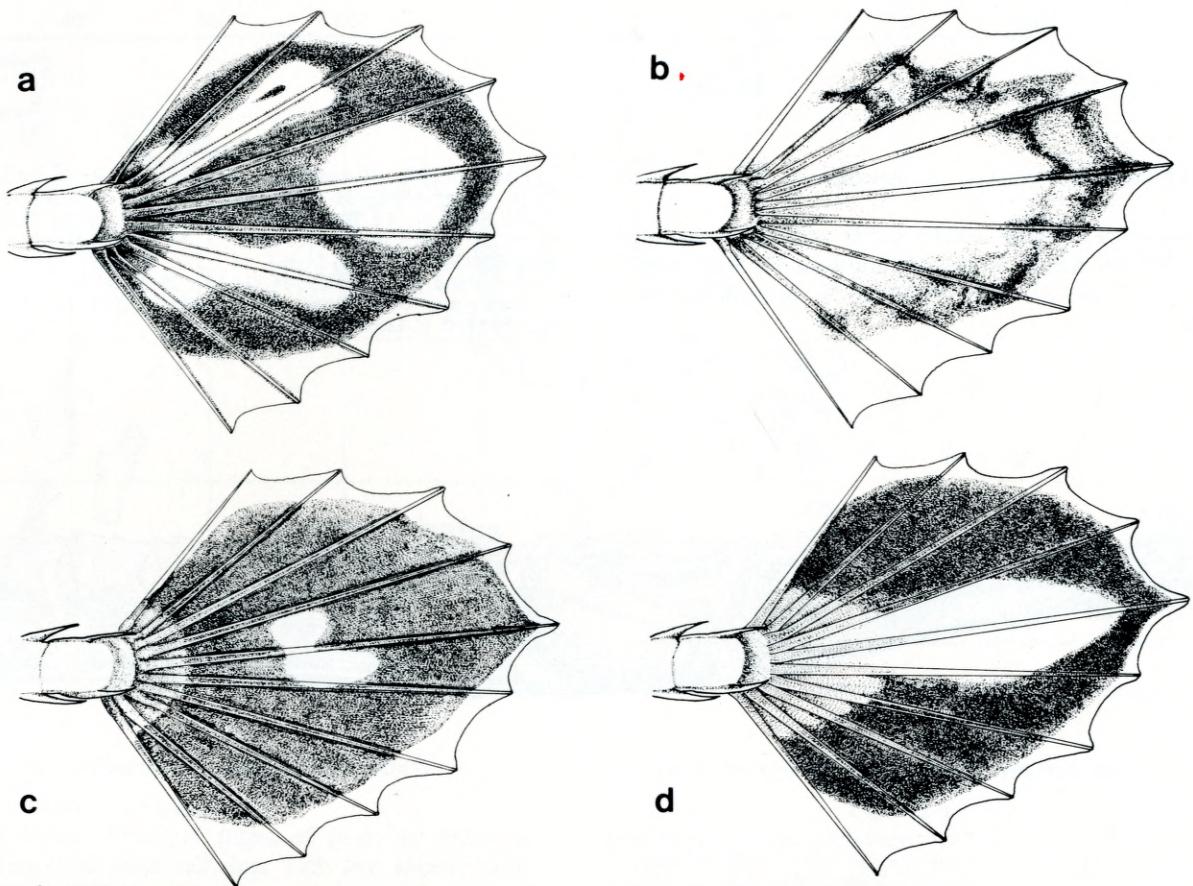


Figure 9. Markings on caudal fins of *Doryrhamphus japonicus* (a), *D. bicarinatus* (b), *D. negrosensis* (c) and *D. janssi* (d).

Doryrhamphus bicarinatus n. sp.

Figs. 8-11

DIAGNOSIS.—Principal ridges of posterior predorsal trunk rings with one distal spine; trunk rings 16; subdorsal trunk rings 2.5-2.0; subadult and adult males with two ventrolateral projections on snout; trunk with narrow dark stripe between superior and lateral ridges.

DESCRIPTION.—Rings 16 + 16-17, dorsal-fin rays 21-23, pectoral-fin rays 19-21, subdorsal rings 2.5-2.0 + 2.75-3.0 = 4.75-5.75; see Tables 1-6 for additional counts. Proportional data based on 7 specimens 42.0-67.0 ($\bar{x} = 55.1$) mm SL follow: HL in SL 4.4-5.3 (4.7), snout length in HL 2.0-2.1 (2.0), snout depth in snout length 5.2-8.2 (6.6), length of dorsal-fin base in HL 1.9-2.2 (2.0), anal ring depth in HL 4.7-6.0 (5.3), length of pectoral-fin base in pectoral-fin length 1.3-1.5 (1.4). Counts and measurements of the holotype (RUSI 10049) are: rings 16 + 16, dorsal-fin rays 23, pectoral-fin rays 20 (each fin), subdorsal rings 2.25 + 3.5 = 5.75, HL 9.8, snout length 4.8, snout depth 0.7, length of dorsal-fin base 5.1, anal ring depth 1.7, trunk depth 2.0, pectoral-fin length 1.9, length of pectoral-fin base 1.3. The holotype is a young male with incompletely developed pouch folds.

The dark stripe on trunk closely follows superior ridge (Fig. 8), covers less than half of space between superior and lateral ridges; see Fig. 9 for markings on caudal fin.

ETYMOLOGY.—Named *bicarinatus*, two-keeled, in reference to the two ventrolateral projections on the snout of subadult and adult males (Fig. 10).

COMPARISONS.—*Doryrhamphus bicarinatus* shares the single spine on principal ridges of the posterior predorsal rings with *D. excisus* and *D. japonicus* but differs from these species in having fewer subdorsal trunk rings (2.5-2.0 versus 5.0-3.0) and in the presence of two (rather than 1-0) ventrolateral projections on the snout of subadult and adult males (also see this section under *D. excisus* and *D. japonicus*). Compared to congeners which have two spines on principal ridges of the posterior predorsal rings and lack ventrolateral projections on the snout of males, *D. bicarinatus* is further distinguished by the absence of a narrow pale stripe on the dorsum (present in *negrosensis*) and by having fewer tail rings than *D. janssi* (32-33 versus 37-39).

REMARKS.—*Doryrhamphus bicarinatus* is sympatric with *D. e. excisus* at Bazaruto I., Mozambique (ca. 21°40'S) where one specimen (RUSI 2478) was taken with 7 adult *D. e. excisus*. Other collections of *D. bicarinatus* are from more southerly localities (ca. 26-27.5°S).

DISTRIBUTION.—Known only from South Africa and Mozambique in the western Indian Ocean (Fig. 11). Two of the seven known collections are recorded from coral reefs and five are from depths of 1.2-28 m.

MATERIAL EXAMINED.—8 specimens, 39.5-67 mm SL.

HOLOTYPE.—RUSI 10049 (45.0 mm SL, subadult male), South Africa, Zululand, Sodwana (= Sordwana) Bay, 12-13 m, 24 Apr. 1979, M. N. Bruton and M. Smale.

PARATYPES.—Mozambique, Bazaruto I.: RUSI 2478 (1, 39.5), Sept. 1953, M. M. Smith. Inhaca I.: GCRL 17064 (1, 61.5), 2 m, 12 Dec. 1970, T. H. Fraser. RUSI 74-82 (2, 60.5-67), 1.2-4.5 m, 5 Dec. 1970, T. H. Fraser. South Africa, Sodwana Bay: GCRL 17063 (1, 57), 1 Apr. 1979, P. C. Heemstra and pty. RUSI 9384 (1, 42), 26-28 m, 17 Apr. 1979, M. Smale and G. R. Allen. RUSI 9937 (1, 53), 10-12 m, 22 Apr. 1979, P. C. Heemstra and pty.

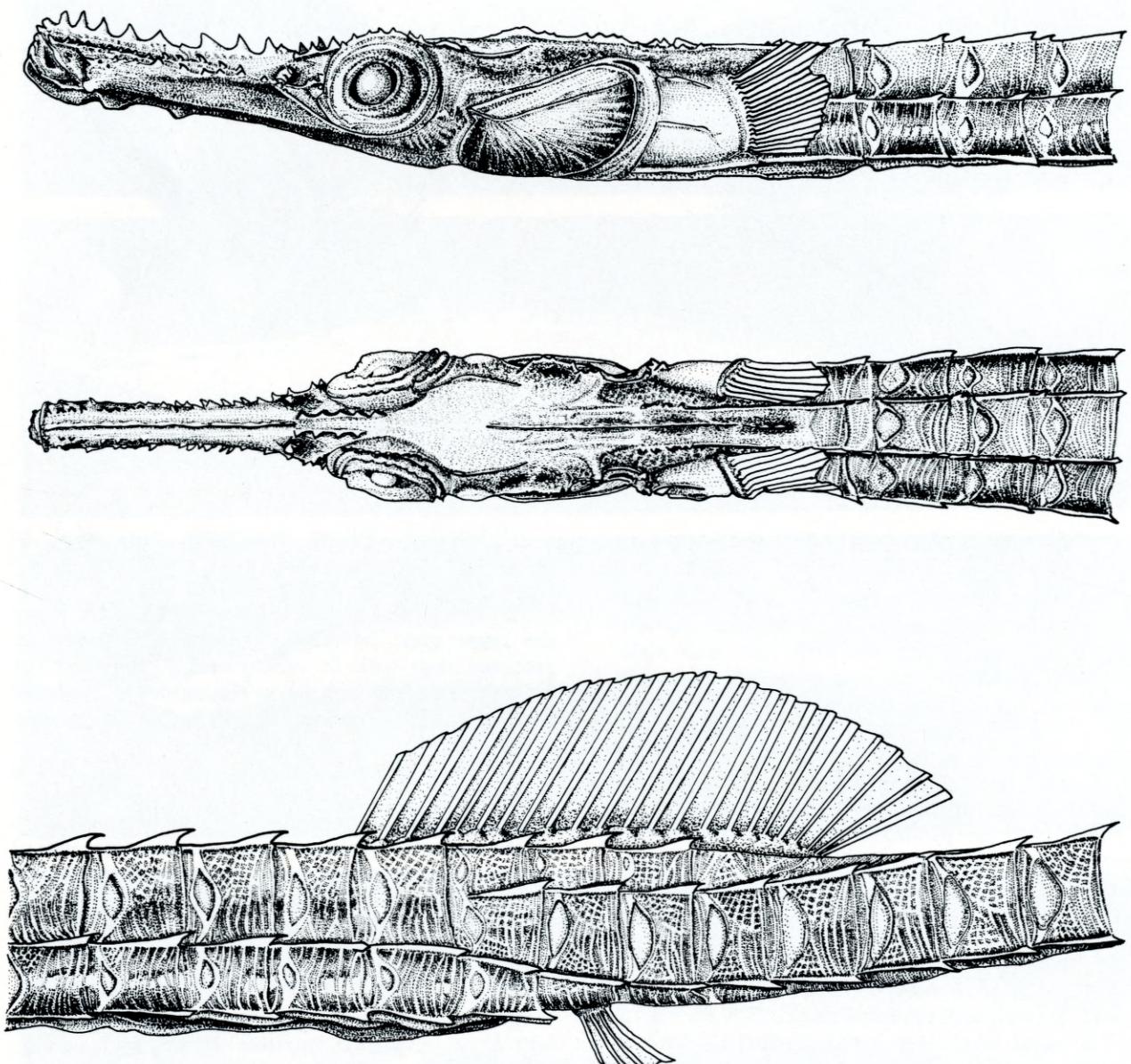


Figure 10. *Doryrhamphus bicarinatus*. Lateral (upper figure) and dorsal (middle figure) aspects of head and anterior trunk rings; note two ventrolateral projections on anterior part of snout. Lower figure, lateral aspect of body. Drawings from 45 mm SL subadult male holotype, RUSI 10049.

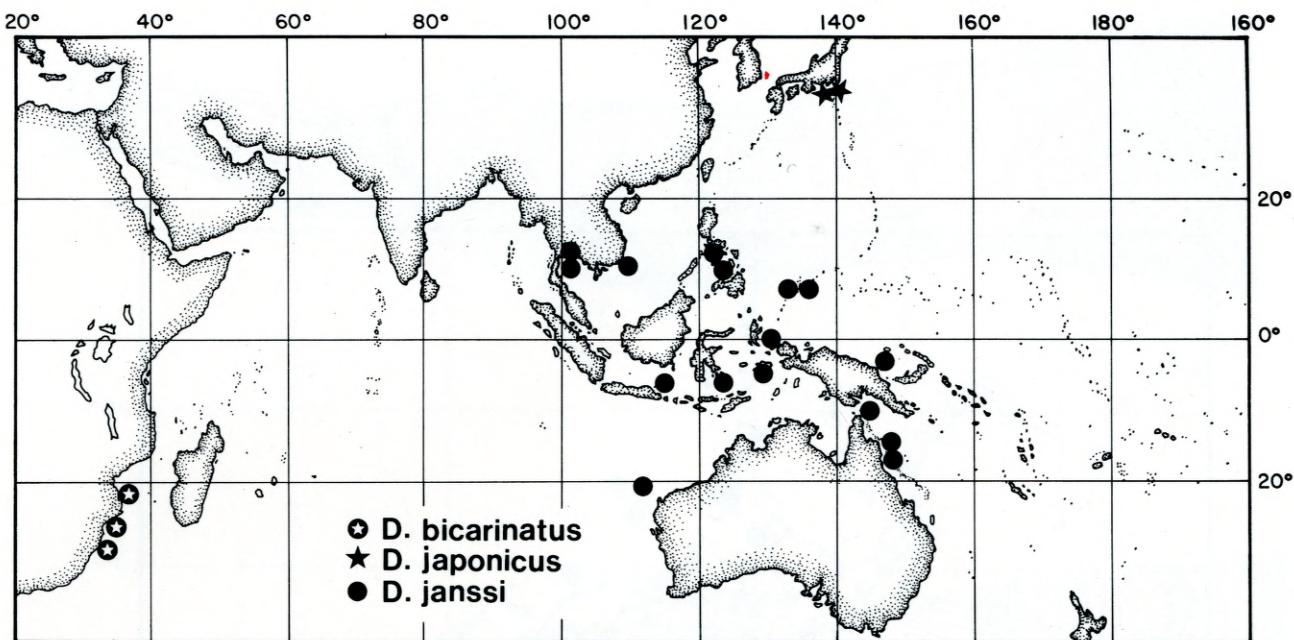


Figure 11. Distributions of *Doryrhamphus bicarinatus*, *D. japonicus* and *D. janssi* based on material examined.

Doryrhamphus negrosensis Herre

SYNONYMY.—See subspecies.

DIAGNOSIS.—Principal ridges of posterior predorsal trunk rings and most tail rings with two spines; trunk rings 14-17 (usually 15-16); total rings 27-32; total subdorsal rings 3.5-5.0; males without bony ventrolateral projections on snout, side of body without a prominent dark stripe; dorsum with a complete or incomplete narrow pale stripe.

COMPARISONS.—The presence of two spines on principal ridges of tail rings, together with 27-32 total rings, 3.5-5.0 total subdorsal rings, absence of ventrolateral projections on the snout of males and presence of a narrow pale stripe on the dorsum distinguishes *D. negrosensis* from all congeners. The presence of two spines on principal ridges of the posterior predorsal rings is shared with *D. janssi*, but *D. negrosensis* typically has two spines on principal ridges of tail rings (one spine in *janssi*) and has fewer total rings (27-32 versus 37-39 in *janssi*).

Compared to congeners with one spine on principal ridges of the posterior predorsal rings, *D. negrosensis* further differs from all species except *D. bicarinatus* in its low number of subdorsal trunk rings (3.0-1.5 versus 5.0-3.0). *Doryrhamphus negrosensis* lacks a narrow, dark, lateral stripe on the trunk and ventrolateral projections on the snout of males (present in *bicarinatus*) and has a narrow pale stripe on the dorsum (absent in *bicarinatus*). Caudal-fin markings, less variable than those of most congeners, usually consist of an irregular, pale, median blotch surrounded by dark brown and a pale outer margin (Fig. 9).

REMARKS.—As interpreted here, *Doryrhamphus negrosensis* includes two subspecies. One is an Australian endemic, whereas the other ranges from the Ryukyu Is. to the New Hebrides in the western Pacific Ocean (Fig. 12). These subspecies are distinguished by differences in meristic values and coloration (see key and diagnoses).

Doryrhamphus negrosensis *negrosensis* Herre

Figs. 12-15

Doryrhamphus negrosensis Herre, 1933:7 (name only, *nomen nudum*); Herre, 1934:28 (orig. descr.; tidepool at Dumaguete (Negros Is.), Philippines); Böhlke, 1953:61 (compiled); Herald, 1953:232, 245 (ref., in key); Herre, 1953:208 (compiled, Philippines and Palau).

Pristidoryrhamphus jacksoni Fowler, 1944:159, figs. 8-9 (orig. descr., New Hebrides); Fowler, 1949:66 (characters); Herald, 1953:232 (= *Doryrhamphus negrosensis*).

DIAGNOSIS.—Trunk rings modally 15; total rings 27-29; dorsal-fin rays usually 17-18 (87% of specimens examined); pale stripe on dorsum ends on caudal-fin base.

DESCRIPTION.—Rings 14-16 + 13-15, dorsal-fin rays 16-19, pectoral-fin rays 17-20, subdorsal rings 3.0-1.5 + 1.0-2.75 = 3.5-4.75, see Tables 1-6 for additional counts. Proportional data based on 19 specimens 22.0-47.0 ($\bar{x} = 36.0$) mm SL follow: HL in SL 3.5-4.2 (3.9), snout length in HL 1.9-2.2 (2.1), snout depth in snout length 4.9-7.2 (6.2), length of dorsal-fin base in HL 2.4-3.3 (2.9), anal ring depth in HL 4.5-6.4 (5.8), trunk depth in HL 2.8-4.8 (4.0), pectoral-fin length in HL 5.6-7.2 (6.3), length of pectoral-fin base in pectoral-fin length 1.1-1.7 (1.3).

Pale median stripe on dorsum (Fig. 14) prominent, extends from tip of snout to caudal-fin base.

COMPARISONS.—*Doryrhamphus n. negrosensis* differs from *D. n. malus* in having modally fewer trunk rings and tail rings (respectively, 15 and 14 versus 16 and 15) as well as fewer total rings (27-29 versus 30-32). This subspecies also has fewer dorsal- and pectoral-fin rays than *D. n. malus* (usually 17-18 versus 19-20). The pale stripe on the dorsum is distinct and reaches the caudal-fin base in *D. n. negrosensis*, whereas this stripe is somewhat diffuse and ends on the anterior third of the trunk in *D. n. malus*. Based on material examined, *D. n. negrosensis* is a rather small pipefish which seldom reaches 50 mm SL. In contrast, 50-60 mm SL specimens of *D. n. malus* are rather common in collections.

REMARKS.—Brood-pouch folds may be developing

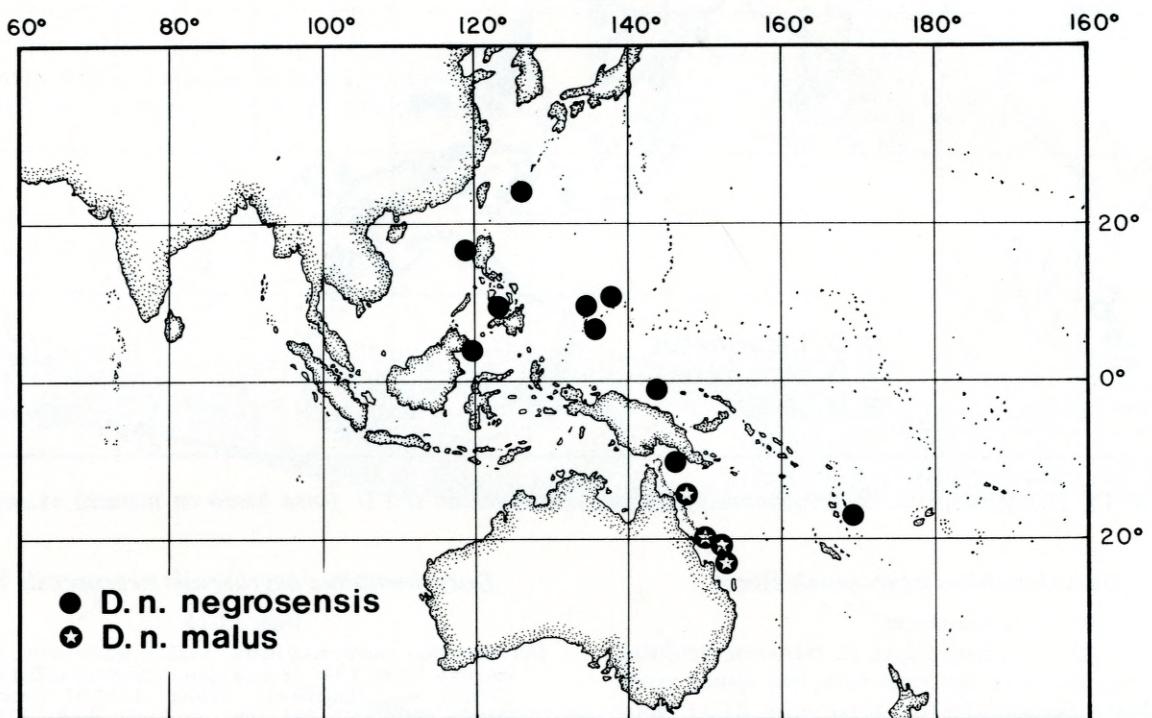


Figure 12. Distributions of subspecies of *Doryrhamphus negrosensis* based on material examined.

on some males at 22 mm SL and they are usually fully developed at 30-35 mm SL. A brooding male (40 mm SL) has eggs deposited in a single layer of four transverse rows and there are 19 eggs in the outer right row.

Spines are single on principal ridges of all rings in 16-mm SL juveniles (Fig. 15), but the characteristic two-spined condition of adults has developed on the superior ridges of most rings at 19-20 mm SL. Some subadults and adults may have single spines on a few tail rings, but most have double spines on the superior tail ridges.

The pale stripe on the dorsum and single pale spot on caudal fin are distinct in some juveniles at 16 mm SL.

DISTRIBUTION.—Western Pacific Ocean from the Ryukyu Is., Philippine Is. and northeastern Borneo, southeastward to the New Hebrides (Fig. 12). This subspecies is unknown from Australia. Available data indicate collections from a variety of habitats including reef pools, a “sand flat between shore and reef”, a “mud flat at edge of mangrove swamp” and a “reef near grass flat.” Recorded depth range is 0-9 m.

MATERIAL EXAMINED.—66 specimens, 16.0-47.0 mm SL.

HOLOTYPE.—CAS-SU 25503 (45 mm SL, male), Philippine Is., Negros I., Dumaguete, tidepool, June 1931, A.W. Herre.

PARATYPE.—CAS-SU 25503 (42.5, female), taken with holotype.

OTHER MATERIAL.—Borneo, Darvel Bay: GCRL 13778 (1, 38.5), USNM 214137 (1, 35.5). Philippines, Luzon I., Bolinao Lagoon: GCRL 17058 (1, 38), USNM 226445 (2, 32-38). Ryukyu Is., Ishigaki I.: YCM P.4127 (1, 40). Palau Is.: BPBM 13620 (1, 38.5), CAS 15539 (1, 22), CAS 15542 (2, 32.4-34), CAS 15543 (16, 23-45.5), CAS 15544 (3, 23.5-30), CAS 15545 (1, 40.5), CAS 15546 (1, 33), CAS 15547 (1, 22.5), CAS 15548 (1, 19.5), CAS 15549 (4, 25-30), CAS 15550 (1, 34), CAS 15551 (3, 39-41.5), CAS 15552 (1, 17.9), CAS 15553 (1, 16.0), CAS 15554 (1, 27.5), CAS 15555 (2, 25-31), CAS 15556 (3, 20.5-27), CAS 15557 (6, 22-30.5), CAS-SU 29409 (3, 27-36.5). Yap I.: CAS 15540 (1, 47), CAS 15541 (1, 43). Hermit Is.: USNM 220711 (1, 30). Papua-New Guinea, Port Moresby: AMS IA.5726 (1, 39.5). New Hebrides Is.: ANSP 71350 (32, male, holotype of *Pristidoryrhamphus jacksoni*), CAS 15558 (1, 31).

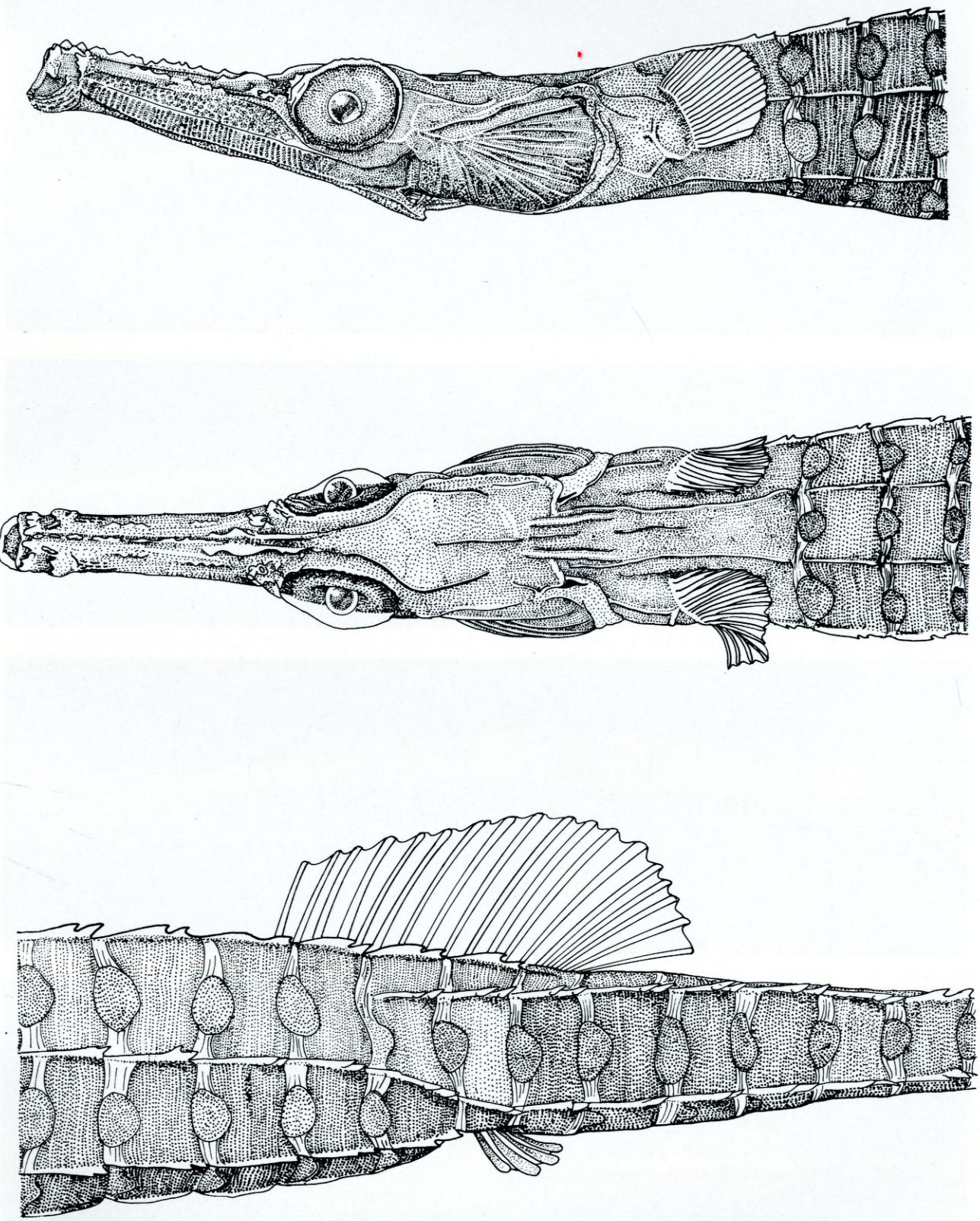


Figure 13. *Doryrhamphus negrosensis negrosensis*. Lateral (upper figure) and dorsal (middle figure) aspects of head and anterior trunk rings; lower figure, lateral aspect of body (note double spines on predorsal trunk rings and tail rings). Drawings from 42.5 mm SL female paratype, CAS-SU 25503.

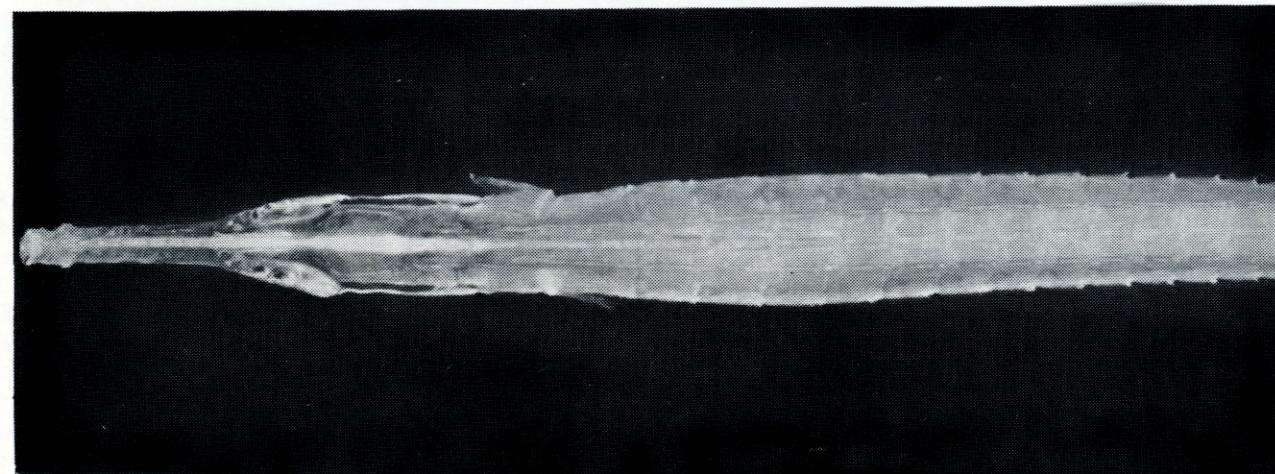
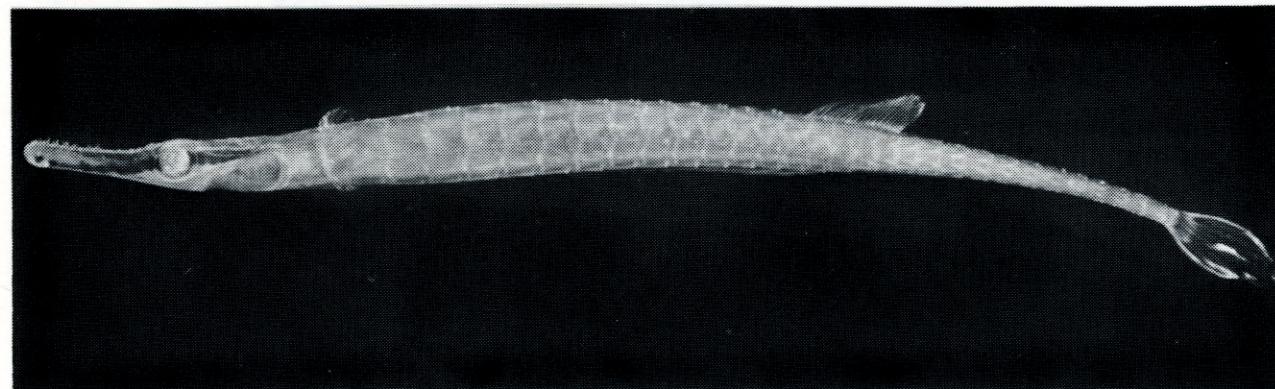
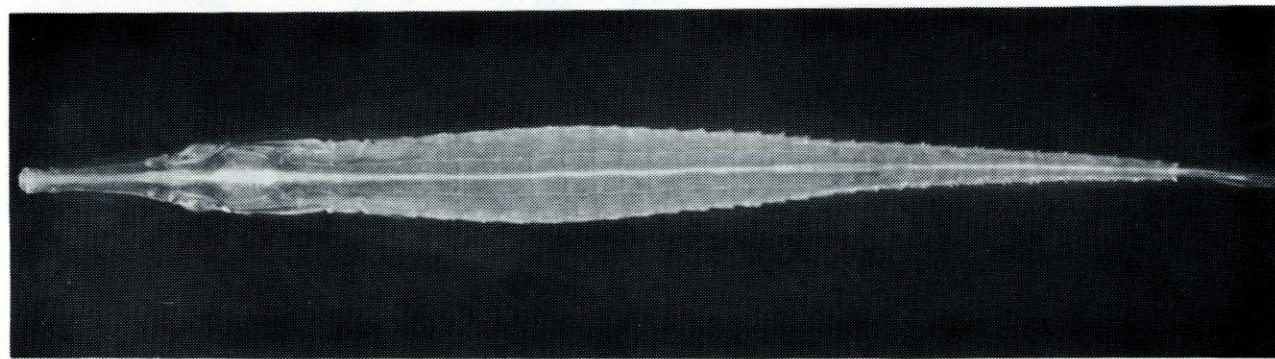
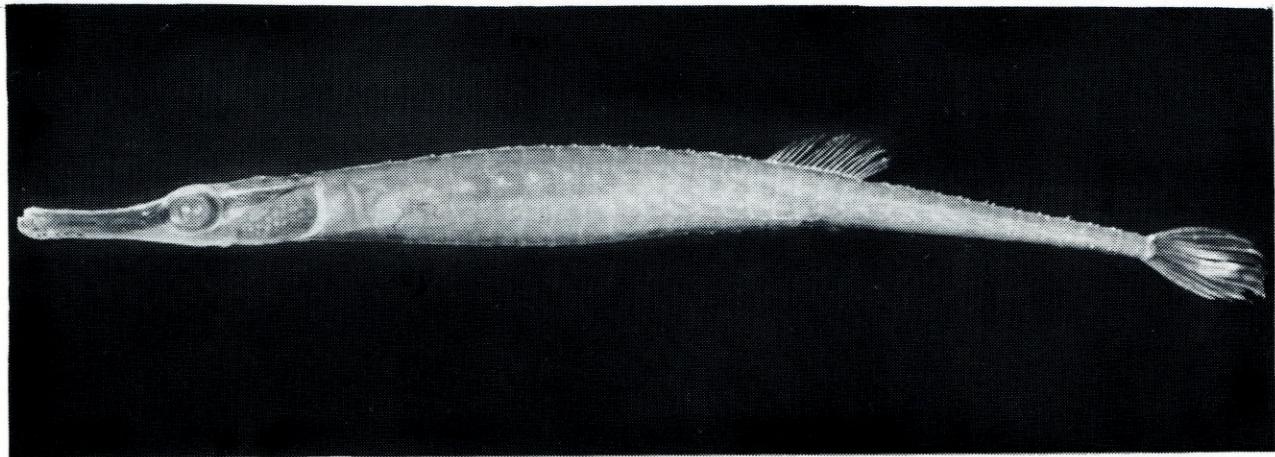


Figure 14. Upper pair – *Doryrhamphus negrosensis negrosensis*, 29 mm SL female, CAS 15543. Lower pair – *D. n. malus*: Above, 51 mm SL male, LACM 33723-61; bottom, dorsal view of front half of 44 mm SL male, AMS I.20486-002.

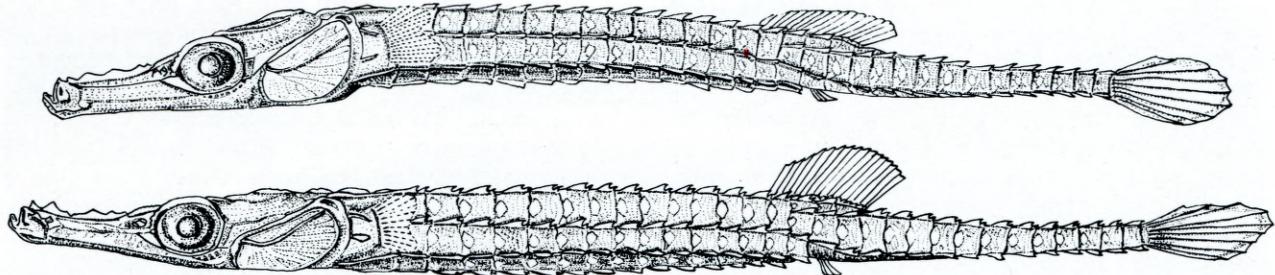


Figure 15. *Doryrhamphus negrosensis negrosensis*. Above — Juvenile (16 mm SL) with single spine on principal body ridges (CAS 15553). Below — Juvenile (19.5 mm SL) with double spines on superior ridge of most trunk and tail rings (CAS 15548).

Doryrhamphus negrosensis malus (Whitley)

Figs. 12 & 14

Choeroichthys suillus malus Whitley, 1954:25 (orig. descr.; Masthead I., Qld., Australia); Munro, 1958:90 (characters); Whitley and Allan, 1958:60 (compiled); Whitley, 1964:38 (compiled); Grant, 1972:80 (ref.); Paxton, 1975:446 (= *Doryrhamphus negrosensis*); Grant, 1978: 156 (color note). *Choeroichthys suillus mallus*. Dawson, 1976:46 (misspelling, ref. only).

DIAGNOSIS.—Trunk rings modally 16; total rings 30-32; dorsal-fin rays usually 19-20 (90% of specimens examined); pale stripe on dorsum ends on anterior third of trunk.

DESCRIPTION.—Rings 16-17 + 14-16, dorsal-fin rays 18-21, pectoral-fin rays 18-21, subdorsal rings 2.75-1.5 + 1.5-3.0 = 3.5-5.0; see Tables 1-6 for additional counts. Proportional data based on 17 specimens 32.5-61.5 ($\bar{x} = 50.1$) mm SL follow: HL in SL 4.0-4.6 (4.3), snout length in HL 2.0-2.1 (2.0), snout depth in snout length 5.4-7.8 (6.5), length of dorsal-fin base in HL 2.3-3.0 (2.7), anal ring depth in HL 5.1-6.8 (5.8), trunk depth in HL 3.0-4.7 (3.6), pectoral-fin length in HL 4.7-7.0 (6.1), length of pectoral-fin base in pectoral-fin length 1.3-1.9 (1.4).

Pale stripe on dorsum (Fig. 14) somewhat diffuse, usually faded posteriad, vestigial or obsolete behind 3rd-4th trunk ring.

COMPARISONS.—See *D. n. negrosensis*.

REMARKS.—Originally described as a subspecies of *Choeroichthys brachysoma* (as *C. suillus*) by Whitley (1954), the holotype was correctly reidentified as *Doryrhamphus negrosensis* by Paxton (1975). Whitley's subspecific name is available and is employed here for the Australian population of *D. negrosensis*.

I am aware of one collection wherein one *D. n. malus* was taken with 12 *D. e. excisus*, but apparent absence of other mixed samples suggests a high degree of niche separation.

The smallest examined male with developed brood-pouch folds is 43 mm SL.

DISTRIBUTION.—From Mackay Reef to Masthead I. (ca. 16°03'-23°32'S), Great Barrier Reef, Queensland, Australia (Fig. 12). Eighty-six percent of examined specimens and 89% of known collections of this pipefish are from One Tree I. (ca. 23°30'S). This area has been sampled extensively, but low frequency of occurrence

in numerous collections from other Barrier Reef localities suggests that actual level of abundance may be highest in the vicinity of One Tree Island. Recorded depth range is 0-6 m.

MATERIAL EXAMINED.—72 specimens, 32.5-62.0 mm SL.

HOLOTYPE.—AMS I.7154 (60 mm SL, female), Australia, Qld., Masthead I., 1909, A. McCulloch.

OTHER MATERIAL.—Australia, Qld., Mackay Reef: AMNH 35916 (1, 32.5). Lindeman I.: AMS IA.6477 (1, 43). Heron I.: AMS IB.4060-1 (7, 46.5-53). One Tree I.: AMS I.15617-002 (3, 49-62), AMS I.15624-002 (1, 48), AMS I.15627-003 (1, ca. 57), AMS I.15633-002 (1, 54), AMS I.15636-004 (1, 50), AMS I.15641-004 (2, 48.5-54), AMS I.15866-004 (1, 53), AMS I.20205-022 (1, 57), AMS I.20211-043 (2, 49.5-61.5), AMS I.20213-034 (2, 44.5-56), AMS I.20463-040 (1, 51), AMS I.20486-002 (1, 44), AMS I.20555-003 (3, 48-62), AMS I.20557-001 (1, 46), AMS I.20789-001 (2, 54-55.5), AMS I.21361-006 (1, 49), ANSP 142685 (1, 51.5), BPBM 13621 (1, 47.5), BPBM 14437 (3, 50.5-51), CAS 13742 (7, 43-57), CAS 13814 (2, 44-45.5), GCRL 16120 (1, 50.5), GCRL 16121 (1, 53), LACM 33723-61 (5, 51-56.5), QM I.11743 (1, 44.5), USNM 208269 (1, 43), USNM 208270 (1, 51.5), USNM 208271 (3, 46.5-56.5), USNM 208272 (7, 46.5-58.5), USNM 208273 (1, 39.5), USNM 208274 (4, 47-55).

Doryrhamphus janssi (Herald & Randall)

Figs. 11, 16, 17

Dentirostrum janssi Herald & Randall, 1972:124, fig. 1 (orig. descr., Palau Is.); Randall et al., 1976:47 (Indonesia).

DIAGNOSIS.—Principal ridges of posterior predorsal trunk rings with two spines; principal ridges of tail rings with one spine; trunk rings 16; total rings 37-39; total subdorsal rings 5.25-6.0; males without ventrolateral projections on snout; trunk with narrow dark stripe between superior and lateral ridges; without narrow pale stripe on dorsum.

DESCRIPTION.—Rings 16 + 21-23, dorsal-fin rays 22-25, pectoral-fin rays 19-21, subdorsal rings 1.75-0.75 + 4.0-4.75 = 5.25-6.0; see Tables 1-6 for additional counts. Proportional data based on 11 specimens 53-127 ($\bar{x} = 90.5$) mm SL follow: HL in SL 4.2-5.2 (4.7), snout length in HL 1.5-1.8 (1.6), snout depth in snout length 7.6-12.6 (10.1), length of dorsal-fin base in HL 2.2-2.6 (2.4), anal ring depth in HL 6.4-9.8 (8.1), trunk depth in HL 5.4-8.9 (6.8), pectoral-fin length in HL 7.5-9.0 (8.2), length of pectoral-fin base in pectoral-fin length 1.1-1.4 (1.2).

Dark stripe on trunk closely follows superior trunk ridge (Fig. 17), covers less than half of space between superior and lateral ridges; see Fig. 9 for markings on caudal fin.

COMPARISONS.—This species is readily distinguished from congeners by the higher number of tail rings (21-23 versus 11-17) and by the longer and more slender snout (snout depth in snout length averages 10.1 versus 4.7-6.6). Subadults and adults of *Doryrhamphus janssi* and *D. negrosensis* have two spines on principal ridges of the posterior predorsal rings, but *D. janssi* differs in having one rather than two spines on principal ridges of the tail rings. The narrow, dark, lateral stripe on the trunk is similar to that of *D. bicarinatus* and *D. japonicus*, but these species lack the double-spined posterior trunk rings of *D. janssi*. This relatively long and slender pipefish differs considerably from congeners in gross morphology, but shared characters dictate its referral to the genus *Doryrhamphus*.

REMARKS.—Early juveniles are not available, but the median dorsal snout ridge is entire in small fish (ca. 53-70 mm SL). In these specimens, the anterior spine is the larger of the two spines on principal ridges of the posterior predorsal rings. The terminal spine is usually the larger in adults.

The smallest examined male with developing brood-pouch folds is 77 mm SL. Brood-pouch eggs are lost from most brooding males, but there are 4 transverse rows of eggs in a 102 mm SL specimen and another (118 mm SL) has eggs in 6 transverse rows.

DISTRIBUTION.—Eastern Indian Ocean (off NW Australia) and western Pacific Ocean from Gulf of Thailand to Philippine Is. southeastward to Queensland, Australia (Fig. 11). Most collections are from depths of 0-15 m, but there is one SCUBA sample from 24-35 m.

MATERIAL EXAMINED.—43 specimens, 53-127 mm SL. For additional data on paratypes, see Herald and Randall (1972).

HOLOTYPE.—CAS 14139 (125.5 mm SL, male), Palau Is., Koror I., 07°19'28"N, 134°30'12"E, 0-15.2 m, 19 Nov. 1957, H. Dewitt and party.

PARATYPES.—Gulf of Thailand: BPBM 11938 (1, 91), CAS 14146 (1, 77), CAS 14147 (3, 61.5-83), CAS 14149 (2, ca. 95-102), CAS 14150 (1, 111.5), CAS 14151 (1, 57.5), CAS 14152 (1, 92), CAS 14153 (1, 105.5), USNM 206654 (2, 78-125.5). Vietnam: BPBM 11939 (1, 93), CAS 14145 (2, 96-107.5). Java: CAS 14144 (1, ca. 95). Palau Is.: AMS I.16144-001 (2, 102-104), BPBM 11937 (2, 81.5-101.5), CAS 14140 (1, 123.5), CAS 14141 (1, 106), CAS 14142 (1, 89.5), CAS 14143 (3, 53-103), SMF 11425 (1, 111). Papua-New Guinea: BPBM 13968 (1, 105). Australia (Qld.): ANSP 119933 (1, 99).

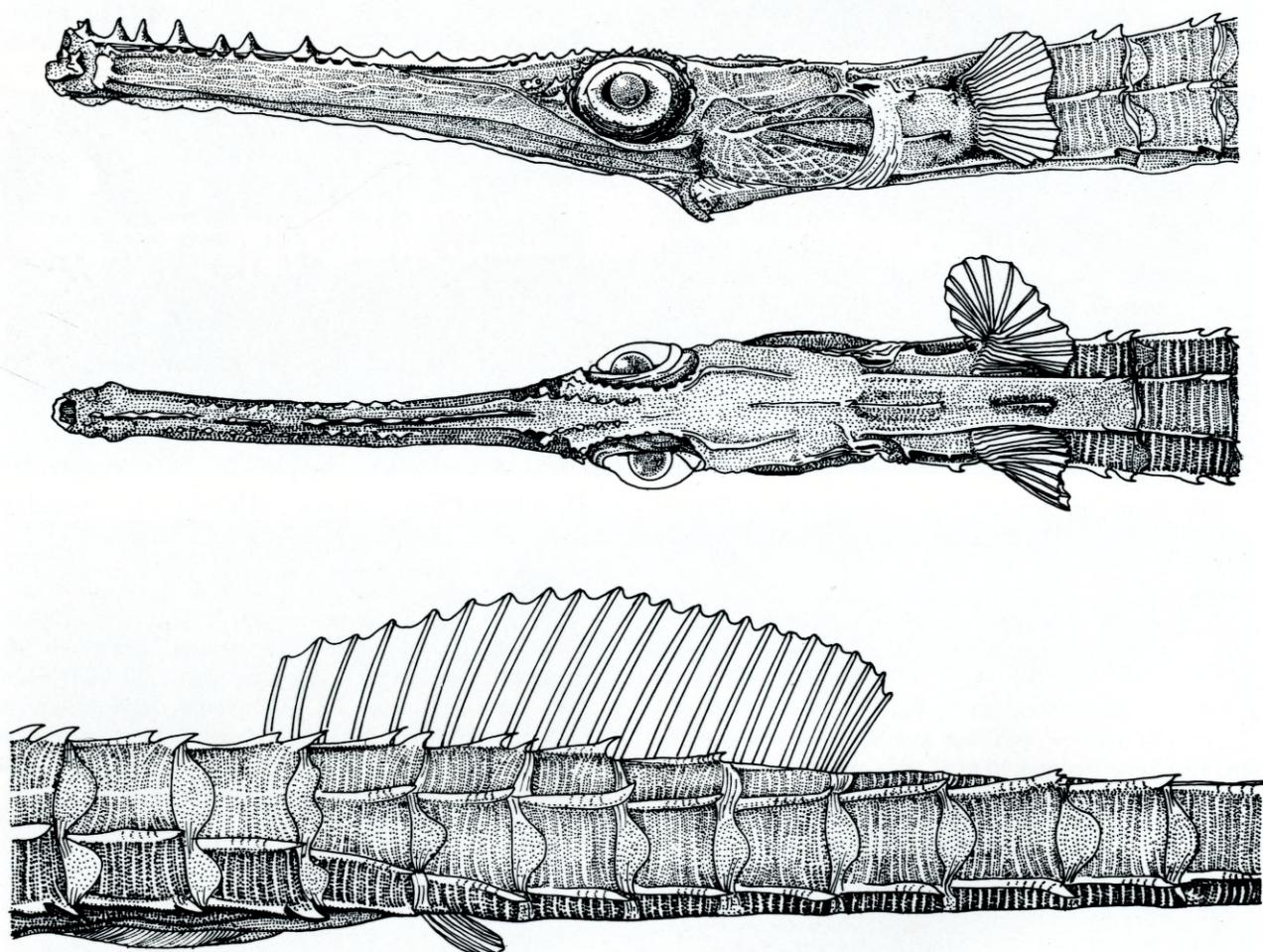


Figure 16. *Doryrhamphus janssi*. Lateral (upper figure) and dorsal (middle figure) aspects of head and anterior trunk rings; lower figure, lateral aspect of body (note double spines on trunk rings and single spines on tail rings). Drawings from 95 mm SL adult male, GCRL 13825.

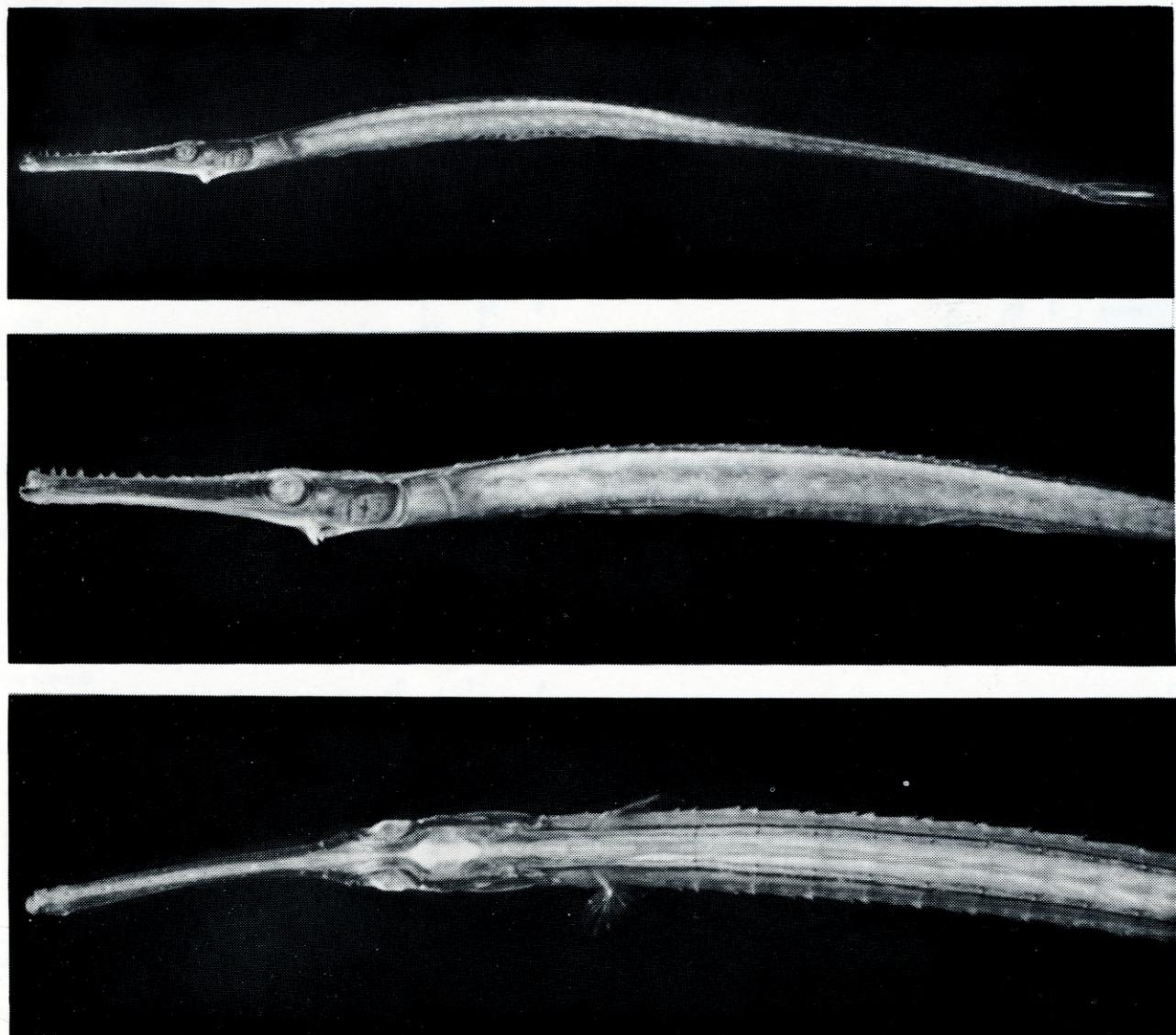


Figure 17. *Doryrhamphus janssi*, 95 mm SL adult male, GCRL 13825.

OTHER MATERIAL.—INDIAN OCEAN, Dampier Arch. (NW Austr.): WAM P.25113-004 (1, 95, photo seen only). PACIFIC OCEAN, Philippines: GCRL 16940 (1, 72.5), GCRL 17065 (1, 78.5), USNM 219149 (1, 61). Celebes Is.: USNM 214280 (1, 127). Saparua I.: GCRL 13825 (1, 95), USNM 210091 (1, 85). Irian Jaya: USNM 222936 (1, 120). Australia (Qld.): AMS I. 20765-001 (1, 102), AMS I.20768-002 (1, 118), AMS I.20769-002 (2, 85.5-115.5).

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TABLE 1. Frequency distributions of trunk rings and tail rings in species of *Doryrhamphus*.

Species	Trunk rings										Tail rings										
	Subspecies	14	15	16	17	18	19	20	11	12	13	14	15	16	17	18	19	20	21	22	23
<i>excisus</i>																					
<i>e. abbreviatus</i>		9	12						10	11											
<i>e. paulus</i>			20	8								20	10	17	17	80	1				
<i>e. excisus</i>				186	350	21						20	171	285							
<i>japonicus</i>						10	1						3	8							
<i>bicarinatus</i>				8										5	3						
<i>negrosensis</i>																					
<i>n. negrosensis</i>		4	60	2								9	56	1							
<i>n. malus</i>			70	2								5	5	64	3						
<i>janssi</i>			38																15	19	4

TABLE 2. Frequency distributions of total rings in species of *Doryrhamphus*.

Species	Total rings													
	Subspecies	26	27	28	29	30	31	32	33	34	35	36	37	38
<i>excisus</i>														
<i>e. abbreviatus</i>		3	13	5										
<i>e. paulus</i>					2	25	1							
<i>e. excisus</i>					14	109	117	242	70	5				
<i>japonicus</i>								3	7	1				
<i>bicarinatus</i>							5	3						
<i>negrosensis</i>														
<i>n. negrosensis</i>		1	8	57			5	62	5					
<i>n. malus</i>														
<i>janssi</i>												15	19	4

TABLE 3. Frequency distributions of dorsal and pectoral fin rays in species of *Doryrhamphus*.

Species	Dorsal-fin rays													Pectoral-fin rays							
	Subspecies	16	17	18	19	20	21	22	23	24	25	26	27	28	29	17	18	19	20	21	22
<i>excisus</i>																					
<i>e. abbreviatus</i>			3	11	4											6	18	6			
<i>e. paulus</i>																3	14	11			
<i>e. excisus</i>							10	34	92	6	3	8	1		19	103	122	41	8		
<i>japonicus</i>							3	2	5							1	2	11	8	1	
<i>bicarinatus</i>							1	5	2							2	7	6			
<i>negrosensis</i>																					
<i>n. negrosensis</i>		1	24	31	7	25	4									12	22	9	4		
<i>n. malus</i>			2	39	25	4										4	24	13	2		
<i>janssi</i>							3	19	14	1						14	23	5			

TABLE 4. Frequency distributions of subdorsal trunk rings in species of *Doryrhamphus*.

Species	Subdorsal trunk rings																		
	Subspecies	5.00	4.75	4.50	4.25	4.00	3.75	3.50	3.25	3.00	2.75	2.50	2.25	2.00	1.75	1.50	1.25	1.00	0.75
<i>excisus</i>																			
<i>e. abbreviatus</i>			2	3	7	3	1	1	1										
<i>e. paulus</i>		1		3	4	3	4	11	1	1									
<i>e. excisus</i>		23	24	78	65	226	73	42	5	7									
<i>japonicus</i>		2	1	2	6						2	3	3						
<i>bicarinatus</i>																			
<i>negrosensis</i>																			
<i>n. negrosensis</i>										1	6	15	20	21	2	1			
<i>n. malus</i>										2	12	15	33	7	2				
<i>janssi</i>														3	8	19	10	2	

TABLE 5. Frequency distributions of subdorsal tail rings in species of *Doryrhamphus*.

Species	Subdorsal tail rings															
	1.00	1.25	1.50	1.75	2.00	2.25	2.50	2.75	3.00	3.25	3.50	3.75	4.00	4.25	4.50	4.75
<i>excisus</i>																
<i>e. abbreviatus</i>	3	3	5	5	2	2		2								
<i>e. paulus</i>					3	32	24	60	107	193	39	4	9	3	3	4
<i>e. excisus</i>													56	13	14	2
<i>japonicus</i>					3	3	2	3								
<i>bicarinatus</i>									2	3	1	2				
<i>negrosensis</i>																
<i>n. negrosensis</i>	2	2	9	15	34	2	1		1							
<i>n. malus</i>			2	4	35	14	13		1							
<i>janssi</i>													17	13	10	2

TABLE 6. Frequency distributions of total subdorsal rings in species of *Doryrhamphus*.

Species	Total subdorsal rings																			
	Subspecies	3.50	3.75	4.00	4.25	4.50	4.75	5.00	5.25	5.50	5.75	6.00	6.25	6.50	6.75	7.00	7.25	7.50	7.75	8.00
<i>excisus</i>																				
<i>e. abbreviatus</i>								2	8	5	1	4								
<i>e. paulus</i>										3	6	32	59	103	143	74	7	31	15	4
<i>e. excisus</i>																				
<i>japonicus</i>										1	1	3	5	1						
<i>bicarinatus</i>						1	2			4	1									
<i>negrosensis</i>																				
<i>n. negrosensis</i>	2	8	27	20	5	4														
<i>n. malus</i>	1	2	20	23	20	4	1													
<i>janssi</i>								16	14	11	1									

TABLE 7. Frequency distributions of trunk, tail and total rings of *Doryrhamphus e. excisus* arranged from west to east.

Locale	Trunk						Tail					Total					
	17	18	19	13	14	15	16	17	30	31	32	33	34	35			
INDIAN OCEAN																	
Gulf of Oman (Bahrain I.)			4				3	1					3	1			
E Africa (Kenya-S. Africa)	18	9		10	16	1			7	14	5	1					
Aldabra-Comore Is.	1	4			2	3			1	1						3	
Seychelles-Amirante Is.	7	28	1	1	24	10	1			4	23	9					
Mauritius	13				3	9	1			3	9	1					
Cargados Carajos Sh.	21	2		1	13	9				13	10					1	
Maldives Is.	1					1											
Chagos Arch.	7	1		2	6				2	5	1						
Sri Lanka	17	1			3	12	3		2	2	13	3					
Cocos Is.			1		1								1				
Cocos-Keeling Is.	7					6	1					6					
Christmas I.	3					2	1					2	1				
PACIFIC OCEAN																	
Gulf of Thailand	1					1						1					
S China Sea	1	1				2						1	1	1			
Philippine Is.	11	3		1	9	4			1	8	3	2				2	
Celebes Is.	2	2			3	1			2	1	1	1					
Ryukyu Is.	5	12			9	8			3	8	8	6					
Caroline Is.	1	21	1		8	15					8	15					
New Guinea	5	1		1	4	1			5	1							
Australia (Qld.)	31	5		3	26	7			3	26	7		33	7			
Mariana Is.	1	39	3		5	32	6		1	2							
Solomon Is.	5				4	1			4	1							
New Hebrides Is.						1						1					
Marshall Is.	35	2			6	29	2				5	29	3				
Gilbert Is.		5				5						5					
Fiji Is.	2	1			2	1				1	2		1	1			
Johnston I.		2				1	1										
Phoenix-Samoa Is.	2	7		1	2	4	3		1	1	2	3	3	3			
Hawaiian Is.	22			1	16	5			1	16	5	1	2	1			
Line Is.	1	3				3	1						6			1	
Cook Is.		6	1				7						2	12	3		
Society-Austral Is.		11	6			6	10	1				2	5	2			
Tuamoto-Marquesas Is.	1	7				1	7										
Mexico-Ecuador*	10	129	6		6	104	35					111	30				

* incl. Galapagos Is.

TABLE 8. Frequency distributions of dorsal-fin rays of *Doryrhamphus e. excisus* arranged from west to east.

Locale	Dorsal-fin rays								
	21	22	23	24	25	26	27	28	29
INDIAN OCEAN									
Gulf of Oman (Bahrain I.)			3	1					
E Africa (Kenya-S. Africa)	2	8	10	2					
Aldabra-Comore Is.		2	2		1				
Seychelles-Amirante Is.	3	15	12	7					
Mauritius	1	5	4	3					
Cargados Carajos Sh.	4	10	7	2					
Maldives Is.				1					
Chagos Arch.	3	4	1						
Sri Lanka	1	1	4		4	1			
Cocos Is.					1				
Cocos-Keeling Is.				3	1	3			
Christmas I.				1	1	1			
PACIFIC OCEAN									
Gulf of Thailand		1							
S China Sea			2						
Philippine Is.	1	1	9	2					
Celebes Is.			1	1	1				
Ryukyu Is.	5	6	3	1	1				
Caroline Is.			5	4	6	2			
New Guinea		3	3						
Australia (Qld.)	3	6	20	4	1				
Mariana Is.				12	11	10			
Solomon Is.	2	1	1	1					
New Hebrides Is.				1					
Marshall Is.			1	10	8	1			
Gilbert Is.		1	1		1				
Fiji Is.	1								
Johnston I.						1	1		
Phoenix-Samoa Is.				2	1	2	1	2	1
Hawaiian Is.				3	9	5	2		
Line Is.				3	1				
Cook Is.						1	1	3	3
Society-Austral Is.	1					4	4	3	2
Tuamoto-Marquesas Is.				1		3	2	2	
Mexico-Ecuador*				4	13	38	45	30	4

* incl. Galapagos Is.

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INDEX

Names in boldface are those accepted as valid

GENERA

<i>Acanthognathus</i>	3	<i>Heraldia</i>	3
<i>Apterygocampus</i>	3	<i>Maroubra</i>	3
<i>Choeroichthys</i>	3, 7, 19	<i>Microphis</i>	2, 6, 9
<i>Dentirostrum</i>	2, 3, 19	<i>Oostehus</i>	2
<i>Doryichthys</i>	5, 9	<i>Pristidoryrhamphus</i>	2, 3, 15
<i>Doryrhamphus</i>	<i>2 et seq.</i>	<i>Syngnathus</i>	4, 9
<i>Dunckerocampus</i>	2, 3		

SPECIES AND SUBSPECIES

<i>abbreviatus</i>	4, 9–10, 22, 23
<i>bicarinatus</i>	3, 11, 12, 13–15, 20, 22, 23
<i>brachysoma</i>	7, 19
<i>californiensis</i>	5, 6
<i>cooki</i>	6, 7, 9
<i>excisus</i>	2, 4–10, 12, 19, 22, 23
<i>extensus</i>	6, 7, 9, 10, 12
<i>jacksoni</i>	2, 15
<i>janssi</i>	2, 4, 11, 13, 15, 19–23
<i>japonica, japonicus</i>	3, 10, 11–12–13, 15, 20, 22, 23
<i>malus</i>	4, 16, 19, 22, 23
<i>mayottae</i>	6, 7
<i>melanopleura</i>	4, 5–7, 9–12
<i>negrosensis</i>	4, 11, 13, 15–19, 20, 22, 23
<i>paulus</i>	4, 9, 10, 22, 23
<i>pleurotaenia</i>	5, 6, 9, 10
<i>suillus</i>	19