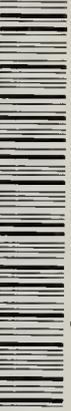


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REVISION, PHYLOGENY,
AND DISCUSSION
OF BIOLOGY AND
BIOGEOGRAPHY
OF THE FISH GENUS
PLESIOPS
(PERCIFORMES:
PLESIOPIDAE)



Randall D. Mooi


ROM



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REVISION, PHYLOGENY, AND DISCUSSION
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Cover: *Plesiops corallicola*, see p. 20, Fig. 13c. Photograph by Robert F. Myers.

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Revision and Phylogeny of the Plesiopid Fish Genus *Plesiops*

Abstract

A revision of the Indo-Pacific coral reef fish genus *Plesiops* Oken, 1817 (Perciformes: Plesiopidae) finds it composed of 17 species, including seven new: *P. auritus* sp. nov. (eastern Indian Ocean, western Malay Archipelago), *P. cephalotaenia* Inger, 1955 (Malay Archipelago, Melanesia), *P. coeruleolineatus* Rüppell, 1835 (East Africa and Red Sea to Line Islands), *P. corallicola* Bleeker, 1853 (eastern Indian Ocean, western Pacific), *P. facicavus* sp. nov. (Sulawesi), *P. genaricus* Mooi and Randall, 1991 (Great Barrier Reef), *P. gracilis* Mooi and Randall, 1991 (Malay Archipelago, Palau Islands, New Guinea, Western Australia), *P. insularis* Mooi and Randall, 1991 (Chesterfield Is., New Caledonia, Norfolk Is., Lord Howe Is., Middleton and Elizabeth Reefs), *P. malalaxus* sp. nov. (Madagascar), *P. multisquamata* Inger, 1955 (southeast Africa), *P. mystaxus* sp. nov. (Madagascar, Comoro Islands, Red Sea, Arabian Sea), *P. nakaharai* Tanaka, 1917 (Japan), *P. nigricans* (Rüppell, 1828) (Red Sea), *P. oxycephalus* Bleeker, 1855 (Malay Archipelago, Melanesia), *P. polydactylus* sp. nov. (Fiji), *P. thysanopterus* sp. nov. (Sumatra), and *P. verecundus* sp. nov. (Malay Archipelago, Melanesia, Australia, South China Sea).

A hypothesized phylogeny of the genus based on osteology and myology places *Plesiops multisquamata* and then *P. malalaxus* as consecutive sister groups to all other species. A clade of three species, with a sequence of relationships of *nakaharai*, *corallicola*, and *nigricans*, is the sister taxon to the remaining species. Among these species, the sister taxa *genaricus* and *insularis* are hypothesized as the sister group to a polytomy of four groups: a single species *verecundus*, the sister species *mystaxus* and *coeruleolineatus*, a clade of three species with a sequence of relationships of *polydactylus*, *thysanopterus*, and *auritus*, and a clade of four species with relationships sequenced as *oxycephalus*, *facicavus*, *cephalotaenia*, and *gracilis*. The latter *oxycephalus* clade exhibits pedomorphic traits involving dentary sensory pores and lateral-line scales.

Large size appears to be primitive within the genus, and, contrary to correlations described in freshwater fishes and some invertebrates, there is an inverse relationship between adult body size and geographic range. Distributions of sister taxa are used to infer modes of speciation prevalent in the genus. Eight of the 13 informative sister-group pairs provided by the hypothesized phylogeny exhibit a high degree of sympatry, suggesting either postspeciational dispersal or sympatric speciation; five of the pairs exhibit allopatry, with three indicative of a peripheral isolates model and two suggestive of vicariant speciation.

The distributions of members of *Plesiops* are compared with distributions of other Indo-Pacific fishes using a historical biogeography approach. Vicariant scenarios are hypothesized based on the breakup of Gondwanaland. Sister species *P. nigricans* and *P. corallicola* have distributions that might be explained by the drift of India through an ancestral Tethyan distribution. *P. genaricus* and *P. insularis* have distributions congruent with the rifting of the Lord Howe Rise from eastern Australia. The possible influence of Pleistocene glacial maxima on the evolution of coral reef fishes is untestable with *Plesiops* phylogenetic and distributional data.

Introduction

Plesiops Oken, 1817 is the type genus of the family Plesiopidae, and recently has been placed in its own subfamily, the Plesiopinae (Mooi, 1993). Mooi (1993) hypothesized relationships among subgroups of the Plesiopidae, including a sister-group relationship between the Acanthoclininae and Plesiopinae, providing the basis for determining monophyly of the genus. *Plesiops* is a group of small fishes ranging from about 50 to 200 mm standard length (SL) (usually 60 to 80 mm), living in shallow coral reef flats or around coral heads of the tropical and subtropical Indo-Pacific. All have long pelvic fins and often have colourful stripes or patterns of blue, red, and yellow on the dorsal and anal fins, features which have given rise to their common names of "longfins" or "prettyfins." They are rarely seen under natural conditions and are apparently nocturnal (Myers, 1989). They feed mostly on crustaceans, gastropods, and other fishes, and occasionally on ophiuroids.

The eggs of the genus are unique within the family (Mooi, 1993): they are elongate and bear filaments originating in pairs from small buttonlike projections that are clustered about the micropyle (Mooi, 1990). The number of filaments varies among species, although a complete survey has not been attempted. As described by Mito (1955), the filaments initially envelop the egg chorion and are arranged along the long axis, coming free of the surface when the egg is laid. Eggs are deposited in a cluster under a rock or other suitable hiding place where the male parent guards them (Mito, 1955), the filaments apparently helping to adhere the eggs to the substrate. Larvae are pelagic, and those of *P. coeruleolineatus* Rüppell, 1835 are described in Leis and Trnski (1989). Little else is known of their biology.

Traditionally, *Plesiops* has been characterized by an unusual scale morphology, by a bifid and thickened first

pelvic-fin ray, and by the absence of features found in other plesiopid taxa. The first pelvic-fin ray is indeed bifid, but it is much more difficult to quantify "thickened." Some species in the genus have very long, delicate first pelvic-fin rays, that, although thicker than other rays of the fin, I would hesitate to call thickened. Furthermore, this feature is shared with the genus *Paraplesiops* Bleeker, 1875.

The scales of members of *Plesiops* have been recognized as unusual since the original description of the type species by Rüppell (1828). These have a distinctly outlined centre from which the radii extend into all but the most posterior fields of the scale (Fig. 1). Some other fishes have a similar scale pattern (e.g., the pseudoplesiopine pseudochromids *Pseudoplesiops rosae* Schultz, 1943 and *P. typus* Bleeker, 1858), but such a scale type is derived within the Plesiopidae.

Plesiops can be demonstrated to be monophyletic by a number of other characters. Osteological synapomorphies include 1) a well-developed cleithral hook; 2) a tenth parapophysis in contact with the first anal pterygiophore; and 3) a well-developed pelvic iliac process. A unique myological feature of the pelvic girdle is an expanded extensor proprius that has two components, one with a lateral origin inserting onto the second and third rays, and the other with a medial origin inserting onto the third and fourth rays. These autapomorphies are treated in more detail below.

Plesiops was last revised by Inger (1955) who recognized six species. Hayashi (1984) and Sano et al. (1984) recently removed *P. nakaharai* Tanaka, 1917 from synonymy with *P. corallicola* Bleeker, 1853c where Inger had placed it, and resurrected it as a valid species. Sano et al. (1984) recognized seven species and provided a key to the five species found in Japanese waters. Mooi and

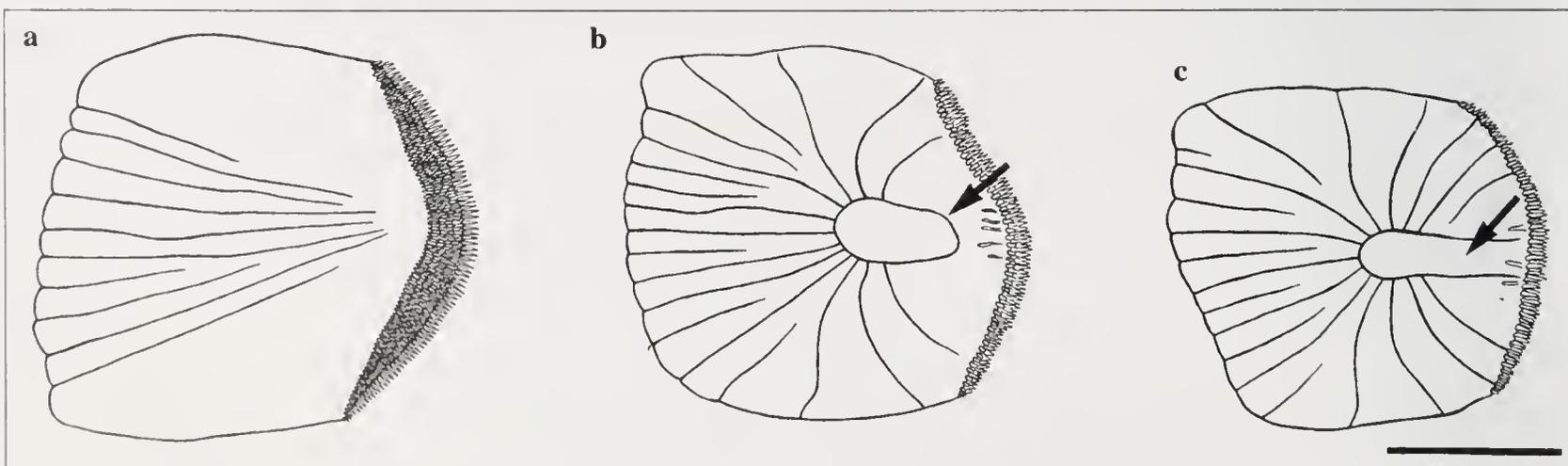


FIG. 1a–c. Body scale morphology of plesiopids. Anterior to left. Scale bar = 2 mm.

a. *Paraplesiops*. No distinct, unmarked centre, and radii only in anterior field.

b. *Plesiops*, closed-centred scale. Distinct, unmarked centre fully circumscribed (arrow), and radii in all but the most posterior fields.

c. *Plesiops*, open-centred scale. Distinct, unmarked centre with open posterior end (arrow) and radii in all but the most posterior fields.

Randall (1991) added three new species found in tropical Australian and adjacent seas. This paper describes seven additional species, and redescribes the 10 currently recognized in order that all species will have comparable descriptions available for future workers. A key is also provided. Biological and distributional information is presented for each species, as well as a synonymy and taxonomic history where appropriate. The synonymies include

only those references that provide an identifiable description or figure of the species; faunal listings are not included. After the species descriptions, characters supporting the monophyly of the genus and a tentative phylogeny of its included species are provided. This phylogeny is used to explore aspects of the development and life history of these fishes, as well as their speciation and biogeography.

Materials and Methods

SPECIES DESCRIPTIONS

Material for descriptions is listed under each species as "Type Material," which includes the holotype and paratype(s), and "Additional Material Examined" if applicable. It is listed alphabetically by major locality, then alphabetically by institutional abbreviation (see below). Detailed locality information is not provided for "Additional Material Examined," but can be obtained from the author or appropriate institution; specimen lengths are occasionally omitted from these data.

Some specimens of new species are not designated as types, but are listed as distributional records. Standard length (SL) in millimetres is used throughout unless otherwise indicated. Symbols before lengths refer to sex: ♂ = male, ♀ = female, ? = examined but undetermined. When no symbol is present the specimen(s) was not examined for sex. For meristic and morphometric characters, the holotype or lectotype value is presented first. When counts varied from one side to the other on the type, both "left" and "right" are provided. The mode (for meristics) or average (for morphometrics) and range are included in parentheses and are separated by a semicolon. When a character value is missing for the holotype owing to specimen damage, only the mode or average and range for the species are provided.

Counts of dorsal-, anal-, and pelvic-fin spines and soft rays are represented as Roman and Arabic numerals, respectively, and separated by a comma. The number of free pectoral-fin rays is defined as the number of rays free of fin membrane for 25 per cent or more of their length (Fig. 2). Caudal-fin rays are counted as principal and procurrent rays. Principal rays include all branched rays and two unbranched rays, one dorsally and one ventrally; the count is presented as upper (those rays associated with hypurals 3, 4, and 5) + lower (those rays associated with hypurals 1 and 2 and the parhypural) rays. Procurrent caudal-fin rays, those anterior to the principal rays, are counted as upper (dorsal) + lower (ventral) rays.

Gill-raker counts are of the outer rakers on the first arch including all rudiments. These are provided in the form of upper + lower rakers, where the former are those

of the upper limb (epibranchial 1), and the latter are those of the lower limb (cerato- and hypobranchials 1). The raker at the angle is included in the lower-limb count.

The lateral line of *Plesiops* is disjunct. There is an upper line that extends from the dorsal gill opening to the end of the soft portion of the dorsal fin, running along the base of the dorsal fin. There is also a lower line that runs midlaterally from about midbody to the caudal base. Counts of tubed scales in each lateral line include intermittent non-tubed scales and empty scale pockets. Lower line counts do not include the pored or tubed scales on the caudal fin (those beyond the posterior margin of the hypural plates, usually two scales). The midlateral series is the scale count from the posttemporal to the caudal base (end of hypural plates), similar to a lateral-line scale count on a fish with a complete lateral line. Cheek scale rows are those counted from the eye to the preopercular angle. Scales are described as closed- or open-centred following Mooi and Randall (1991, fig. 1) (Fig. 1b,c).

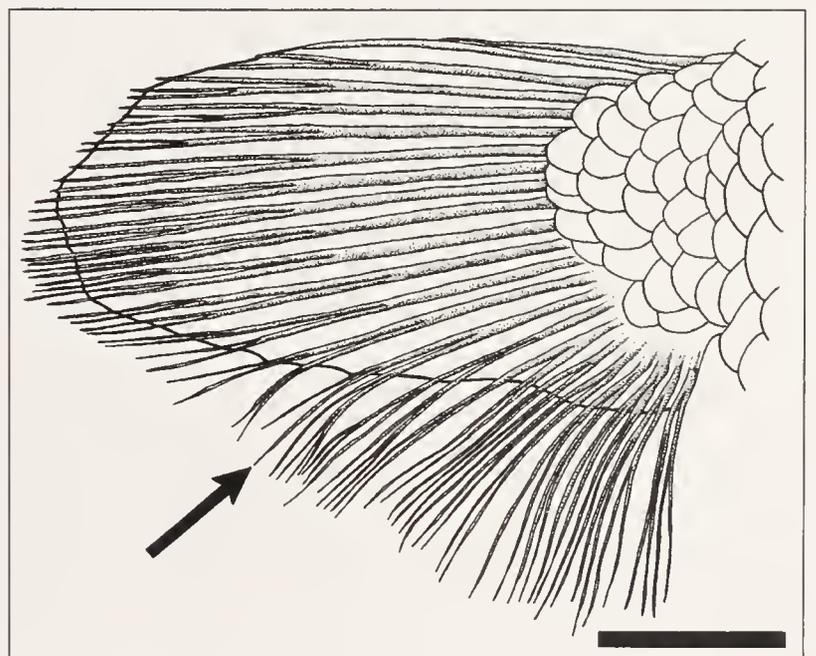


FIG. 2. *Plesiops insularis*. Right pectoral fin of holotype BPBM 14762, 80.5 mm. Arrow points to ninth pectoral ray counting from ventrally, the last free ray, defined as the dorsalmost ray with more than 25 per cent of its length free of the fin membrane. From Mooi and Randall (1991:380, fig. 4). Scale bar = 5 mm.

Dentary sensory pores are defined as those ventral to a hypothetical line drawn between the posteroventral tip of the maxilla and the anteroventral tip of the preopercle. The number of dentary pores is counted on one side (left or right), then divided by SL (mm) to create a dentary pore:SL ratio.

Measurements were made with dial calipers to the nearest tenth of a millimetre and recorded as percentages of SL or head length (HL). Morphometric measurements are either standard, following Hubbs and Lagler (1949), or are self-explanatory.

Vertebral counts are divided into precaudal and caudal; the first caudal vertebra being the anteriormost vertebra with a haemal spine, and the last being the urostylar complex. Dorsal formulae follow the format of Ahlstrom, Butler, and Sumida (1976), and span only the first five interneural spaces. Neural spines are represented by slashes; each supraneural (predorsal) bone is represented by a "0"; and pterygiophores are represented by a "2" (when bearing two supernumerary spines) or a "1" (when bearing only one spine).

Sex was determined externally (Fig. 3), and when possible, verified by internal examination. Sex ratios were produced by counting the number of males and females identified. Individuals identified as males that were smaller than the smallest identified female were excluded from the ratio calculation under the assumption that females below this length might not exhibit the external secondary sexual characteristics of more mature individuals, and might be incorrectly assigned as males.

Colour descriptions were taken from colour transparencies, published photographs, or field notes on particular specimens. Catalogue numbers provided in the descriptions refer to those specimens for which colour slides were available.

INSTITUTIONAL ABBREVIATIONS

Institutional abbreviations follow Leviton et al. (1985): AMS, Australian Museum, Sydney; ANSP, Academy of Natural Sciences of Philadelphia; BMNH, The Natural History Museum, London; BPBM, Bernice P. Bishop Museum, Honolulu; CAS, California Academy of Sciences, San Francisco; FMNH, Field Museum of Natural History, Chicago; FMRI, Central Marine Fisheries Marine Research Institute, Mandapam Camp, India; FUMT, Department of Fisheries University Museum, University of Tokyo, Tokyo; IOP, Izu Oceanic Park, Shizuoka; IORD, Institute of Oceanographic Sciences, Tokai University; LACM, Museum of Natural History, Los Angeles County, Los Angeles; MMNH, Musée d'Histoire Naturelle, Marseille; MNHN, Muséum National d'Histoire Naturelle, Paris; MPM, Milwaukee Public Museum, Milwaukee; NMNZ, National Museum of New Zealand, Wellington; NSMT, National Science Museum, Tokyo; RMNH, Rijksmuseum van Natuurlijke Historie, Leiden; ROM, Royal Ontario Museum, Toronto; RUSI, J. L. B. Smith Institute of Ichthyology, Grahamstown, South Africa; SMF, Natur-Museum und Forschungs-Institut Senckenberg, Frankfurt-am-Main;

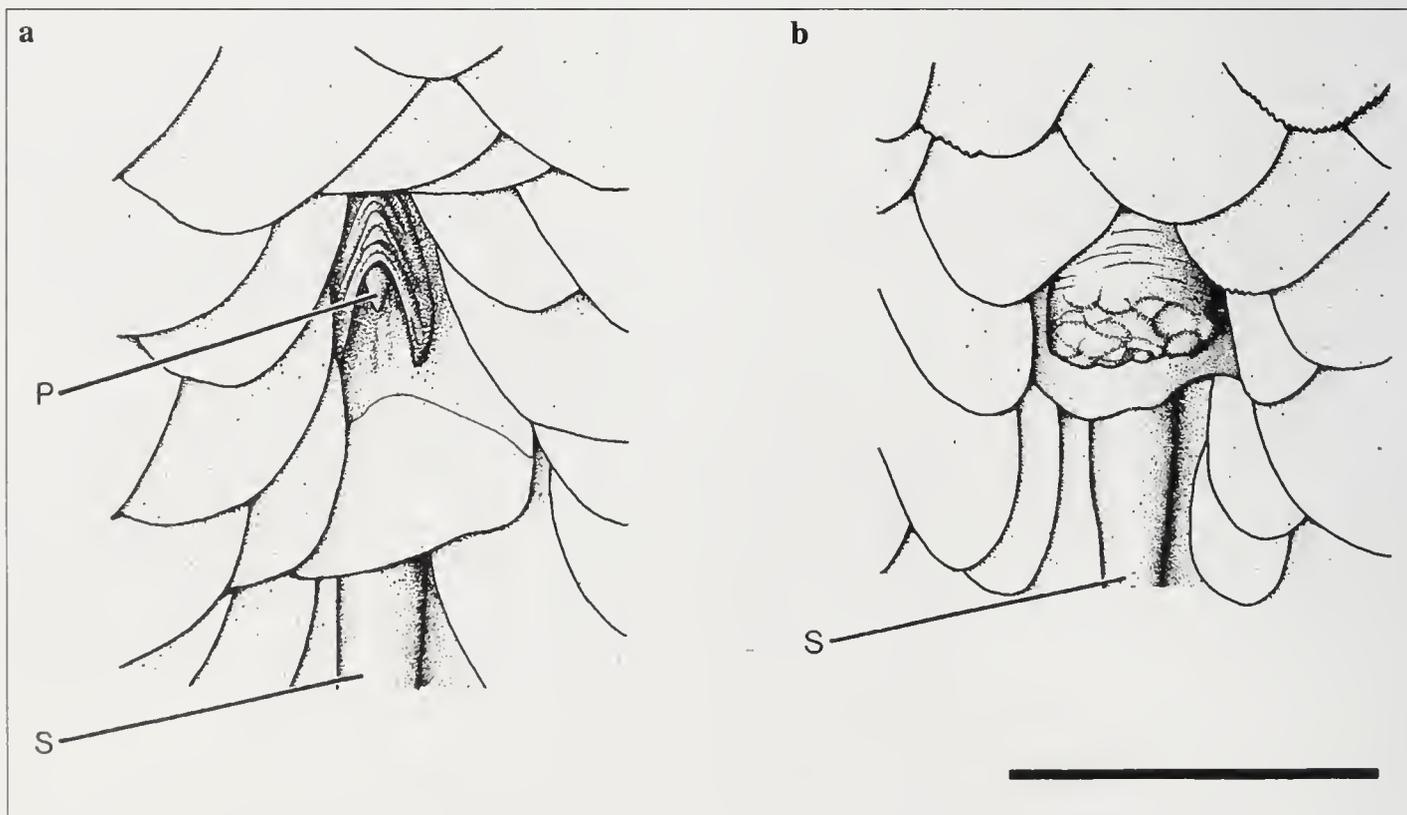


FIG. 3a-b. *Plesiops corallicola*. Urogenital regions. Anterior towards top. S = base of first anal spine, P = urogenital papilla. Scale bar = 5 mm.

a. Male, USNM 154392, 111.2 mm. Urogenital papilla visible.

b. Female, AMS 1.13846-51, 102.0 mm. Urogenital papilla obscured.

TAU, Tel-Aviv University, Tel-Aviv; UMMZ, University of Michigan Museum of Zoology, Ann Arbor; USNM, National Museum of Natural History, Washington; WAM, Western Australian Museum, Perth; YCM, Yokosuka City Museum, Yokosuka; ZIL, Academy of Sciences, Leningrad (St. Petersburg); ZUMT, Department of Zoology University Museum, University of Tokyo, Tokyo.

STATISTICAL ANALYSIS

The frequency of the dentary pore:SL ratio was plotted for selected species. Because this ratio varies with size, larger individuals were used for interspecific comparison, arbitrarily chosen to be specimens no smaller than 40.0 mm. A nonparametric pairwise test, the Mann-Whitney U-test (following Sokal and Rohlf, 1981:433), was performed to discover if the pore:SL ratio distributions of specimens over 40.0 mm were significantly different. The total number of dentary pores was also regressed against standard length for selected species using the general linear models procedure of SAS/PC 6.03 (SAS Institute Inc., Box 8000, Cary, NC, 27511-8000). An analysis of covariance (ANCOVA) was performed pairwise to determine if the slopes of the lines for the species were significantly different from each other. Populations of species exhibiting geographic variation in dentary pore:SL ratios were tested pairwise for significant difference using ANCOVA, but regressions were not plotted.

Observed sex ratios were tested for a difference from a 1:1 ratio using a log likelihood ratio test (Sokal and Rohlf, 1981:696). This is a G-test where

$$G = 2 \ln L$$

$$\ln L = f_m \ln(f_m / \hat{f}_m) + f_f \ln(f_f / \hat{f}_f)$$

f_m = observed frequency of males

f_f = observed frequency of females

and $\hat{f}_m = n(0.5)$

$\hat{f}_f = n(0.5)$

where n = no. of specimens

0.5 = expected probability of males and females.

This value was compared to that of a Chi-square distribution using one degree of freedom to test for significance.

OSTEOLOGICAL AND MYOLOGICAL PREPARATIONS

Osteology of plesiopids and other taxa was examined by two methods. The majority of specimens were cleared and stained with trypsin and counterstained for bone and cartilage following the methods of Dingerkus and Uhler (1977) or Taylor and Van Dyke (1985). These specimens were dissected to various degrees, but usually the suspen-

sorium, suborbitals, hyoid apparatus, and gill arches were removed first, followed by the pectoral and pelvic girdles. Occasionally, the cranium was removed from the axial skeleton, and for some species a spine-bearing dorsal-fin pterygiophore was removed.

Some specimens were examined using soft X-rays. Fishes were placed on Kodak AA5 or SR X-ray film sealed in lightproof plastic bags and exposed to an X-ray source in a Hewlett-Packard Faxitron series 43805 N for between 30 seconds and 5 minutes at 35 KVP. Films were developed and viewed as negatives under a binocular microscope using transmitted light. A list of osteological preparations examined is provided in Appendix.

Cheek musculature was examined by removing the eye, suborbitals, and skin on one side of the head and staining the muscles using a variation on Lugol's solution (Bock and Shear, 1972). Muscle bundles were identified, drawn under a binocular dissecting microscope through a camera lucida, then removed to reveal more medial muscle groups. Pelvic musculature was examined after the pelvis was removed from the fish, stained, and dissected. Both muscle groups were often examined prior to clearing and staining for osteological study. Specimens examined for muscle anatomy are listed in Appendix. Muscle terminology follows that of Winterbottom (1974).

PHYLOGENETIC ANALYSIS

External, osteological, and myological characters were analysed following the principles of phylogenetic systematics (cladistics). Wiley (1981) best summarizes the techniques and philosophy that I embrace. The outgroup method of Watrous and Wheeler (1981) was used to polarize characters and provide evidence of relationships based on derived (apomorphic) features. Mooi (1993) provided a hypothesis of relationships among members of the Plesiopidae, where the family was expanded to include the former family Acanthoclinidae. This hypothesis provided a sister group (primary outgroup) to *Plesiops* (placed in its own subfamily Plesiopinae), the Acanthoclininae, followed by a secondary outgroup, the Fraudellinae, and successively more remote outgroups, including the Paraplesiopinae, Assessorinae, and Trachinopinae (Fig. 4). Such a phylogeny permits use of global parsimony arguments of Maddison, Donoghue, and Maddison (1984) in situations where character states appear in both the ingroup and some outgroups. For expediency, all non-plesiopine plesiopids are termed immediate outgroups in the text in order to differentiate them from more distantly related outgroups (e.g., Pseudochromidae); all outgroups were examined independently during character analysis. Within *Plesiops*, functional ingroup/functional outgroup (FIG/FOG) argumentation is used extensively. However, similarities in the morphology

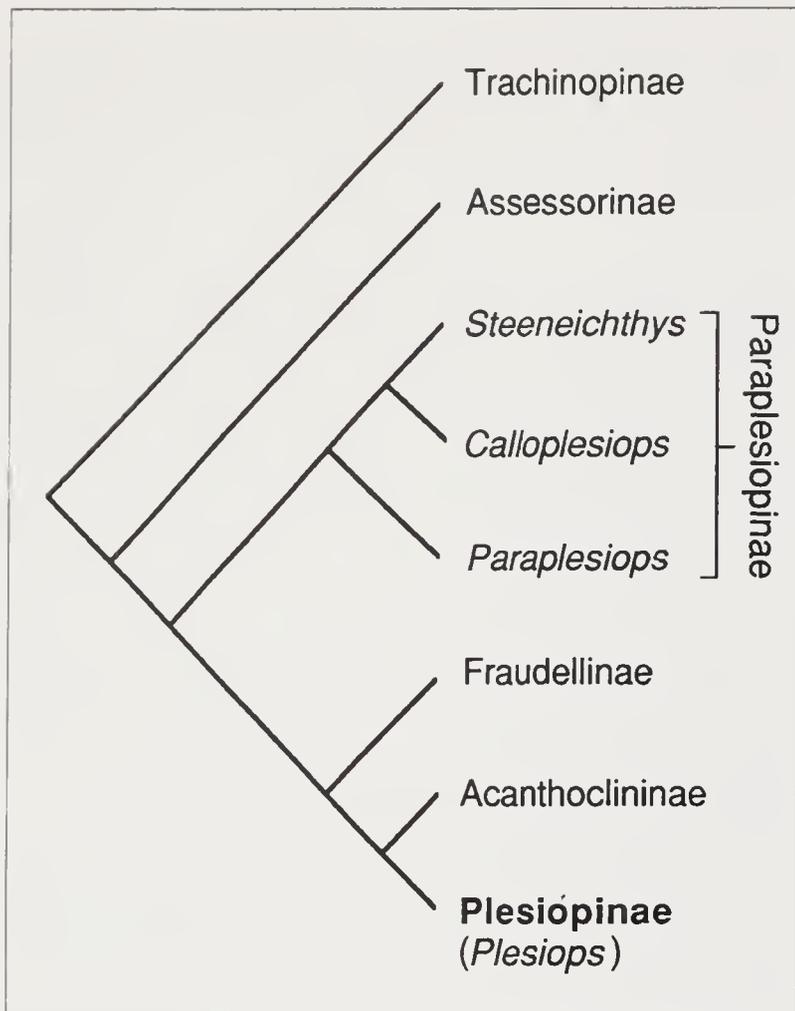


FIG. 4. Hypothesized phylogeny of the family Plesiopidae (after Mooi, 1993). Outgroup relationships shown for the subfamily Plesiopinae (bold-face) indicated as comprising a single genus, *Plesiops*.

of immediate outgroups and other percoid families are discussed when deemed of interest. Gill and Mooi (1993) provided evidence to suggest that the Notograptidae are related to the Acanthoclininae, either as a sister taxon or as an internal clade. Possible addition of the Notograptidae to the Plesiopidae does not alter the interpretation of the characters used here to hypothesize relationships among species of *Plesiops*, but character states in notograptid are discussed where relevant.

Features are discussed first as their primitive state under "Plesiomorphy," and then as the derived condition under "Apomorphy." When homoplasies (incongruences) could not be redefined on the basis of ontogenetic or other morphological criteria during analysis, these are discussed under the heading "Homoplasies" and sometimes further explored under "Remarks" for a given character. For some features, the global parsimony techniques of Maddison, Donoghue, and Maddison (1984) were employed, although biological explanations of homoplasy were preferred over parsimony explanations. Initial cladistic analyses via Hennigian argumentation were corroborated by analysis employing the branch-and-bound option of PAUP (Phylogenetic Analysis Using Parsimony), version 2.4.1, of D. L. Swofford

(LMS/MSC/NMNH, Smithsonian Institution, Washington, DC 20560). This option is guaranteed to generate the shortest tree(s). A consistency index and a retention index (Farris, 1989) are presented for the analysis.

Plesiops Oken, 1817

Plesiops Oken (ex Cuvier), 1817:1182.—Cuvier, 1816:266; Cuvier, 1829:264; Bleeker, 1876:322.

Pharopteryx Rüppell, 1828:15, pl. 4 (fig. 2).

Pseudochromichthys Schmidt, 1931:180, fig. 1

DIAGNOSIS

Dorsal fin XI–XII, 7; spinous and soft portion of dorsal united; spinous portion of dorsal with membranes often deeply incised; anal fin III, 8; pelvic fin I, 4 with first ray bifid, elongate, and sometimes thickened; scales with distinct centre from which radii extend to all fields (except occasionally posterior field); lateral line interrupted, the upper portion running from posttemporal along the base of dorsal fin and ending at or just beyond the base of the last dorsal soft ray, the lower line running along the midlateral body from about the level of the anal-fin origin to the caudal base; no basihyal teeth; no scales on maxilla; extensor proprius pelvici with lateral and medial muscle fibres, the former inserting on the 2nd and 3rd rays, the latter inserting on the 3rd and 4th rays; well-developed cleithral hook; well-developed iliac process; 10th parapophysis in contact with the 1st anal-fin pterygiophore; eggs oblong with filaments arising in pairs from button-like knobs clustered around the micropyle.

TYPE SPECIES

Plesiops nigricans (Rüppell, 1828) by subsequent designation (Bleeker, 1876).

DESCRIPTION

Body compressed; origin of dorsal fin slightly behind pelvic base; bony-interorbital narrow (< 10 per cent head length); anterior nares tubed and usually smaller than posterior nares; maxilla extends to or beyond posterior orbit margin; head naked anteriorly from just posterior to orbit; scales of cheek, opercle, nape, dorsal-fin base, anal-fin base, and anterior to pectoral- and pelvic-fin base cycloid, the remainder ctenoid; all scales on adult with distinct centre with radii emanating from it; all scales relatively large with a distinct, unmarked centre, those of opercle much larger than on rest of body and always closed-centred, those of body open- or closed-centred (Fig. 1b,c; p. 2); pored lateral line interrupted, forming 2 lines, the upper one from posttemporal along dorsal-fin base to or just beyond last soft ray, lower one along midlateral body from level of anal-fin origin to caudal-fin base; upper lateral-line scales 18–30, primary anterior pore of each scale covered

or not covered by preceding scale; lower lateral-line scales 7–18, anterior primary pore never covered by preceding scale; predorsal scale rows 5–11; cheek scale rows 3–7; dorsal and anal fins in scale sheaths, mostly cycloid; dorsal formula 0/0/2/1+1/1 or 0/0/1/1+1/1, hence either 1 or 2 supernumerary spines on first dorsal pterygiophore; spinous and soft portions of dorsal fin united, XI–XII,7; membrane of spinous portion of dorsal fin incised, the incision often to spine bases in larger specimens, usually first 6–8 spine intermembranes joined with following spine at or close to base, incisions then gradually becoming less pronounced until only tip of spine free of membrane; dorsal-fin spines with fleshy tips; anal-fin spine membranes only slightly incised; both dorsal- and anal-fin spines increase in length posteriorly; dorsal-fin spine-bearing pterygiophores articulate with spines via interlocking bony rings; dorsal soft-ray pterygiophores trisegmented; dorsal and anal stay present; anal fin III,8; caudal fin rounded, 10 + 9 principal caudal-fin rays except on smaller individuals, 4–6 + 4–6 procurrent caudal-fin rays; pectoral fins rounded, with or without the ventralmost rays free of membrane for much of their length, if so, forming a tassled fringe, pectoral-fin rays 17–30; pelvic fins I,4, first ray bifid and much longer than other rays, often very obviously thickened, particularly in larger specimens; extensor proprius with 2 muscle bundles, 1 lateral and 1 medial; adductor superficialis pelvici to spine and first ray only; well-developed iliac process; large subpelvic shelf; lower lip interrupted at symphysis; 5 suborbitals, subocular shelf present; gill rakers on first arch short, 3–6 + 7–14; branchiostegals 6, membranes not fused across isthmus; numerous teeth on palatine; jaw teeth in 2–6 rows, 3 larger canines on each premaxilla, all teeth but canines hinged and posteriorly depressable; teeth on dentary, vomer, and palatine also small and in many rows; no tongue (basihyal) teeth; interarcual cartilage present; well-developed cleithral hook; well-developed metapterygoid lamina; vertebrae 10 + 15 (rarely 10 + 14, 10 + 16); first 3 vertebrae smooth on ventral surface; parapophysis on 10th vertebra in contact with 1st anal-fin pterygiophore; preural centrum 2 haemal spine autogenous; epurals 2–3; hypurals 1 + 2, 3 + 4, 5, with 3 + 4 fused to compound ural centrum; parhypural fused to hypural plate 1 + 2.

TAXONOMIC REMARKS

The genus was first described as “LES PLESIOPS” by Cuvier (1816:266), apparently without any specimens available. Oken (1817:1182) was the first to Latinize the name and is given authorship, although Paxton et al. (1989:526) cited Bosc (1818). Rüppell (1828:16) had originally recognized the similarity between Cuvier’s description of *Plesiops* and his new genus and species *Pharopteryx nigricans*, but balked at that part of Cuvier’s description that stated that the fish was a “*Chromis*.” Rüppell noted that the mouths of his specimens were not at all like *Chromis* Cuvier, 1814, and rejected a synonymy. However, in an index to his collected works on North Africa, Rüppell (1830:141, footnote 4) stated that he believed *Pharopteryx* [*sic*] to be identical with *Plesiops* on the strength of a comparison of his material with that in Paris labelled *Plesiops*. The specimens Rüppell examined were very likely those of Kuhl and van Hasselt, which had been collected at least six years after Cuvier’s description, and were never described. Because Rüppell (1830) maintained the name *Pharopteryx* (ruled as an incorrect spelling of *Pharopteryx* in Opinion 1082 of the International Commission of Zoological Nomenclature, 1977), I do not consider this a designation of a type species for *Plesiops*. In 1835, Rüppell formally adopted the name *Plesiops* for his species, but simultaneously described a second species. Bleeker (1876:322) finally designated *Plesiops nigricans* (Rüppell, 1828) as the type species for the genus. Jordan and Seale (1906) attempted to rectify this taxonomic problem by considering Cuvier’s (and Oken’s) *Plesiops* as a *nomen nudum* and accepting *Pharopteryx* Rüppell, but their recommendation was ignored by subsequent authors. A ruling of the International Commission of Zoological Nomenclature (1910) in Opinion 19 provisionally accepted *Plesiops* as the senior synonym of *Pharopteryx* in accordance with Rüppell’s own conclusion. Apparently unaware of the ICZN ruling, Smith (1952:139) commented: “The recognition of this genus as valid over *Pharopteryx* Rüppell, 1828, with the type species described 11 [*sic*] years later than the genus, appears somewhat anomalous, but is apparently generally accepted.” The gender of the genus name is masculine, following Article 30(a)(ii) of the International Commission on Zoological Nomenclature (1985).

Key to the Species of *Plesiops*

- 1a. Upper lateral-line scales 26–30; scales in midlateral series 29–33; circumpeduncular scales 22–24 (east coast, South Africa) *multisquamata*, p. 42
- 1b. Upper lateral-line scales 18–23; scales in midlateral series 23–25; circumpeduncular scales 16, rarely 15 or 17 2
- 2a. Dorsal spines XI (< 2 per cent with X or XII), always only 1 supernumerary spine on first dorsal pterygiophore (dorsal formula 0/0/1/1+1/1); scales in midlateral series 23–24; total number of branches on 6 ventralmost pectoral-fin rays fewer than 15, usually 12 (only 6 per cent with 15 or more) 3
- 2b. Dorsal spines XII (very rarely XI or XIII), 2 supernumerary spines on first dorsal pterygiophore (dorsal formula 0/0/2/1+1/1); midlateral scale series almost always 24 (rarely 23 or 25); total number of branches on 6 ventralmost pectoral-fin rays often more than 15 4
- 3a. Pectoral-fin rays 19–24 (usually 21–23, < 2 per cent with 24); total gill rakers on first arch usually 11 or 12 (9–15, < 10 per cent with 14–15); almost always 3–4 gill rakers on upper arch (only 3 per cent with 5–6); predorsal scale rows 5–8 (< 1 per cent with 5) (Indo-West Pacific, from Red Sea and East Africa to Japan, Gilbert Is., Western Samoa, and Great Barrier Reef) *coeruleolineatus*, p. 18
- 3b. Pectoral-fin rays 26–28; total gill rakers on first arch 13–18; 4–5 gill rakers on upper arch; predorsal scale rows 5–6, usually 5 (Fiji) *polydactylus* sp. nov., p. 53
- 4a. Dark ocellus greater than or about equal to $\frac{3}{4}$ eye diameter on ventral portion of opercle, sometimes extending onto subopercle (eastern Indian Ocean to Ryukyus, southeast to Cook Is., then west to northern New Guinea) *corallicola*, p. 25
- 4b. No dark ocellus on ventral portion of opercle, although some species with a small spot on subopercle 5
- 5a. Pectoral-fin rays 26 or more (sometimes 25); 11 free pectoral rays or more (rarely fewer than 10); predorsal scale rows 4–6 6
- 5b. Pectoral-fin rays fewer than 26 (rarely 25); fewer than 10 free pectoral rays (Fig. 2, p. 3); predorsal scale rows 6–11 7
- 6a. Pectoral-fin rays 28–30; cheek scale rows 4; body and head generally dark, no dark spot on dorsal opercle; dorsal-fin spine tips dark or dusky; sensory pores on head small and abundant, dentary pore:SL (mm) ratio > 1.0 (northern Sumatra) *thysanopterus* sp. nov., p. 55
- 6b. Pectoral-fin rays 25–27; cheek scale rows 2–3; head with dark spot on dorsal portion of opercle just posterior to dorsal tip of preopercle, giving “eared” appearance; body often pale, scales with darker posterior margins giving a spotted or banded pattern, especially on caudal peduncle; dorsal-fin spine tips pale; sensory pores on head small but not greatly abundant, dentary pore:SL ratio < 1.0 (Sri Lanka, western Malay Peninsula, Greater Sundas) *auritus* sp. nov., p. 12
- 7a. Caudal-fin membranes with pale spots; body scales with single central pale spots becoming crescent-shaped dorsally, smaller pale spots on scales of nape, cheek, and opercle; cheek scale rows 6–7 (rarely 5); predorsal scale rows 9–10 (rarely 7–8) (Red Sea, Gulf of Aden) *nigricans*, p. 48
- 7b. Caudal-fin membranes without pale spots; body scales with or without pale central spots; cheek scale rows 3–5 (rarely 6); predorsal scale rows either 6–8 (rarely 9) (7 species) or 9 or more (3 species) 8
- 8a. Three or more posterior upper lateral-line scales with anterior pore not covered by preceding scale (Fig. 5); pectoral-fin rays 17–19, sometimes 20; dentary pore:SL ratio < 0.5, number of dentary pores on each side usually fewer than 20, always fewer than 25 9
- 8b. Fewer than 3 upper lateral-line scales with anterior pore not covered by preceding scale; pectoral-fin rays usually 20 or more, sometimes 19; dentary pore:SL ratio often > 0.5, and most species with more than 20 dentary pores when greater than 35 mm SL 11
- 9a. Predorsal scale rows 7–8; cheek scale rows 3–4; 5–23 dentary pores on each side usually more

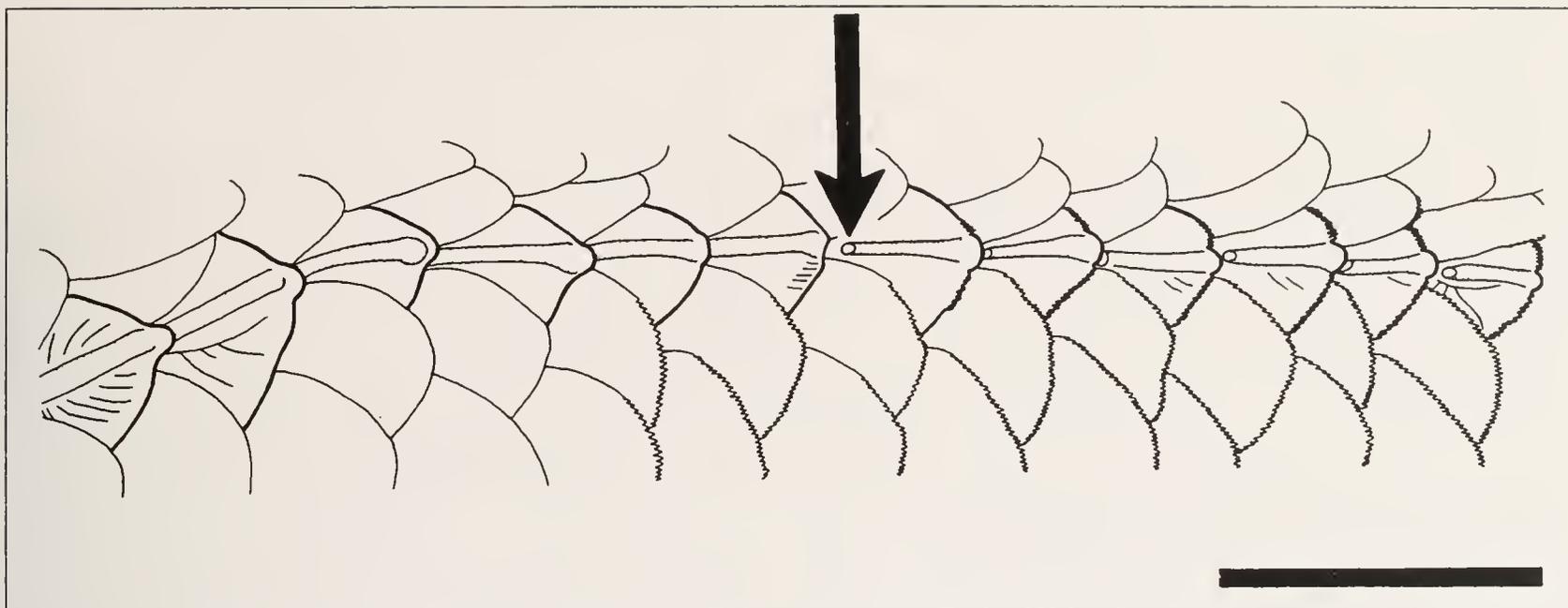


FIG. 5. *Plesiops gracilis*. Fourth to 15th upper lateral-line scales of paratype CAS 67421, 62.0 mm. Lateral-line scales outlined in bold. Arrow indicates first exposed anterior sensory canal pore. Sensory canal with stippled margins. Note that the anterior sensory canal pore is covered by the preceding scale on scales 5–9, and not covered by preceding scale on scales 10–15. Note also the medial flap or lobe on the posterior margin of most lateral-line scales. Scale bar = 5 mm.

- than 7; anteroventral preopercular sensory pore not enlarged (Solomons, north coast of New Guinea, eastern Indonesia, Philippines, southern Ryukyu Is.) *cephalotaenia*, p. 14
- 9b. Predorsal scale rows 9–11; cheek scale rows 4–5; 5–9 dentary pores on each side rarely more than 7; anteroventral preopercular sensory pore enlarged or not 10
- 10a. Anterior part of head densely speckled with small (0.5 mm), brown spots; sensory pores on head sparse and large, especially those of interorbital (about 1 mm); only 5 large dentary pores; sensory pore at anteroventral end of preopercle not enlarged in comparison with other pores (Togian Is., Sulawesi)
..... *facicavus* sp. nov., p. 29
- 10b. Anterior part of head not speckled; many small sensory pores in interorbital region; usually 6 (5–9) dentary pores, not enlarged; sensory pore at anteroventral end of preopercle enlarged (Fig. 6) (Palawan, Palau Islands, Yap Island, northern coast of New Guinea, Rowley Shoals of Western Australia) *gracilis*, p. 35
- 11a. Maxilla and supramaxilla with a dark dorsal margin, but no dark stripe on the ventral cheek just dorsal to the maxilla (Madagascar, Comores, Red Sea, Oman) *mystaxus* sp. nov., p. 44
- 11b. Maxilla and supramaxilla without a dark dorsal margin, but often a dark stripe on ventral cheek bordering maxilla, and sometimes a dark stripe or smudge at posterior end of maxilla but positioned midlaterally 12
- 12a. Predorsal scale rows 9–11; pectoral-fin rays 19–21, usually 20; nape with a mottled or dendritic pattern; body usually pale with dark spots, often congregated to form 4–6 bands, 4 on body, 2 on peduncle (west coast of Sumatra, Vietnam, southern Ryukyu Islands, Philippines, Moluccas, north coast of New Guinea, New Hebrides) ...
..... *oxycephalus*, p. 51
- 12b. Predorsal scale rows 6–8; pectoral-fin rays 20 or more, usually 22 or more; nape without a mottled or dendritic pattern; body usually dark without bands 13
- 13a. Dorsal-fin spines with obviously pale tips (red in life) except in specimens < 30 mm; total number of branches on lower 6 pectoral-fin rays rarely more than 20, usually 12; branches on ventralmost ray 1–2, rarely 3; no pale central spot on body scales (southern Ryukyus, Vietnam, Philippines, southern Indonesia, Western Australia, Great Barrier Reef, New Guinea, Solomons, New Hebrides, New Caledonia, Fiji) *verecundus* sp. nov., p. 57
- 13b. Dorsal-fin spines without obviously pale tips, sometimes lighter than rest of fin, but always dusky; total number of branches on lower 6 pectoral-fin rays rarely fewer than 20 (never < 16), usually 23 or more; branches on ventralmost ray

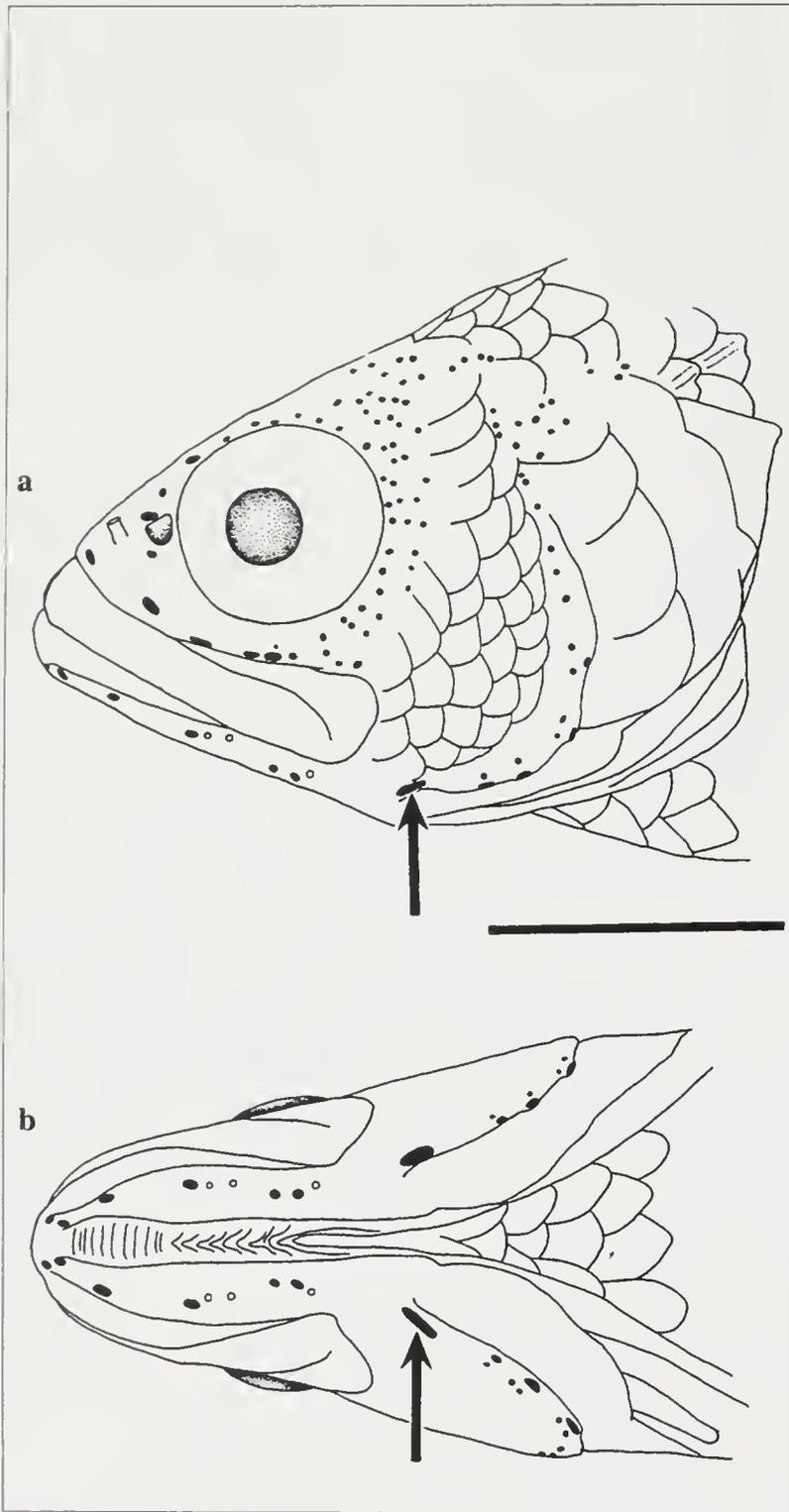


FIG. 6a–b. *Plesiops gracilis*. Cephalic sensory pores of paratype CAS 13985, 60.1 mm. Pores in black. Arrow points to enlarged pore at anteroventral end of preopercular series. This specimen possesses the highest number of dentary pores recorded for this species; pores not normally found on other specimens are indicated as open circles. From Mooi and Randall (1991:376, fig. 2). Scale bar = 10 mm.

a. Left lateral view
b. Ventral view.

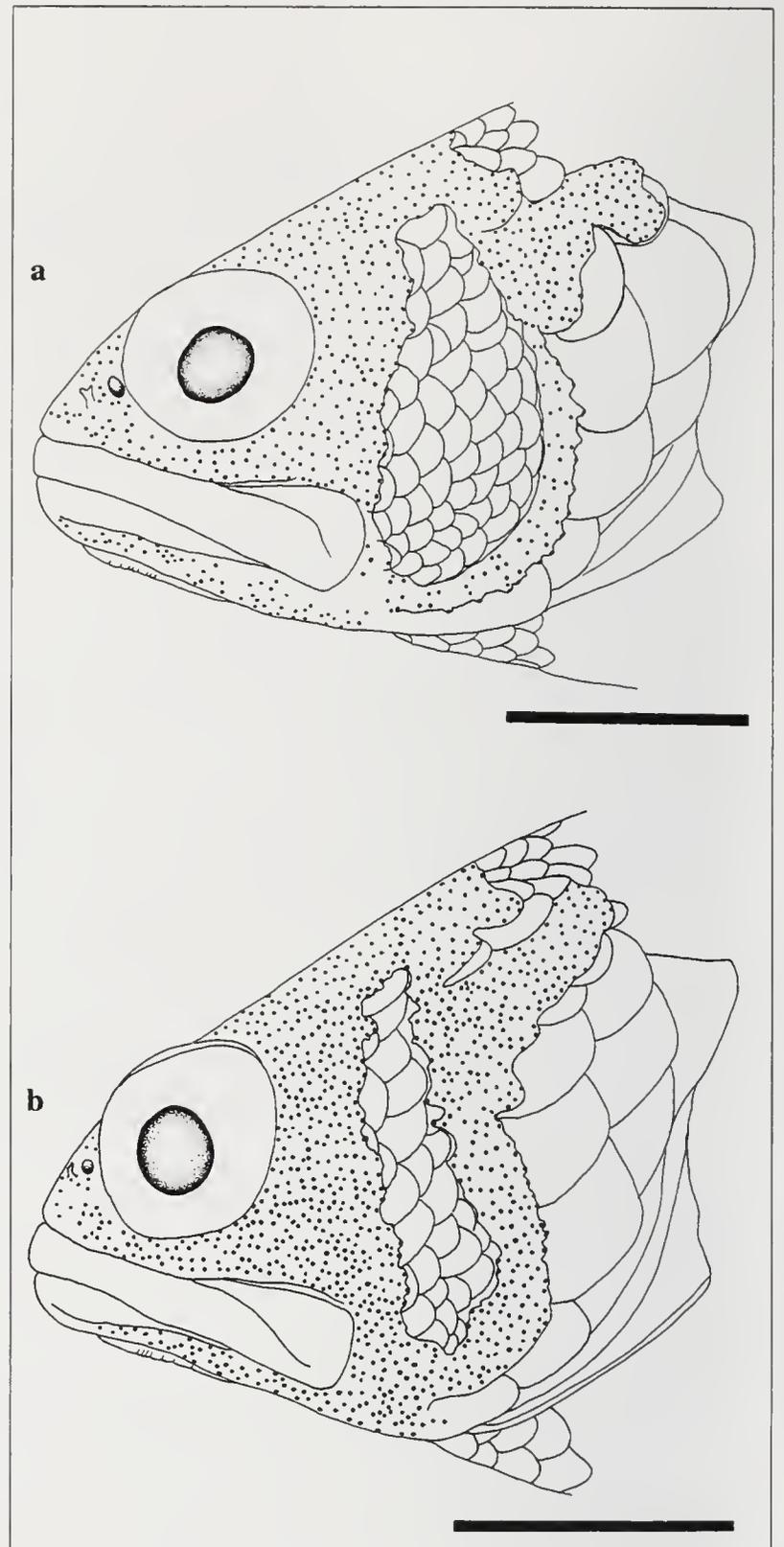


FIG. 7a–b. *Plesiops*. Left lateral view of the cephalic sensory pores of two similar species. Note the large number of pores posterior to the maxilla that make the suborbital, preopercular, and dentary series continuous and the fewer visible cheek scales in (b) compared with (a). From Mooi and Randall (1991:380, fig. 5). Scale bars = 10 mm.

a. *P. insularis*, paratype AMS I.17363-004, 76.5 mm.
b. *P. genaricus*, paratype USNM 274570, 70.3 mm.

- 3 or more (rarely 2); with or without pale central spots on body scales **14**
- 14a. Pale central spots on body scales, spots blue in life; in life, head mottled with blue spots less than pupil diameter, preserved specimens lose pale head spots and replace them with 4–5 preopercular spots and occasionally a small spot on ventral opercle (west coast of Honshu and Shikoku) *nakaharai*, p. 46
- 14b. No pale spots on body scales; no blue mottling on head in life and/or no preopercular spots ... **15**
- 15a. Spot on pectoral-fin base (sometimes obscure); adductor mandibulae with a sheet of fibres originating from cranium (sphenotic and pterotic) ..
..... **16**
- 15b. No spot on pectoral-fin base; adductor mandibulae without a sheet of fibres originating from cranium (Madagascar)
..... *malalaxus* sp. nov., p. 40
- 16a. Skin bearing pore series posterior to eye and on skin of preopercle not expanded (Fig. 7a); cheek scale rows 5 (4–6), visible as far anteriorly as posterior tip of maxilla; few sensory pores immediately posterior to tip of maxilla, suborbital sensory pore series not continuous with those of preopercle or dentary (Fig. 7a); dentary pore:SL ratio generally < 1, averaging 0.76 (Chesterfield Is., New Caledonia, Norfolk Is., Lord Howe Is., Elizabeth and Middleton Reefs)
..... *insularis*, p. 37
- 16b. Skin bearing pore series posterior to eye and on skin of preopercle expanded, resulting in a smaller area of visible cheek scales (Fig. 7b); cheek scale rows 4 (3–5), not visible as far anteriorly as posterior tip of maxilla; many sensory pores present immediately posterior to maxilla, resulting in a continuous preopercular, dentary, and suborbital pore series (Fig. 7b); dentary pore:SL ratio > 1 in specimens greater than 40 mm, averaging 1.8 (Great Barrier Reef)
..... *genaricus*, p. 31

Species Descriptions

Plesiops auritus sp. nov.

Figs. 8, 9; Tables 1–5

Plesiops sp. 1—Mooi, 1993:286.

TYPE MATERIAL

Holotype. USNM 295539, ♂ 73.8, Sri Lanka, Weligami, 180 m offshore from resthouse (E of resthouse), rotenone, 0.5–3 m, C. C. Koenig, 14 Feb. 1970.

Paratypes. 57 specimens, 29.5–75.9—INDONESIA: ANSP 166921, ♀? 41.0, ♂ 58.5, Mentawai Is., Pulo Mega, 04°01' S, 101°01'30" E, 0.3–2.0 m. SRI LANKA: ROM 60180, 6♀:53.4–65.5, 6♂:59.8–68.5, Galli, coral heads SE end of bay, 6–10 m, C. C. Koenig, 16 Feb. 1970; USNM 274552, 7♀:46.7–61.0, 8♂:37.8–75.9, 4?:33.6–46.0, 450 m S of resthouse, 4–6 m, C. C. Koenig, 15 Feb. 1970; USNM 274556, ♀ 62.3, ♂ 60.6, 2?:42.4–55.4, Hikkaduwa, 1 km offshore, 1.5 km S of resthouse, 12 m, C. C. Koenig, 13 Feb. 1970; USNM 295538, ♀ 51.1, ♂ 61.1, 450 m S of resthouse, 4–6 m, C. C. Koenig, 15 Feb. 1970; USNM 295540, ♀ 50.7, ♂ 61.2, ? 55.3, Eastern Province, Batticaloa District, Korali Pattu, Passakuday Bay, reef 450 m NE of outlet of small stream over which a low bridge passes on road to coconut estate, 7°56' N, 81°34' E, 6–8 m, T. Iwamoto, 10 Jan. 1970; USNM 295545, 3♀:40.5–49.9, Hikkaduwa, 1.5 km S of coral gardens, 1.5 km offshore, C. C. Koenig, 12 Feb. 1970; USNM 295550, ♂ 45.5, Hikkaduwa, 1.5 km N of resthouse, 1.5 km offshore, 15 m, C. C. Koenig, 13 Feb. 1970; USNM 295549, ♂ 46.6, Batticaloa District, Korali Pattu, Kalkuda Bay, 7°54'54" N, 81°34'30" E, 2–3 m, T. Iwamoto, 6 Jan. 1970; USNM 313025, 4♀:51.6–65.0, 3♂:29.5–71.8, collected with holotype. THAILAND: BPBM 22790, 2:42.7–58.9, Andaman Sea, Similan Is., Ko Miang Is. (NW of Phuket), N side of rocky shore grading to coral and sand, 0–2 m, rotenone, J. E. Randall, G. R. Allen, R. Steene, Pitiwong Tantichodok, and Anawat Nateewathana, 14 Feb. 1979; BPBM 28697, ♂ 44.2, Phuket Is., Laem Sai off Kata Beach, large *Porites* boulders and scattered small corals, 3 m, rotenone, R. Lubbock and N. Polunin, 20 Mar. 1977.

ADDITIONAL MATERIAL EXAMINED

4 specimens, 28.5–59.3—INDONESIA: USNM 295530 (♀ 59.3) Scribu Is., 313021 (♂ 52.4) Bawean Is. SRI LANKA, Weligami: ANSP 166920 (2♂:28.5–32.5).

DIAGNOSIS

Dark spot of about eye diameter on opercle just posterior to dorsal tip of preopercle and a second but usually less obvious spot on ventral portion of opercle; pectoral-fin

rays 26 (25–27); number of free pectoral-fin rays 11 (10–14); cheek scale rows 3; predorsal scale rows 5 (4–6); relatively few sensory pores on head, dentary pore:SL ratio 0.44–1.1, average 0.76.

DESCRIPTION

Meristic and morphometric data based on 58 type specimens (29.5–75.9).

Fins. Dorsal-fin spines, rays XII,7; longest dorsal-fin ray 5th; anal-fin spines, rays III,8; longest anal-fin ray 6th; pectoral-fin rays 27 left, 26 right (26; 25–27); total number of branches of lower 6 pectoral-fin rays 13 left, 12 right (12; 11–19); ventralmost ray branches 2 (2; 1–2, rarely 3); pectoral fins with ventralmost rays free of membrane to form a fringe, number of free pectoral-fin rays 12 left, 14 right (11; 10–14, rarely 8); pelvic-fin spines, rays I,4; first pelvic-fin ray elongate but relatively short for *Plesiops*, and noticeably thickened, first pelvic-fin ray extends to 2nd anal-fin ray (1st–8th); principal caudal-fin rays (upper + lower) 9 + 9 (10 + 9; 8–11 + 7–10); procurent caudal-fin rays (upper + lower) 6 + 5 (5 + 5; 3–6 + 4–6).

Gill rakers. Upper + lower 3 + 9 (4 + 9; 3–5 + 8–13); total 12 (13; 11–16).

Scales. Body scales always closed-centred. Lateral-line scales with simple tube, no midposterior fleshy flap or lobe on upper line, a midposterior notch on lower line. Often small pores present along margins of tube. Upper lateral-line scales 19 (19; 18–20); lower lateral-line scales 14 (14; 10–16); midlateral series 24, rarely 23; scales above upper lateral line to origin of dorsal fin 3 (2; 2–3); scales below upper lateral line to origin of anal fin 9 (9; 8–9); predorsal scale rows 5 (5; 4–6); cheek scale rows 3 (3; 2–3); circumpeduncular scales 16; primary anterior pore of each upper lateral-line scale covered by preceding scale, except occasionally the last; all lower lateral-line scales with anterior pores uncovered; first ctenoid upper lateral-line scale 7th (7th; 4th–12th); first ctenoid scale below upper lateral line 3rd (3rd; 2nd–7th). Anterior body scales cycloid, but becoming ctenoid further anteriorly than in most other members of the genus, i.e., ahead of the pectoral- and pelvic-fin bases. Cheek scales visible anteriorly to the posterior tip of maxilla.

Cephalic sensory pores. Small and quite numerous. Dentary pore number varies with SL and ranges from 12 to 83 (holotype 70), and forms a ratio with SL of usually < 1 (\bar{x} = 0.76, range = 0.44–1.1, holotype 0.95). Pores present posterior to maxilla, but preopercular, dentary and suborbital pore series remain separate and distinct.

General morphology. As percentage of SL: body depth at anal-fin origin 29 (29; 25–31); body width at pectoral-fin base 20 (18; 15–21); caudal-peduncle length 20 (19;

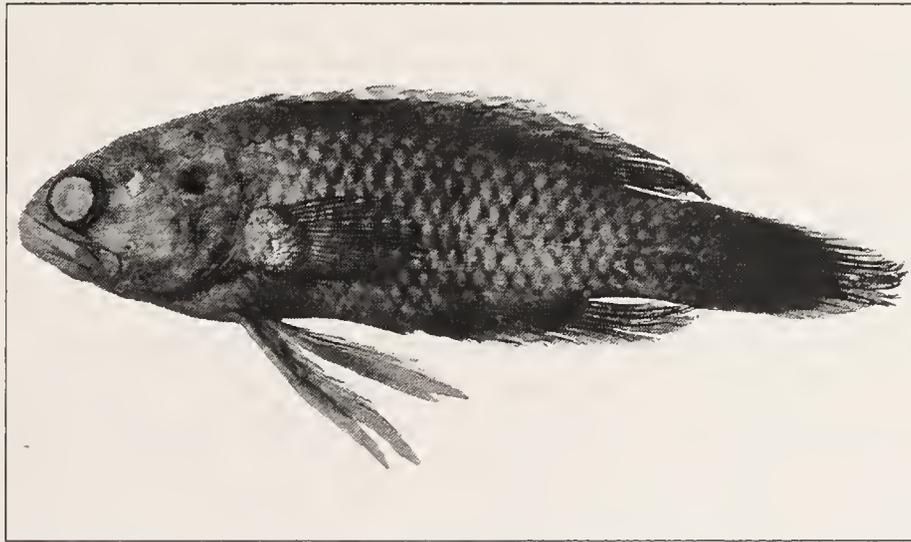


FIG. 8. *Plesiops auritus* sp. nov. Holotype USNM 295539, ♂, 73.8 mm, Sri Lanka.

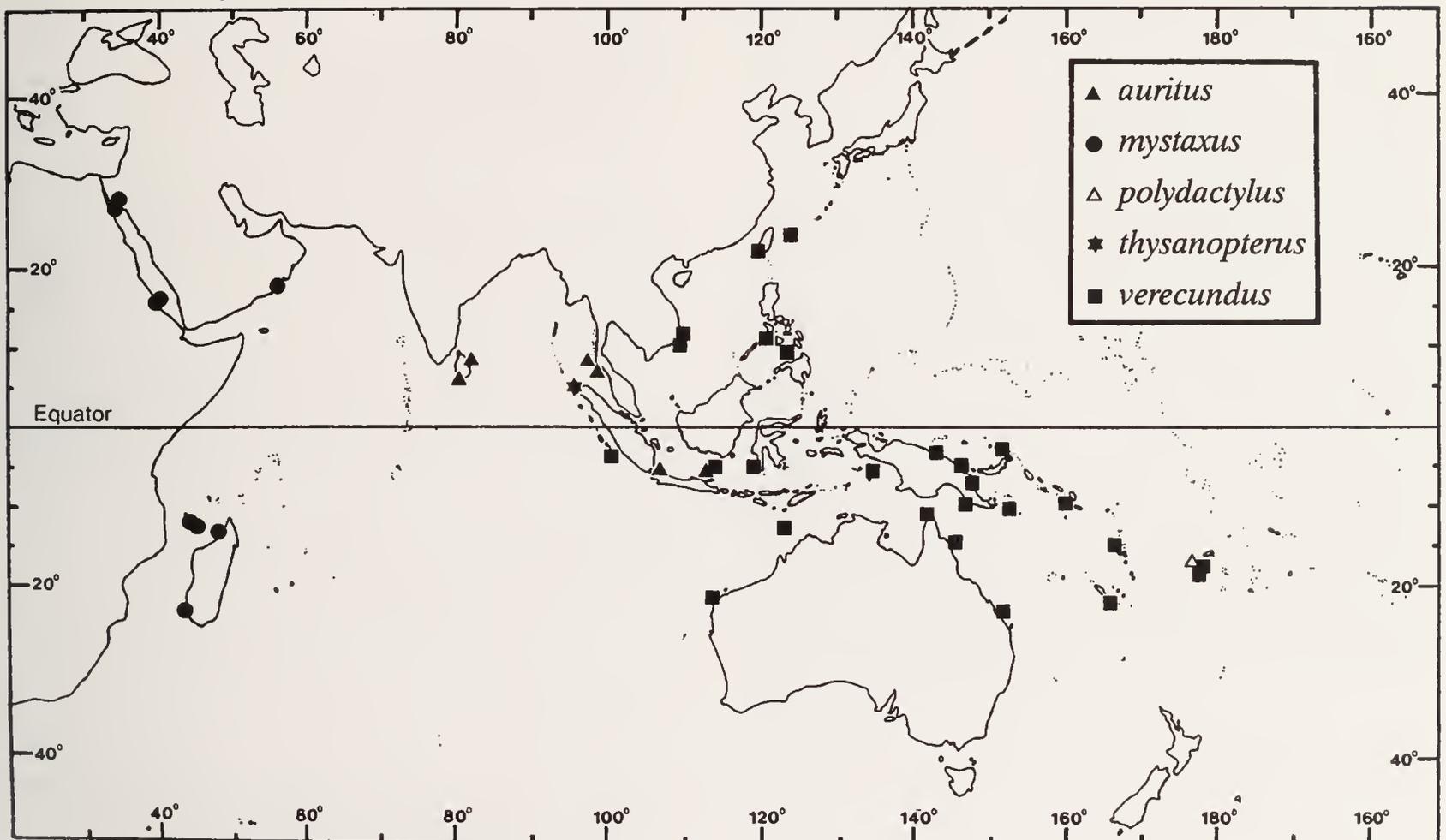


FIG. 9. Distribution of five species of *Plesiops*.

17–22); caudal-peduncle depth 15 (14; 13–16); predorsal length 37 (38; 36–40); preanal length 63 (63; 58–66); pre-pelvic length 35 (35; 32–39); dorsal-fin base 54 (53; 43–56); longest dorsal-fin ray 21 (22; 18–26); anal-fin base 21 (21; 17–25); longest anal-fin ray 21 (22; 19–27); pectoral-fin length 25 (25; 23–27); pelvic-fin length 36 (40; 32–46); head length 38 (39; 36–42).

Head. Rounded. Maxilla extends to or beyond posterior margin of orbit. Bony interorbital narrow. As percentage of HL: snout length 18 (17; 15–21); upper-jaw length 46 (46; 43–53); bony-interorbital width 8 (8; 5–10); pos-

terior internasal width 16 (15; 13–17); orbital diameter 28 (30; 25–33); head depth at posterior margin of orbit 56 (53; 50–61); head depth at posterior margin of preopercle 76 (71; 63–78); head width at dorsal tip of preopercle 57 (54; 49–61).

Osteology and myology. Dorsal formula 0/0/2/1+1/1; epurals 3, occasionally 2; epaxial musculature extends onto frontals anterior to sphenotic, lateral muscle bundles in advance of dorsal (medial), the latter not reaching frontals; adductor mandibulae with an additional thick sheet of fibres originating from sphenotic and pterotic, as

well as usual main body originating from posterior part of suspensorium.

Colour when fresh. From slide of BPBM 22790, 58.9 mm, Thailand. Body pale brownish-grey with scattered darker scales anteriorly, on peduncle darker scales form 3 incomplete bands; nape and anterior part of head darker, upper lip with 2 paler bands; posterior to eye, 2 short, dark stripes, 1 posterodorsal, the other posteroventral, and a narrow stripe running from the ventral edge of orbit parallel to the maxilla, ending dorsal to its posterior tip; trace of a dark spot just posterior to the dorsal tip of the preopercle; posterior part of cheek, interopercle, subopercle, and opercle washed with yellow, scattered scales in this region retaining a dark base; branchiostegal membranes grey; dorsal-fin spines with pale tips; dorsal fin otherwise dark with a blue median stripe running from the first spine to the 4th soft ray; above the blue stripe, a faint dark reddish "stripe" from about the 4th spine to near the tip of the 5th ray, interrupted anteriorly by the incised membrane of the spinous portion of the fin; anal fin similar to dorsal, dark with blue median stripe running to about 4th soft ray, with a faint reddish stripe distal to it; caudal fin dark with pale base; pectoral fins dark; pelvic fins pale with dark chevrons or stripes on membranes; iris of eye red directly around pupil, bluish on periphery.

Colour of holotype (in ethanol). See Fig. 8. Body pale brown or sepia, scales with darker posterior margins giving body a spotted appearance; posterior caudal peduncle scales darker than those on body; head light brown, interorbital region darkest; 2 dark splotches behind eye, 1 posterodorsal and 1 posteroventral, and a thin dark line running posteriorly from the midventral eye margin parallel to maxilla and ending slightly beyond posterior end of maxilla; dark spot of about eye diameter on dorsal part of opercle, just posterior to dorsal tip of preopercle; a smaller and less obvious dark mark on ventral part of opercle; branchiostegal membranes dark, particularly ventrally; no spot on scales of pectoral-fin base; dorsal fin black, tips of dorsal-fin spines paler but dusky, fleshy posterior portion light-coloured; soft portion of dorsal fin black with narrow light margin; anal-fin spines and rays black, spines with lighter tips; caudal black; pectoral fins dark; pelvic fins dusky grey. Paratypes similar to holotype, differing in the following ways: dorsal opercular spot usually more obvious; lower opercular spot often absent; caudal peduncle with 2 or 3 series of dark, elongate spots in bands, each "band" with 3–6 spots; 1 paratype with only 2 caudal peduncle spots, 1 below lower lateral line and the other above lower lateral line at hypural bases; some smaller specimens with 7 dark bands on body including 3 on caudal peduncle; on adult specimens, dark scale margins produce a reticulated pattern on body; scattered dark scales on cheek sometimes retained.

DISTRIBUTION AND HABITAT

This species is known only from Sri Lanka to the west coast of the Malaysian Peninsula near Phuket, and south along the western coast of Sumatra to north of Java (Fig. 9). Found in collections made in coral heads, on reefs or in rocky areas, to depths of 15 m but usually shallower.

COMPARISONS

This species is most similar to *P. thysanopterus* which likely has an overlapping distribution (known from only one locality; Fig. 9), but the latter has more pectoral-fin rays (28–30 vs. 25–27), more dentary pores (dentary pore:SL ratio > 1.0 vs. ratio usually < 1.0), and is much darker, without spots on the body or head nor pale tips to spines of the dorsal fin. *P. polydactylus*, known only from Fiji, has a similarly high pectoral-fin ray count (26–28) and low predorsal scale row count, but can be distinguished by having only 11 dorsal-fin spines (vs. 12), a single supernumerary spine on the first dorsal-fin pterygiophore (vs. 2), and usually a higher number of gill rakers on the first arch (13–18 vs. 11–14, rarely 16). Otherwise, *P. auritus* can be distinguished from all other members of the genus by its high number of pectoral-fin rays, few predorsal scales, and a dorsal opercular spot.

BIOLOGICAL REMARKS

Of the 62 specimens available, 51 were assigned a sex; 25 were females and 26 were males. This is not significantly different from a 1:1 sex ratio ($G = 0.020$, $0.75 < p < 0.90$). The size range of females was 40.0–65.5 mm, and the largest individual available, at 75.9 mm, was male. However, a number of females exceeded 60 mm SL, and it seems likely that the maximum size attainable is similar for both sexes. Specimens have been collected in only four months of the year, January, February, March, and April; gravid females were found only in February and April collections.

ETYMOLOGY

This species possesses a dark spot at the upper edge of the opercle and appears eared, hence the Latin for eared, "auritus" (to be treated as a noun in apposition).

Plesiops cephalotaenia Inger, 1955

Figs. 10, 11; Tables 1–5

Plesiops cephalotaenia Inger, 1955:272, figs. 1b, 4.—
Munro, 1967:283; Sano et al., 1984:15, Pl. 6c; Masuda et al., 1984:141, pl. 125L; Mooi, 1990:fig. 5a.

Plesiops corallicola (non Bleeker, 1853c)—Masuda, Araga, and Yoshino, 1975:224, pl. 53C.

Plesiops corallicola—Masuda, Araga, and Yoshino, 1975:pl. 53C (caption).

TYPE MATERIAL

Holotype. FMNH 44708, ♀ 49.5, Philippine Is., Sulu Archipelago, Sitankai, A. W. Herre, 1931.

Paratypes. 19 specimens, 23.1–52.8—INDONESIA: USNM 162704, 2♂:41.1–42.3, Tomahu Is., Bouro [Buru], Moluccas, “Albatross,” 12 Dec. 1909. PAPUA NEW GUINEA: USNM 123384, ♂ 43.2, Tanamera Bay (N coast of N.G.), Lt. O. Barton USNR, Dec. 1909. PHILIPPINES: FMNH 47293, 3♂:26.6–52.8, Sitankai, A. W. Herre, 1931; USNM 146460, 36.1, Rapu Rapu Is., Luzon, “Albatross,” 22 June 1909; USNM 146462, 31.7, Mantacao Is., Bohol west coast, “Albatross,” 8 April 1908; USNM 146464, 44.7, San Miguel Is., “Albatross,” 21 April 1908; USNM 146466, ♀ 35.5, 6?:23.1–52.4, Cataingan Bay, Masbate, “Albatross,” 18 April 1908; USNM 146467, ♂ 43.3, Maculabo Is., Luzon, “Albatross,” 14 June 1909; USNM 146469, ♂ 36.4, Sitankai Reef (stated locality as Borneo on cat. label, but is officially Philippines territory), 24 Sept. 1909; USNM 151323, 35.8, Tara Is., “Albatross,” 15 Dec. 1908.

ADDITIONAL MATERIAL EXAMINED

40 specimens, 13.7–62.1—INDONESIA: CAS 62495 (20.0) Flores; USNM 209674 (♀ 37.8, 2♂:30.3–39.0, ? 27.8) Ceram, 210278 (? 28.2) Ambon, 245698 (♂ 37.8) Irian Jaya, 274544 (2♀:36.0–41.5, ♂ 38.2) Moluccas, 299026 (2♂:35.5–42.1) Kabaena Is., Sulawesi, 299028 (♀ 32.8) Ceram, 299030 (♀ 36.3, 2♂:27.4–34.2) Indonesia. JAPAN, Ryukyu Is.: BPBM 19106 (2♂:22.3–53.3); IORD 76-439 (♂ 41.3), 83-231 (♀ 40.4), 83-232 (♀ 36.7, ♂ 32.2, ? 13.7), 83-233 (♂ 46.2), 83-253 (♂ 42.9). PAPUA NEW GUINEA: AMS I.17089-048 (♀ 38.9) Madang Harbour; ANSP 157375 (20.3), Keraward Is., 157395 (♀? 30.7) Bougainville; CAS 65926 (40.1) Masas (Little Pig) Is.; USNM 299032 (♀ 43.4, ♂ 29.9) Hermit Is. PHILIPPINES: BPBM 11661 (2♂?:45.8–53.4) Sitankai; CAS SU28523 (♂ 62.1) Sitankai; ROM 1325CS (55.7) Siquijor Is., 60202 (♀ 49.3) Siquijor Is.; UMMZ 100294 (3♂:28.6–59.4) Sitankai; USNM 313014 (♀ 33.6) Bararin Is. SOLOMON Is.: BPBM 1201 (23.8) Shortland Is.; CAS 65919 (43.3) Nagada Harbour.

DIAGNOSIS

Twelve dorsal-fin spines with light tips when in ethanol, pale yellow in life; 6–8 (rarely 9) predorsal scale rows; cheek scales 3–4; last 3–11 upper lateral-line scales with primary anterior pore uncovered; pectoral-fin rays 18–20; fewer than 20 total branches on 6 ventralmost pectoral-fin rays; usually 8–9 longitudinal stripes on body, becoming about 7 between soft portions of anal and dorsal fins, and 5 on caudal peduncle; no spots in membranes of anal, dorsal or caudal fins; no dark dorsal margin to maxilla; usually more than 7 dentary pores, and anteroventral preopercular pore not enlarged.

DESCRIPTION

Morphometric and meristic data based on 58 specimens (13.7–62.1), including all type material.

Fins. Dorsal-fin spines, rays XII,7 (XII,7; XI(once)–XII,6–7); longest dorsal-fin ray (5th; 4th–6th); anal-fin spines, rays III,8 (III,8; III,7–10, extremes occurred only once); longest anal-fin ray (6th; 4th–6th); pectoral-fin rays 19 (19; 18–20); total number of branches of lower 6 pectoral-fin rays (10–14; fewer than 15–19); ventralmost ray branches (1; 1–2); pectoral fins with ventralmost rays usually not free of membrane, usually no free pectoral-fin rays, occasionally 4 or 5 free; pelvic-fin spines, rays I,4; first pelvic-fin ray elongate, but not always noticeably thickened, first pelvic-fin ray extends to (past 8th anal ray; 1st–past 8th); principal caudal-fin rays (upper + lower) 10 + 9 (10 + 9; 9–10 + 7–10); procurent caudal-fin rays (upper + lower) 4 + 4 (5 + 5; 4–6 + 3–6).

Gill rakers. Upper + lower 4 + 10 left, 4 + 11 right (4 + 10; 3–5 + 8–13); total 14 left, 15 right (14; 11–17).

Scales. Body scales open- or closed-centred. Lateral-line scales with simple tube, with or without a midposterior flap or lobe on upper line, a midposterior notch on lower line. Often small pores present along margins of tube. Upper lateral-line scales 20 (19; 18–20); lower lateral-line scales 12 (12; 7–13); midlateral series 24 (24; 23–25); scales above upper lateral line to origin of dorsal fin 3 (3; 2–4); scales below upper lateral line to origin of anal fin 9 (9; 8–10); predorsal scale rows 6 (7; 6–8, once 9); cheek scale rows 3 (4; 3–4); circumpeduncular scales 16; number of upper lateral-line scales with anterior pore not covered by preceding scale 7 (8; 3–11); all lower lateral-line scales with anterior pores uncovered; first ctenoid upper lateral-line scale 8th (9th; 6th–13th); first ctenoid scale below upper lateral line 6th (6th; 4th–8th). Cheek scales visible anteriorly to the posterior tip of maxilla.

Cephalic sensory pores. Always small, but number varies with SL. Dentary pore number ranges from 5 to 23 (holotype 23), and forms a ratio with SL of $\ll 1$ ($\bar{x} = 0.26$, range = 0.12–0.46, holotype 0.46).

General morphology. As percentage of SL: body depth at anal-fin origin 36 (32; 29–37); body width at pectoral-fin base 20 (18; 11–22); caudal-peduncle length 18 (17; 15–20); caudal-peduncle depth 16 (15; 14–17); predorsal length 40 (40; 37–44); preanal length 66 (66; 60–70); pre-pelvic length 33 (36; 33–40); dorsal-fin base 55 (54; 50–58); longest dorsal-fin ray (26; 21–30); anal-fin base 20 (21; 18–24); longest anal-fin ray (26; 21–33); pectoral-fin length (29; 23–34); pelvic-fin length (48; 38–57); head length 38 (40; 38–44).

Head. Rounded. Maxilla extends to or beyond posterior margin of orbit. As percentage of HL: snout length 17 (19; 15–23); upper-jaw length 49 (48; 42–53); bony-

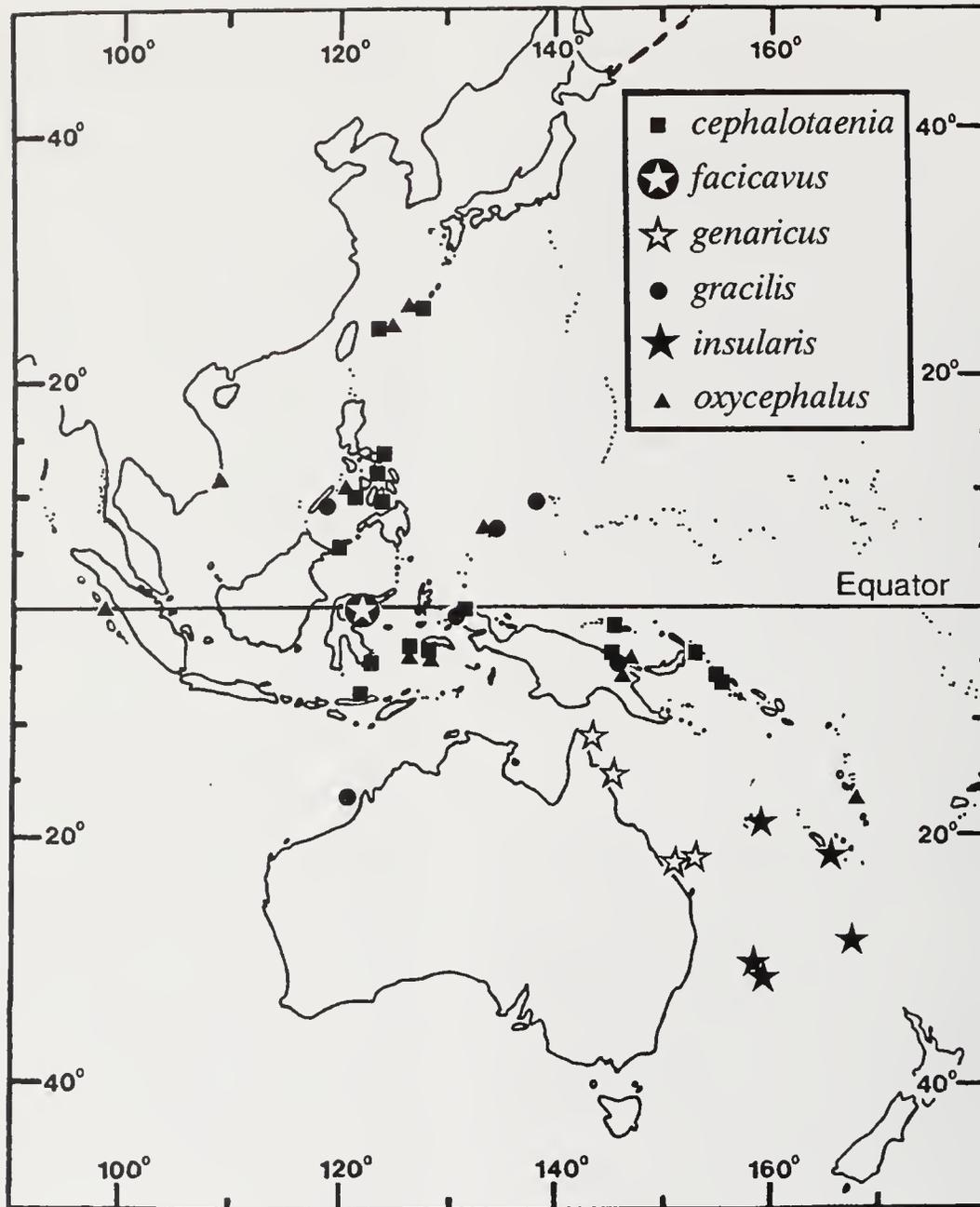


FIG. 10. Distribution of six species of *Plesiops*.



FIG. 11. *Plesiops cephalotaenia*. IOP 2739, 53.0 mm TL, Ryukyu Islands. From colour slide by H. Senou.

interorbital width 6 (7; 5–8); posterior internasal width 12 (13; 10–16); orbital diameter 35 (35; 31–44); head depth at posterior margin of orbit 64 (64; 59–72); head depth at posterior margin of preopercle 85 (77; 70–86); head width at dorsal tip of preopercle 61 (51; 35–64).

Osteology and myology. Dorsal formula 0/0/2/1+1/1, once 0/0/1/1+1/1 (but deformed); epurals 2 (2; 2–3); epaxial musculature extends onto frontals anterior to sphenotic, dorsal (medial) muscle bundles in advance of lateral fibres; adductor mandibulae with an additional thick sheet of fibres originating from sphenotic and pterotic, as well as usual main body originating from posterior suspensorium.

Colour when fresh. From slide of IOP 2739, Fig. 11. Body black with 9 pale longitudinal stripes, 7 such stripes between the soft portions of the dorsal and anal fins, and 5 stripes on the caudal peduncle; head sepia; 2 dark oblique bars extending from eye to edge of preopercle, one posterdorsal and the other posteroventral to eye, both continuing onto opercle; narrower stripe running from midventral margin of eye to just beyond posterior tip of maxilla; a series of 4 white spots on preopercle, 1 on subopercle; dorsal fin sepia with wide pale stripe running medially through fin to last spine; tips of dorsal-fin spines pale, white proximally and yellow most distally; soft portion of dorsal fin dark brown; anal fin brown, spine tips pale; caudal fin dark brown; pectoral fins dark; pelvic fins pale sepia with dark brown spots.

A photograph in Masuda, Araga, and Yoshino (1975, pl. 53C), labelled *P. corallidora* [sic], is *P. cephalotaenia* (Sano et al., 1984). This specimen has a sepia body with a similar longitudinal stripe pattern as that described above; head dark sepia dorsally, becoming white abruptly on subopercle and ventral part of preopercle; eye with red iris immediately around pupil, then blue peripherally; bar and stripe pattern behind eye similar to above, ventral part of opercle with apparent continuation of posteroventral eye bar, producing a dark spot (but not ocellus); cheek with small area of orange-yellow; branchiostegals copper-yellow proximally and dark brown distally; gular region copper-yellow; maxilla pale; dorsal fin brown with paler median stripe running from base of first spine up to middle of 5th ray; dorsal-fin spine tips pale, white proximally and pale yellow distally; anal fin brown with median paler region to 4th ray, spine tips pale; caudal fin yellow-copper; pectoral fin dark; pelvic fins dark proximally, with yellow tips.

Colour notes on the label data of BPBM 19106, collected on the north side of Sesoko Island, Ryukyus Islands: "Brown with narrow gray stripes; yellowish over cheek; branchiostegal membranes yellow, shading outwardly to gray; D spine tips yellow; C fin yellowish brown. Iris blue with inner edge above and below yellow."

Colour of holotype (in ethanol). Body uniform red-brown with trace of about 6 lighter longitudinal stripes running from behind opercle to caudal-fin base; head with 2 dark bars, one posterdorsal and one posteroventral to eye, and narrow dark stripe running from midventral eye just dorsal to maxilla and ending at posterior tip of maxilla; dorsal and anal fins uniformly dark red-brown; caudal and pectoral fins dark; pelvic fins dark with spotted pattern. Paratypes similar to holotype, but body stripes sometimes absent, and pelvic fins either uniformly dark or with chevron pattern. Non-type material with body stripes variously obvious to inconspicuous depending on darkness of background colour, usually 9 such stripes on body, 7 between soft portions of dorsal and anal fins, and 5 on caudal peduncle; head as in holotype, posteroventral bar becoming a dark spot on lower part of opercle; sometimes with pale cheek and branchiostegal membranes; dorsal fin dark with light tips to spines; anal, caudal, and pectoral fins dark; pelvic fins usually spotted or with chevron pattern.

DISTRIBUTION AND HABITAT

Ryukyu Islands south to Flores, and east to the Solomon Islands (Fig. 10). This species is found at depths of 12 m or less in dead coral, reef flats, and on coral heads—habitats with somewhat less wave energy than inhabited by other members of the genus.

COMPARISONS

This species is most similar to *P. gracilis*, *P. facicavus*, and *P. oxycephalus*, all of which have overlapping distributions (Fig. 10). It can be distinguished from the former 2 species by the number of predorsal scale rows (6–8 vs. 9–11), usually more dentary pores (7–23 vs. 5–7), and fewer cheek scale rows (3–4 vs. 4–5). *P. cephalotaenia* also has a rounder head profile whereas *P. gracilis* has a pointed head. *P. facicavus* is unique among *Plesiops* species in having the anterior part of the head densely dotted by small brown speckles. *P. oxycephalus* has spots on the body rather than stripes (when a pattern is visible), has more predorsal scale rows (8–11 vs. 6–8) and cheek scale rows (4–5 vs. 3–4), and has fewer uncovered anterior pores in the upper lateral line (0–3 vs. 3–11). Other members of the genus rarely have 20 or fewer pectoral-fin rays, never have longitudinal body stripes, and always have fewer uncovered anterior pores in the upper lateral line.

BIOLOGICAL REMARKS

Of 35 specimens for which a sex could be determined, 23 were male and 12 were female. This apparent 2:1 sex ratio is not significantly different from 1:1 ($G = 3.50$, $0.05 < p < 0.10$). Females ranged from 30.7–49.3 mm, and gravid females were found in the months of January, March, May, and November. The largest male examined

was 62.1 mm. No secondary sexual characters were noted in this species.

ETYMOLOGY

Inger (1955) apparently named this species for the pattern of head stripes, hence the combination of "cephalo" (head) and "taenia" (stripes), which he incorrectly believed was diagnostic for the species.

Plesiops coeruleolineatus Rüppell, 1835

Figs. 12, 13a–b, 14; Tables 1–9

- Plesiops coeruleo-lineatus* Rüppell, 1835:5, pl. 2 (fig. 5).
Plesiops melas Bleeker, 1849:9.—Snyder, 1912:498; Weber and de Beaufort, 1929:378, fig. 91; Fowler, 1931:332; Fowler, 1932:8–9; Aoyagi, 1941:428; Smith, 1949:187; Marshall, 1950:175; Schultz et al., 1953:400; Palmer, 1970:224.
Plesiops coeruleolineatus—Bleeker, 1853a:116; Klunzinger, 1871:517; Inger, 1955:270, figs. 2a, 3a; Schultz, Woods, and Lachner, 1966:163; Munro, 1967:283, pl. 35; Masuda, Araga, and Yoshino, 1975:224, pl. 53A; Grant, 1982:254, pl. 124; Masuda et al., 1984:140, pl. 126I; Sano et al., 1984:17, pl. 7a; Shen, 1984:45, pl. 294–1a,b; Smith and Heemstra, 1986:543; Masuda and Allen, 1987:136; Leis and Trnski, 1989:204, fig. 45; de la Paz, Aragonés, and Agulto, 1988:252, fig. 23; Mooi, 1990:458, table 2; Mooi, 1993:figs. 5, 10, 14, 16, 17, 22–24.
Plesiops caeruleo-lineatus—Günther, 1861:363.
Plesiops nigricans var. *apoda* Kner, 1868:346.
Plesiops nigricans (non Rüppell, 1828)—Bleeker, 1875:27 [in part]; Boulenger, 1895:340 [in part]; Fowler, 1928:188 [in part]; Fowler and Bean, 1930:313 [in part]; Vivien, 1973:235, 294.
Pharopteryx melas—Jordan and Seale, 1906:261, pl. 38 (fig. 3).
Plesiops semeion Tanaka, 1917:200.—Mito, 1955:95–99.
Pharopteryx semeion—Tanaka, 1918 and 1935 (2nd ed.):500, pl. 137 (fig. 382).
Plesiops corallicola (non Bleeker, 1853c)—Shen, 1984:45, pl. 294–2.
Pseudochromichthys riukianus Schmidt, 1931:180, fig. 1.
Plesiops caeruleolineatus—Fourmanoir, 1957:247; Smith, 1952:143, fig. 1 [in part, lapsus]; Smith, 1961:187; Rofen, 1958:168; Jones and Kumaran, 1980:233; Dor, 1984:107; Myers, 1989:113.

TYPE MATERIAL

Holotype. SMF 1696, ♀ 44.2, Red Sea, Massaua (= Massawa, Ethiopia, 15°37' N, 39°28' E), E. Rüppell, December (1834?).

ADDITIONAL MATERIAL EXAMINED

1869 specimens, 9.1–69.5—ALDABRA: USNM 264168 (60+:15.0–53.4) Picard Is. AMERICAN SAMOA: ANSP 151648 (12♀:28.7–40.3, 16♂:19.7–48.2) Apia, 157392 (12:12.4–26.8) Tuitila Is.; FMNH 4768 (45:19.1–43.5) Apia. AUSTRALIA: AMS I.20755-007 (2:15.0–39.0) Cape Melville, I.21260-002 (59.2) Cape Tribulation, I.21315-023 (2♂:33.9–36.7, 2?:19.8–25.8) Timor Sea, I.22628-013 (2:42.8–44.9) Escape Reef North, I.26748-004 (5♀:32.4–40.9, 10♂:22.9–52.2) Timor Sea, I.26750-010 (5♂:40.2–49.3) Timor Sea; ANSP 134697 (38:14.9–51.1) Cocos-Keeling Is., 134707 (4♀:25.4–42.5, 28♂:20.5–53.0) Cocos-Keeling Is.; CAS 13777 (8♀:34.5–38.9, 12♂:31.0–50.4, 46?:10.0–26.5 mm) One Tree Is.; USNM 299033 (12♀:32.9–43.5, 10♂:32.6–49.8, 9?:20.5–26.2) One Tree Is. CAROLINE ISLANDS: CAS 38837 (♂ 37.7) Ulithi Atoll, 57656 (21.0) Ifaluk Atoll, 67843 (4:41.0–51.0) Kapingamarangi Atoll, 67849 (59:13.6–51.0) Ifaluk Atoll, 67850 (23:21.0–44.0) Ifaluk Atoll, 67855 (7:42.9–52.5) Kapingamarangi Atoll; NSMT 22914 (48.4) Truk, 41153 (♀ 32.6, ♂ 42.4) Pohnpei, 44987 (2) Truk, 44996 (72:11.5–45.0) Pohnpei; USNM 154384, Yap Is., 224315 (4♀:31.8–37.8, 6♂:31.3–38.8, 38?:14.4–30.0) Pohnpei. COMORES: ROM 58402 (2♀:31.5–31.6, 8♂:36.0–42.0, 15?:9.9–13.1) Isle Malandzamiayatsini, 58403 (4♀:32.5–42.7, 4♂:34.2–50.2) Oueniefou Is., 58404 (55:9.7–46.0) Chissioua Dzaha, 58405 (41:9.1–41.5) Moheli. EAST AFRICA: LACM 30297-41 (3♀:29.6–45.4, ♂ 31.2) Kenya; RUSI 3818 (2♀:30.1–36.5, ♂ 42.1, ? 30.5) Mozambique. FIJI, Viti Levu: BPBM 11490 (29:36.0–55.0); ROM 40217 (6♀:31.6–40.1, 3♂:41.7–47.6, 8?:17.5–27.6), 46840 (28:20.5–47.9), 46841 (4♀:32.5–40.1, 21♂:17.7–48.8), 46842 (5♀:28.8–38.8, 12♂:28.0–41.7, 16?:16.0–27.0), 46843 (3♂:29.9–40.3); USNM 257640 (♀ 45.7, 3♂:30.0–48.7) Totoya Is. GILBERT ISLANDS: AMS I.18052-059 (29.4) Abaiang Atoll; BPBM 10534 (36.3) Tarawa; NSMT 23586 (5) Abemama Atoll, 23656 (2:23.4–25.7) Abemama Atoll, 23685 (3) Abemama Atoll. HONG KONG: CAS 67901 (57:12.7–48.9) Pratas Reef. INDIA: FMRI 161 F.111/156 (6♀:36.8–51.7, 4♂:35.2–56.2) Laccadive Islands. INDONESIA: ANSP 157385 (3:31.7–39.7) Mentawai Is.; BPBM 20899 (2:26.4–40.7) Bali; CAS SU 28035 (♀ 35.8, 6♂:27.2–46.9) Irian Jaya; MNHN A.2975 (36.6) Sumatra, A.8065 (52.0) Moluccas; RMNH 20107 (41.0), 20266 (3:35.0–45.0), 20335 (46.0), 20737, 21169 (40.2), 21185 (47.5), 21285, all Timor, 20109 Tidore (= Soasui), 20167 (4:32.5–38.0) Obilatu, 20637 (5:23.5–31.0) Obilatu, 21065 (3:29.0–44.5) Talaud, 21076 (5:18.2–47.5) Talaud, 25284 Irian Jaya, 32427 (25:29.2–52.0), 32432 (42.2) Bali (holotype of *Plesiops melas* Bleeker, 1849); USNM 144551, 210947, 228463, 245692, 278185 all Moluccas, 295531 (2♂:32.7–46.0) Bawean Is.; YCM

P.12297 Sanur Beach. JAPAN: BPBM 18702 (♀ 66.0, ♂ 64.5) Okinawa, 18989 (♀ 44.0, ♂ 33.8) Miyakejima; CAS 29923 (21:17.4–53.8) Okinawa; FUMT-P 3859 (51.0) Shionomisaki; IORD 76-183 (♀ 33.2), 76-306 (♂ 45.1), 76-307 (♀ 29.9), 76-308 (♀ 30.0), 76-333 (♂ 36.4), 76-416 (35.0), 77-106 (♂ 49.3), 83-229 (♂ 46.8), 83-230 (19:14.2–41.5), 83-254 (♂ 39.3), 83-255 (20:19.2–41.1), 85-50 (5♂:45.1–59.6), all from Ryukyu Is.; NSMT 17831 (1) Yakushima Is., 17925 (14:21.5–69.5) Oosumi Is., 18185 (2) Bonin Is.; USNM 071397 (53:9.9–51.0) Okinawa, 264999 (♀ 45.1, 2♂:34.3–52.3, 2?:22.8–27.5) Okinawa; ZIL 23413 (50.8) Okinawa (holotype of *Pseudochromichthys riukianus* Schmidt, 1931); ZUMT 3358 (41.8), 26940 (63.0), 29620 (43.5), 39998 (38.4), 40071 (60.6), 43017 (67.8), 54386 (59.5) Tanabe Wakayama Pref. (holotype of *Plesiops semeion* Tanaka, 1917). MADAGASCAR: ANSP 157396 (2:17.3–19.0), 157398 (5♀:34.7–42.5), both Nosi-Bé; MNHN 1965-381 (47.4) Tuléar; UMMZ 185567 (7♀:41.4–50.2 mm, 9♂:24.0–58.0, ? 17.4), 185921 (2♀:36.0–46.2, 4♂:24.5–43.5), 186010 (2♀:41.8–43.5 mm, 11♂:27.7–53.2), all Tuléar. MALAYSIA: ANSP 157393 (14.6) Darvel Bay; BPBM 21987 (4:22.0–48.2) Tioman Is.; FMNH 51754 (11♂:25.8–45.3) Sabah; USNM 82992 (31.8) Balabac Passage. MALDIVES: BMNH 1962.1.22:19 (♂ 28.4) G'an; CAS 58738 (10:27.9–48.6) Male Atoll. MARIANA ISLANDS: ANSP 89287 (♀ 32.4) Guam, 117245 (35.8) Saipan; RMNH 2323 (49.0) Guam; UMMZ 198048 (♀ 42.2), 198327 (4♂:30.9–48.8), both Guam. MARSHALL ISLANDS: BPBM 8013 (4:28.3–48.5), 12188 (42.9), 29117 (5♂:25.2–42.4), all Enewetak; FMNH 44330 (12:9.5–32.9) Rongelap, 44335 (2♀:41.2–45.7, 4♂:40.5–49.5) Enewetak; LACM 6674-44 (9♀:33.2–42.9, 12♂:29.0–48.4, 2?:15.3–25.0), 7376 (♀ 34.7, 3♂:38.6–46.4), both Enewetak; NSMT 45001, 45005, Majuro. MAURITIUS: ANSP 157388 (♀ 42.4) Port Louis; BPBM 20203 (2:28.0–40.8) Palmar. NEW CALEDONIA AND LOYALTY ISLANDS: BPBM 28644 (2:22.5–38.7) Nouméa; MNHN 1980-140 (2:53.4–54.1), 1980-339 (32.1), 1980-341 (2:25.6–50.1). PALAU ISLANDS: CAS 67869 (24.7), 67879 (8:21.6–40.0); NSMT 45007 (28.6) Babelthuap Is. PAPUA NEW GUINEA: AMS I.16671-042 (♂ 49.9) Madang Harbor, I.17102-013 (♀ 33.4, 5♂:18.0–38.2) Trobriand; USNM 122982 Bougainville, 245691 (2♂:28.7–30.5, ? 10.4) Bagabag Is., 245697 (2♀:28.7–31.1, 2♂:25.5–38.1, 6?:14.0–20.2) Umboi Is., 278156 Pinipel Is., 295546 (2♂:26.5–40.3) Basilaki Is., uncat. Ninigo Is. PHILIPPINES: CAS 30499 (2:18.6–21.9) Luzon, SU 30058 (32) Sangihe Is., SU 38947 (5:34.0–48.0) Palawan, SU 69028 (10:13.2–20.3) Negros; LACM 42485-8 (4:17.7–41.3) Lingayen Gulf; ROM 60204 (3♀:27.0–41.5, 7♂:28.2–45.5), 60203 (2♀:41.5–43.6, 3♂:34.3–44.4), 60205 (♂ 32.5), 55453 (7♀:30.2–36.8, 10♂:30.1–44.8, 3?:9.8–27.7), all Siquijor

Is.; USNM 146449, 146450, both Batan, 273857 (7♀:33.5–47.8, 5♂:41.1–52.5) Mindanao, 313023 (18♀:27.4–38.2, 18♂:27.5–42.5, 6?:13.1–22.5) Cuyo Is. RED SEA AND GULF OF ADEN: BMNH 1951.1.16:204–223 (♀ 40.0, 18♂:31.5–60.0) Abu Zabad, 1985.7.9:107–8 (2:30.8–38.3) Port Sudan; BPBM 21535 (2:17.2–19.0) Maskali Is.; MNHN 1977-721 (20.7) Gulf of Tadjourah; TAU P.9094 (♂ 24.1, 2?:15.7–16.5) Sinai; USNM 274547 (5:10.7–14.3) Gulf of Aqaba, 274548 (25.0) Ethiopia, 275549 (♂:33.2, ? 24.4) Massawa, 274561 (♀ 46.7) Sha'b al Fanadir Reef, 313011 (♀ 36.3, 3♂:27.7–46.2) Ethiopia. ST. BRANDON'S SHOALS: USNM VGS 76-4 Frigate Island, 274950 Cargados. SEYCHELLE ISLANDS: ANSP 106624 (10♀:29.4–36.6, 20♂:14.4–47.1, 4?:11.3–17.1) Amirante Is., 108721 (25♀:27.3–49.1, 33♂:25.5–54.7, 13?:10.0–22.6) Mahé; CAS 58542 (4:42.1–47.1) Mahé. SOLOMON ISLANDS: AMS I.15360-042 (3♀:31.0–41.2, ♂ 30.9) Malaita Is., I.17490-041 (3♀:34.1–43.8, ♂ 45.2, ? 45.8) Savo Is.; BPBM 16042 (3:31.4–42.3) Guadalcanal; CAS 57658 (10.0) Vanikoro Is.; NSMT 23322 (34.0) Guadalcanal, 23868 (5:31.9–43.0) Florida Is. SRI LANKA: ANSP 157377 (16.3); USNM 295532 (2:16.5–21.0), 290192. TAIWAN: BPBM 23263 (29.0) San Shieh Tai; USNM 274560 (5♀:40.7–58.3, 5♂:26.3–63.9) Ta-Fan-Lieh. THAILAND: ANSP 157378 (♀ 32.7) Similan Is.; BPBM 22836 (2♀:32.8–45.0, 2♂:26.8–43.4) Similan Is.; CAS 67886 (50.0) Aoa Kating Bay, 67887 (3) Ko Tao; WAM P.26507-001 (4♀:32.5–37.7, ♂ 45.5, ? 19.0) Similan Is. TONGA: BPBM colour photo (no specimen) (38.0) Vava'u. VANUATU (NEW HEBRIDES): AMS I.6427-28 (4) Banks Is., I.13852-53 (6♂:25.4–44.6); ANSP 91582 (3) Aneityun Is.; FMNH 22556, 22558–22567 (7♀:30.5–43.9, 4♂:24.1–60.9) Malo Is. VIETNAM: CAS 57663 (6♀:38.3–48.7) Ilot du Sud (Cu Lao Hon), 67897 (2:43.0–47.0) Hon Mieu, 67898 (5:31.5–49.2) Bai Dua.

DIAGNOSIS

Dorsal spines XI, always only 1 supernumerary spine on first dorsal pterygiophore; usually with a distinctive colour pattern on spinous portion of dorsal fin of red tips (distal 1/4 to 1/3) bordered proximally by a narrow black stripe, followed by a narrow pale stripe, and then a black base, with a narrow blue stripe in the basal 1/3 of the fin; when preserved, red is pale and blue is black, otherwise spinous dorsal pattern similar, resulting in a pale, dark, pale, dark sequence from distal to proximal; cheek scale rows 3–4; predorsal scale rows 7–8; no light spots on body scales; no opercular ocellus; maxilla sometimes with dark smudge near posterior tip, but not along dorsal margin; few dentary pores, dentary pore:SL ratio of less than 0.5, averaging 0.33; pectoral-fin ray count 21–23, rarely 19–20 or 24 (less than 5 per cent); almost always fewer than 15 branches in total on 6 ventralmost pectoral-

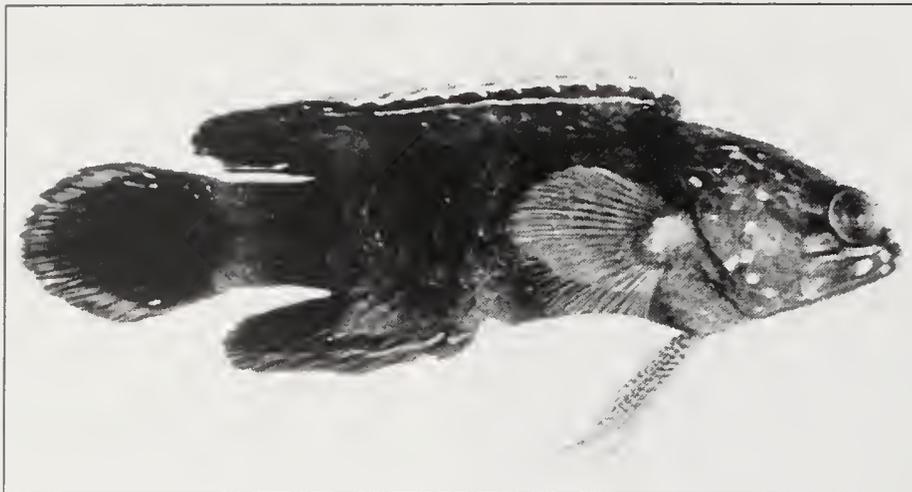


FIG. 12. *Plesiops coeruleolineatus*. BPBM 12188, 42.9 mm, Marshall Islands. From colour slide by J. E. Randall.

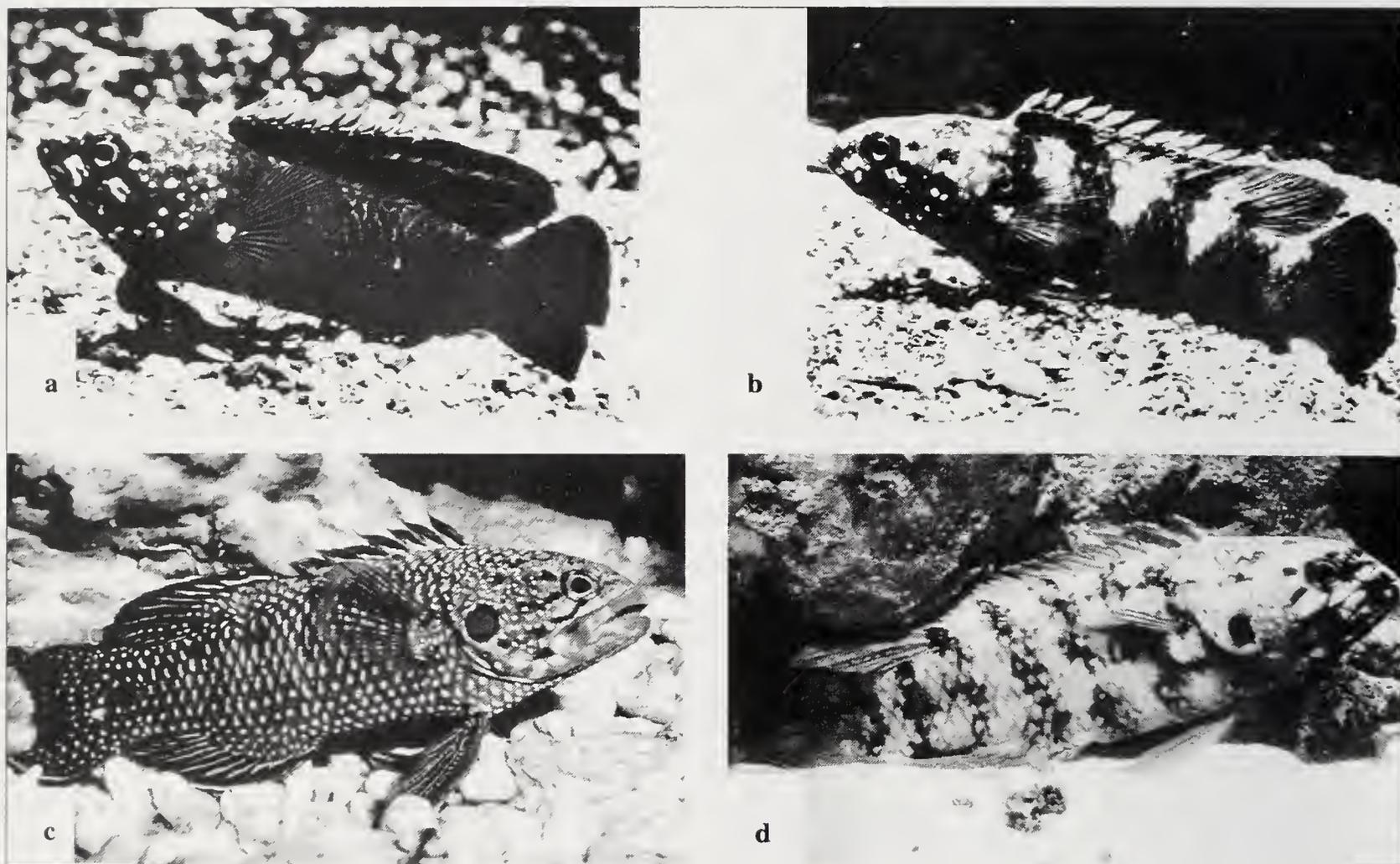


FIG. 13a-d. Colour changes in species of *Plesiops*.
 a, b. *P. coeruleolineatus*. Same aquarium specimen showing 2 colour patterns, Izu Islands (no voucher). From colour prints by M. Hayashi.
 c, d. *P. corallicola*. Same aquarium specimen showing 2 colour patterns, Guam (no voucher). From colour slides by R. F. Myers. Fig. 13c appears in colour in Myers (1989:pl. 37B).

fin rays (only 7 per cent with 15 or more); usually 12 or fewer total gill rakers (70 per cent), and only 3 per cent have more than 4 gill rakers on upper arch.

DESCRIPTION

Meristic data based on 273 specimens (20.2–66.0), except for number of dorsal spines based on 1870 specimens (9.1–69.5). Morphometric data based on 68 specimens (20.2–66.0).

Fins. Dorsal-fin spines, rays XI,7 (XI,7; X–XII,6–8); 5th dorsal-fin ray longest (4th–6th); anal-fin spines, rays III,8; 6th anal-fin ray longest (6th; 5th–7th); pectoral-fin rays 22 left, 21 right (22; 19–24); total number of branches on ventral 6 pectoral-fin rays 12 (12; 10–24); branches on ventralmost pectoral-fin ray 2 (2; 1–3); pectoral fins with ventralmost rays free of membrane to form a fringe, number of free pectoral-fin rays 7 (5–9); pelvic-fin spine, rays I,4; first pelvic-fin ray elongate and noticeably thickened, first pelvic-fin ray extends to base of 3rd anal-fin ray (4th ray; 1st–8th ray); 4th pelvic-fin ray branched; principal caudal-fin rays (upper + lower) 10 + 9 (10 + 9; 9–10 + 8–9); procurent caudal-fin rays (upper + lower) 5 + 5 (5 + 5; 4–6 + 4–6).

Gill rakers. Upper + lower 3 + 8 left, 4 + 8 right (3 + 8; 3–6 + 6–11); total 11 left, 12 right (11; 9–15).

Scales. Body scales open- or closed-centred. Lateral-line scales with simple tube, often with a midposterior lobe on upper line, a midposterior notch on lower line. Upper lateral-line scales 20 (19; 18–21); lower lateral-line scales 11 (11–12; 7–14); midlateral series 23 (23; 22–24); scale rows above upper lateral line to origin of dorsal fin 3 (3; 2–3); scale rows below upper lateral line to origin of anal fin 8 (9; 7–10); predorsal scale rows 7 (7; 5–8); cheek scale rows 4 (4; 3–5); circumpeduncular scales 16; primary anterior pore of each upper lateral-line scale covered by preceding scale, except occasionally the last; anterior pores of lower lateral-line scales usually uncovered; first ctenoid upper lateral-line scale 11th (8th; 4th–11th); first ctenoid scale below upper lateral line 4th (4th; 2nd–7th). Anterior body scales cycloid, usually remaining so above upper lateral line, but occasionally becoming ctenoid by between the 7th and 18th upper lateral-line scale. Below upper lateral line, cycloid scales end at 4th (4th; 2nd–7th) scale and extend forward to pectoral-fin base and then ventrally to pelvic-fin base. All scales posterior to this line ctenoid. Cheek scales visible anteriorly to the posterior tip of maxilla.

Cephalic sensory pores. Small and sparse. Dentary pore number varies with SL and ranges from 6–33 (holotype 12), but generally forming a ratio with SL of < 1 ($\bar{x} = 0.33$, range = 0.20–0.61, for SL > 40 mm, holotype 0.27). No pores posterior to maxilla linking preopercular or dentary pore series to suborbital series.

General morphology. As percentage of SL: body depth

at anal-fin origin 36 (26; 27–36); body width at pectoral-fin base 19 (18; 11–21); caudal-peduncle length 18 (18; 16–20); caudal-peduncle depth 16 (16; 14–18); predorsal length 36 (35; 34–42); preanal length 62 (65; 60–70); pre-pelvic length 30 (34; 30–41); dorsal-fin base 58 (53; 50–58); longest dorsal-fin ray (23; 18–28); anal-fin base 21 (21; 18–25); longest anal-fin ray 20 (24; 17–31); pectoral-fin length 24 (23; 18–28); pelvic-fin length 42 (45; 37–51); head length 37 (36; 34–41).

Head. Rounded. Maxilla extending to or beyond posterior margin of orbit. As percentage of HL: snout length 17 (20; 14–23); upper-jaw length 48 (51; 42–54); bony-interorbital width 8 (8; 6–10); posterior internasal width 14 (16; 11–18); orbital diameter 30 (27; 26–48); head depth at posterior margin of orbit 56 (53; 52–71); head depth at posterior margin of preopercle 77 (71; 59–78); head width at dorsal tip of preopercle 56 (48; 41–60).

Osteology and myology. Dorsal formula 0/0/1/1+1/1 (one specimen with 0/0/1/2+1/1); epurals 3 (rarely 2); epaxial musculature extends onto frontals anterior to sphenotic, lateral muscle bundles in advance of dorsal (medial); adductor mandibulae with an additional sheet of fibres originating from sphenotic and pterotic as well as usual main body originating from posterior suspensorium.

Colour when fresh. From slide of BPBM 12188, Fig. 12. Body and base of median fins dark sepia, almost black; head dark sepia dorsally; 2 obscure dark blotches behind eye, 1 posterodorsal and the other posteroventral; also a stripe running from the midventral orbit just above maxilla; preopercle with 5 silver-white spots, 1 on subopercle; maxilla with 2 pale bars; iris of eye blue peripherally, and orange-red around pupil; dorsal-fin spines with bright red tips, this bordered proximally by a narrow black stripe, then a pale stripe, a more proximal dusky region, a bright blue stripe, and finally a dark base; the pale stripe angles upward slightly to form the pale margin of the soft portion of dorsal fin; the blue stripe angles upward and continues to 4th ray, and soft portion of dorsal fin also has blue stripes in membranes of 4th–7th rays running parallel to the rays; otherwise soft dorsal fin dark; anal-fin spines and rays with pale tips, bordered proximally by a dark region, then with blue stripes of same pattern as dorsal; caudal dark with narrow, submarginal, orange-yellow band; pectoral-fins dark; pelvic-fins brown with numerous pale chevron markings.

Colour photographs of other specimens (BPBM 8013, Marshall Islands; BPBM 21997, Malaysia; ROM 58402, 58401, Comores; ROM 60203, 2, ROM 55453, 4, Philippines; Masuda et al., 1984, pl. 126I, Japan) are similar, but can be slightly paler, have yellow branchiostegal membranes, dark centres to the preopercular spots, and/or pale bases to the anal and dorsal fins.

Some specimens have quite different colouration, particularly on the dorsal and anal fins. The Tonga specimen

has a spinous dorsal fin pattern, from distal to proximal, of pale tips, dark stripe, dusky reddish stripe, blue stripe, and finally a dark base. A Ryukyu Islands specimen (BPBM 7393) has a spinous portion of the dorsal fin with crimson tips bordered by a dusky region, followed by a pale region, a narrow dark stripe, then a wider reddish area, a narrow blue stripe, and finally a wider yellowish basal stripe bordered proximally by a dusky base. This pattern, except for the crimson tips, continues onto most of the soft portion of the dorsal fin. Philippine specimens can also vary from common patterns. Rather than having the dark basal portion as found in the Marshall Islands specimens described above, they often have a yellow or yellow-red base which extends well onto the soft portion of the dorsal fin (ROM 60203, 2, ROM 55453, 4). The anal fin also can have a broad yellow base. Variation also occurs in the caudal fin. It ranges from being completely dark with a narrow pale margin to having a wide yellow crescent in the distal third of the fin. The head is often very yellow, with the cheeks and opercle usually brightest (BPBM 7393, Ryukyu Islands; ROM 60203, 55453, Philippines).

Colour of holotype (in ethanol). Entirely straw-coloured except for darker caudal, last rays of dorsal and anal fins, and 2 post-orbital spots. Other specimens have body background ranging from almost black to pale brown with scales having darker centres giving a spotted or reticulated appearance; occasionally body with alternating dark and light bars, about 3 of each; head pale to dark, sometimes with paler cheeks and opercle; preopercle often with 3–5 white spots, these sometimes black; 2 black blotches behind eye, one posterodorsal, one posteroventral; a narrow stripe running from midventral orbit margin parallel to maxilla and ending just at or beyond its posterior tip; occasionally a dark median stripe or spot on posterior end of maxilla, but never on dorsal margin; often a pair of white or pale marks on maxilla; dorsal fin with pale tips, bordered proximally by black, then another pale stripe, and a dark base; soft portion of dorsal with a narrow pale margin, the remainder usually dark, although sometimes a pale base; anal fin with a narrow pale margin, remainder dark, sometimes with pale base; caudal fin dark with pale margin or subterminal pale band; pectoral fins dark; pelvic fins usually brown or grey with pale spots or chevrons.

These fishes can change colour, as notes of J.E. Randall suggest (BPBM 8013, Marshall Islands): "A single individual may vary in colour from dark brown to light gray with dark bars." Photographs by M. Hayashi of the same specimen in an aquarium also show that the barred and unbarred condition can be displayed by the same individual (Fig. 13a,b; p. 20).

DISTRIBUTION AND HABITAT

This species has the widest distribution of all *Plesiops* species (Fig. 14), and overlaps at least parts of the ranges of all other species except *P. multisquamata* (east coast, South Africa). In addition to the material examined, reliable literature records include Pariaman, Sumatra (Bleeker, 1853a:117), Prigi, Java (Bleeker, 1857:479), and Delagoa Bay, Maputoland (Mozambique) (Smith and Heemstra, 1986:542). Smith (1946) provides a record of *P. melas* (= *P. coeruleolineatus*) for Durban, but his identification is not substantiated. Like other species, *P. coeruleolineatus* is generally a shallow water dweller of coral interstices, and is rarely seen. Randall comments on a specimen label (BPBM 8013): "A secretive fish. None were observed underwater. All were caught accidentally from beneath rocks when squirting quinaldine for young *Epinephelus merra*." Myers (1989:113) finds that: "It is a common, but seldom seen inhabitant of exposed outer reef flats and outer reef slopes to a depth of 23 m. It ventures out in the open at night to feed on small crustaceans, fishes, and gastropods." Most specimens are collected within 3 m of the surface.

COMPARISONS

Plesiops coeruleolineatus is one of only 2 species of the genus with 11 dorsal spines. Those rare specimens that have 12 spines can be identified by having only 1 supernumerary spine on the first dorsal pterygiophore (vs. 2). This species also has, on average, the fewest gill rakers on the first arch (11 or 12), and very rarely has more than 4 rakers on the upper limb (only 3 per cent have 5 or 6) (Table 3). *P. polydactylus*, the other 11-spined species (having only 1 supernumerary spine on the first dorsal-fin pterygiophore), has a higher pectoral-fin ray count (26–28 vs. 19–24, < 2 per cent with 24), more gill rakers on the first arch (13–18 vs. 11–15, < 10 per cent with 14–15), usually more rakers on the upper limb (equally 4 or 5 vs. 3–6, 3 per cent with 5–6), fewer predorsal scale rows (almost always 5, sometimes 6 vs. 5–8, < 1 per cent with 5), and perhaps a higher dentary pore:SL ratio (\bar{x} of 0.41 vs. 0.33) (Tables 1, 3, 4, 5).

The 2 most similar species having 12 dorsal-fin spines, *P. verecundus* and *P. mystaxus*, like all other members of the genus, have a higher midlateral scale count (24 vs. 23). Additionally, *P. verecundus* usually has a higher dentary pore:SL ratio (\bar{x} of 0.57 vs. 0.33), and more gill rakers on the first arch (mode of 15 vs. 11), especially on the upper arm (mode of 5 vs. 3) (Tables 3, 6). *P. mystaxus* has a black margin to the posterodorsal maxilla, which *P. coeruleolineatus* never has, although it might have a dark mark running down the middle of the posterolateral maxilla. All other members of the genus lack the flame red tips to the dorsal spines, have consistently higher total lower pectoral-fin ray branch counts (i.e., > 12) (Table 2),

and more gill rakers, among other features.

The low spine count and average pectoral-fin ray count make it difficult to confuse *P. coeruleolineatus* with other species.

BIOLOGICAL REMARKS

Despite its wide range, *P. coeruleolineatus* exhibits very little geographic variation. Pectoral-fin ray number varies between 21 and 23 in almost all populations (Table 7). Cocos-Keeling Islands, Mauritius, New Caledonia, Ryukyu Islands, and Thailand populations might have more individuals with high pectoral-fin ray counts than others, while the Carolines, Marianas, and Marshalls populations tend to have lower counts. The total number of pectoral-fin ray branches is very consistent, and only the high counts in the Tuléar population are notable (Table 7). Gill raker counts are also very consistent, although higher than average counts are common in the Marshalls and Great Barrier Reef (Table 8). Dentary sensory pore:SL ratios vary between populations as well (Table 9), although even the most disparate populations (Tuléar, Great Barrier Reef) do not exhibit significantly different correlations between pore number and SL (ANCOVA, $p < 0.01$).

Almost all specimens of this species that I have examined have 11 dorsal-fin spines. Only 23 of 1870 individuals (1.2 per cent) had 12 dorsal-fin spines, and only 8 (0.4 per cent) had 10. Even these anomalous specimens have

only 1 supernumerary spine on the first dorsal-fin pterygiophore. Of the 23 individuals with 12 dorsal-fin spines, 15 had a XII,6 arrangement, rather than the usual one of XI,7. The conservation of number of fin elements suggests that what would normally have been the first soft ray has transformed into a spine, thus increasing the spine number by 1 and reducing the ray number by 1, and maintaining the same number of fin elements. Examination of X-ray radiographs provides evidence for this explanation, as the twelfth spine on these XII,6 specimens is supported by a soft ray pterygiophore; i.e., the pterygiophore has separate proximal, medial and distal elements. The last spinous pterygiophore in *Plesiops* normally has only its distal element autogenous. Individuals with a XII,7 arrangement have inserted a new single spine element and shifted the soft portion of the fin back 1 interneural space, or have 1 deformed precaudal centrum that bears 2 neural spines and has an extra pterygiophore and spine accompanying this abnormality. Specimens that have reduced the number of spines to 10 have merely failed to produce a pterygiophore and spine in one of the interneural spaces and have a gap, but the soft portion of the fin still fills the normal interneural positions.

Of the 568 specimens that were sexed, 363 were male and 205 were female. This produces a sex ratio that is highly significantly different from 1:1 ($G = 44.5$, $p < 0.001$). However, for two large collections, ANSP 108572

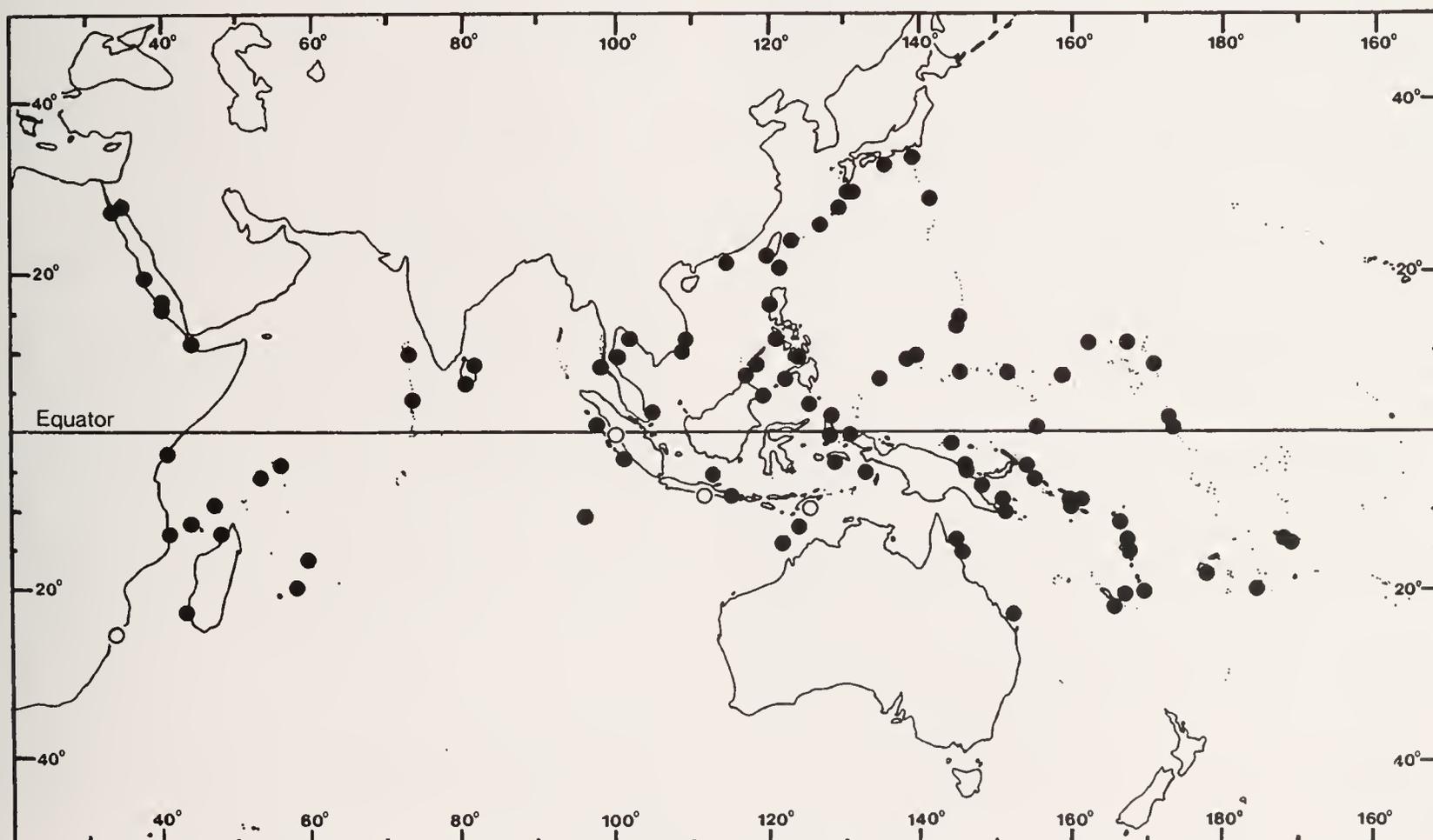


FIG. 14. Distribution of *Plesiops coeruleolineatus*. Closed circles indicate localities for material examined by the author; open circles indicate reliable literature records.

(Seychelles: 33 males, 25 females; $G = 0.55$, $0.50 < p < 0.75$) and USNM 295533 (Philippines: 18 males, 18 females), the sex ratios are not significantly different from 1:1. In light of this, it is difficult to interpret a sex ratio based on collections spanning the entire range collected at different times of the year. Perhaps sampling at the same reef is required before definite conclusions about sex ratios can be reached.

Externally identifiable females ranged from 25.4–66.0 mm, and males reached 64.5 mm. The smallest gravid female was 27.0 mm. It appears that little or no sexual dimorphism in size occurs, and no detectable difference in colour was found. However, within most collections the largest individuals are usually males.

TAXONOMIC REMARKS

Bleeker (1849) described *P. melas* from a single specimen (54 mm TL) from Bali. He (1853a) synonymized this species with *P. coeruleolineatus* Rüppell and combined the *P. melas* holotype with 6 other specimens he identified as *P. coeruleolineatus*. This species and *P. corallicola* were synonymized with *P. nigricans* Rüppell by Bleeker in 1875. Bleeker (1875) believed that his small specimens were juvenile *P. nigricans* that had not yet obtained the blue spots on the body. As pointed out by Inger (1955), all of Bleeker's material was from the East Indies, meaning that he had no true *P. nigricans* (endemic to the Red Sea) in his possession, and all the larger specimens with spots would have been *P. corallicola*. The smaller "juveniles" were actually adult *P. coeruleolineatus*, as even small *P. corallicola* possess the opercular ocellus and blue spots, at least on the caudal. Weber (1913; cited in Weber and de Beaufort, 1929:379) showed that the ocellus and spots "are wanting independent of age...[and] independent from sex" in *P. coeruleolineatus*, which he knew as *P. melas*. At that time, the Red Sea species of Rüppell, *P. nigricans* and *P. coeruleolineatus*, were considered to be the same, whereas the Indonesian and West Pacific *P. melas* described by Bleeker (1849) was considered valid. This was rectified by Smith (1952), who returned to the decision of Bleeker (1853a), and synonymized *P. melas* with *P. coeruleolineatus* once again, and recognized the species as valid.

When Bleeker (1875) synonymized *P. coeruleolineatus* (including *P. melas*) and *P. corallicola* with *P. nigricans*, he combined all the specimens into a single lot. Most of these specimens (36 of 42) were obtained by the Rijksmuseum van Natuurlijke Historie in Leiden (see Taxonomic Remarks of *P. corallicola* for a more detailed history of Bleeker's *Plesiops* specimens). Among these specimens, one individual referable to *P. coeruleolineatus* of appropriate size (approximately 52 mm TL) showed signs of detailed examination by Bleeker, having a slit through the right suspensorium. This has been used by

other authors (Gill, 1995; Whitehead, Boeseman, and Wheeler, 1966) to identify Bleeker type material. Unfortunately, the specimen is in poor condition and lacks scales, so other possible evidence such as pencil marks for scale counts could not be obtained. However, based on the slit opercular region, this specimen is identified as the holotype of *P. melas* Bleeker, and is now catalogued as RMNH 32432.

The Staatliches Museum für Naturkunde in Stuttgart (SMNS) held "several" specimens and a skeleton of *P. coeruleolineatus* donated by Bleeker in 1861 (Fricke, 1991:50). Conceivably, these might have held the type of *P. melas*, given Bleeker's habit of replacing types that were in poor condition when he obtained better specimens (Mees, 1962). However, I am convinced that the RMNH specimen is correctly identified as the holotype of *P. melas*, for the reasons outlined previously. In any event, the SMNS specimens are lost, probably during World War II (Fricke, 1991), or from poor curatorial practices (Fricke, pers. comm.).

Kner's (1868) *Plesiops nigricans* var. *apoda* from Kandavu, Fiji, appears to be based on a damaged or aberrant specimen lacking pelvic fins. The type specimen cannot be located. Although a specimen in the Naturhistorisches Museum Wien with the correct catalogue number exists (Godeffroy Nr. 838, now NMW 22241), this specimen has pelvic fins and is more likely to be Kner's Godeffroy Nr. 838b or 838c (B. Herzig, pers. comm.). Without the type, the identification of var. *apoda* relies on Kner's original description which states that the specimen had 11 dorsal-fin spines. Such a count suggests 1 of 2 recognized species, *P. coeruleolineatus* or *P. polydactylus*, both of which are known from Fijian waters. The former is a more common species, and as the Kner species has been synonymized with *P. coeruleolineatus* in the past, I opt for retaining this status until the type specimen is available for examination.

Pseudochromichthys riukianus Schmidt, 1931 (catalogued as ZIL 23413), was originally synonymized with *Plesiops corallicola* by Inger (1955), probably because of its 12 dorsal spines. However, it has a XII,6 arrangement, with a dorsal formula of 0/0/1/1+1/1, and the 12th spine supported by a typical soft ray pterygiophore. It also has a pectoral-fin ray count of 21. This suggests that it is one of the rare instances of a 12-spined *P. coeruleolineatus*, so I have changed its synonymy accordingly.

ETYMOLOGY

The name "coeruleolineatus" is Latin for "blue stripe," and Rüppell was apparently referring to the blue lines present in the dorsal and anal fins, which have since been found not to be unique among species of the genus.

***Plesiops corallicola* Bleeker, 1853c**

Figs. 13c–d, 15, 16; Tables 1–5, 10–11

Plesiops corallicola Bleeker, 1853c:280.—Rüppell, 1835:5; Günther, 1861:364; Day, 1871:685; Günther, 1873–1910:87; Vaillant, 1889:57–60; Inger, 1955:266, figs. 1a, 2b,c, 3c; Schultz, Woods, and Lachner, 1966:163; Munro, 1967:283, pl. 35 (fig. 506); Masuda et al., 1984:141, pl. 126M; Sano et al., 1984:17, pl. 7b; Myers, 1989:113, pl. 37b; Mooi, 1990:458, table 2; Mooi, 1993:figs. 15, 21.

Cirrioptera corallicola Van Hasselt [*icon inedit, nomen nudum*].—Bleeker, 1853c:281.

Plesiops nigricans (non Rüppell, 1828).—Bleeker, 1875:27, pl. 3, fig. 3 [in part]; Bleeker, 1875–8:pl. 390, fig. 3; Day, 1875:127–8, pl. 31; Day, 1889:78; Boulenger, 1895:340 [in part]; Weber and de Beaufort, 1929:375 [in part]; Fowler, 1928:188 [in part]; Fowler and Bean, 1930:313 [in part]; Fowler, 1932:7; Schultz, 1943:111–2; Marshall, 1950:175; Schultz et al., 1953:399; Munro, 1955:116–117; Palmer, 1970:224; Shen, 1984:45, pl. 294–3.

Pharopteryx nigricans—Jordan and Seale, 1906:260 [in part].

Plesiops caeruleolineatus—Smith, 1952:143 [in part].

TYPE MATERIAL

Lectotype. RMNH 6352, 86.3 (114.0 TL), Priaman [as reported by Bleeker (1853c) = Pariaman?, 0°38' S, 100°08' E], Sumatra, I. Pfeiffer, 1853?.

Paralectotype. RMNH 32450, 114.5 (153.5 TL), collected with lectotype.

ADDITIONAL MATERIAL EXAMINED

399 specimens, 11.5–142.6—AUSTRALIA: ANSP 134704 (♂ 75.8), 134706 (♂ 38.0), 134708 (2♂:20.5–33.8), 134710 (♂ 56.1), all from Cocos-Keeling Is.; WAM P21766-001 (♂ 98.8) Christmas Is. CAROLINE ISLANDS: BPBM 28317 (♂ 71.0) Kosrae; CAS 67819 (22:44.5–108.0), 67824 (40.2), 67826 (30:14.5–61.3), 67828 (32.0), all near Ifalik Atoll, 67832 (25:22.7–97.2) Kapingamarangi Atoll; USNM 154389 (4:53.5–90.0) Yap, 313004 (2♂:18.0–32.4) Pohnpei. COOK ISLANDS: AMS IA.2465 (130.0), IA.4741 (126.0), both from Suwarow Atoll. FIJI: BPBM 11496 (♂ 71.6) Viti Levu; FMNH 47920 (♂ 96.3); ROM 46758 (5♀:63.6–120.0) Nairai Is., 46759 (♂ 30.0), 46760 (♀ 79.8, ♂ 34.6, ? 35.2), both from Great Astrolabe Reef; USNM uncat., Rotuma Is. GILBERT ISLANDS: AMS IB.5550 (85.0) Tarawa, IB.5551 (97.0) Tarawa; ANSP 105469 (3:78.2–99.5) Kings Mills; BMNH 1969.8.26.154 (♀ 65.5) Tarawa; BPBM 3987 (♂ 84.2); USNM 167344, Onotoa. INDIA: AMS I.37 (♂ 106.5) Andaman Is.; CAS SU 37199 (2♂:70.9–78.0) Andaman Is. INDONESIA: CAS

SU 28032 (3) Waigeo Is.; MNHN A.8065 (2:82.5–129.0), A.8073 (90.0), both Moluccas; RMNH 2326 (2) Java, 5036 (105.7), 25221, both from Irian Jaya, 5052 Timor, 10006 (78.0), 20001 (2:70.0–72.0), 31262 (8:34.0–108.5). JAPAN: IORD 76-199 (142.6) Ryukyu Is.; ZUMT 3359 (72.2). MARIANA ISLANDS: ANSP 85970 (♂ 83.2) Guam, 114716 (♀ 64.7, ♂ 40.3, ? 32.8), 114739 (2♀:70.0–80.0, ♂ 86.0), 114741 (2♀:88.7–124.0), 114747 (2♀:111.0–124.8), all Saipan; BPBM 3988 (♂ 93.2) Guam; UMMZ 197950 (4♀:69.7–89.1, 3♂:47.0–89.5), 198038 (♀ 101.0), both Guam; USNM 139733 Rota, 154392 (3♀:58.2–86.0, 8♂:23.0–110.0, 2?:11.5–13.2) Guam. MARSHALL ISLANDS: FMNH 44706 (♀ 87.0, 2♂:38.5–80.7) Rongelap Atoll; LACM 6674-139 (3♀:48.5–93.6, 3♂:42.0–105.9) Enewetak Atoll; UMMZ 176824 (♂ 109.3) Kwajalein Atoll; USNM 140712 (4:64.0–107.8) Bikini Atoll, 166737 (8♂:16.7–84.7) Arno Atoll, 196125 Enybar Atoll, 274574 (2♀:65.5–70.0, 3♂:37.2–79.7, 2?:43.1–61.5) Kwajalein Atoll. PALAU ISLANDS: CAS 14302 (80.0), 67836 (122.0); USNM 154390. PAPUA NEW GUINEA: BMNH 1974.5.25:980–1 (2:56.0–57.8) Trobriand Is.; USNM 274969 Bismark Arch., uncat. Trobriand Is. PHILIPPINES: CAS SU 20690 (4♂:34.0–115.3) Calayan, SU 32352 (4) Batangas, SU 51518 (38.7) Panay Is., 52466 (97.0) Dumaguete, 57654 (2♂:43.4–71.0) Negros; USNM uncat. Batangas. PHOENIX ISLANDS AND VICINITY: ANSP 65292 (♀ 87.8) Howland Is., 105324 (97.7) Baker Is.; BPBM 3989 (♂ 106.5) Howland Is., 3990 (♀ 102.3) Baker Is.; USNM 115388 Canton Is., 115390 (4♀:82.3–92.7, ♂ 92.3) Hull (Orona) Is. SAMOA: AMS I.7284 (♀ 97.5); ANSP 122597 (4♀:71.9–88.5, 2♂:48.9–87.0) Apia; FMNH 4769 (2♀:75.6–96.2, 5♂:45.0–103.0) Apia; USNM 52437 (6♀:54.7–102.1, 9♂:54.0–107.0) Apia, 115391 Tutuila Is. SOLOMON ISLANDS: AMS I.15360-208 (5♀:65.1–88.0, 4♂:72.3–90.3) Malaita Is.; ANSP 83963 (♀ 105.7) Shortland Is., 157401 (2♀:60.0–70.1) Santa Cruz Is.; BPBM 1158 (♀ 91.4) Shortland Is., 11494 (♀ 31.5, 4♂:23.0–82.0) Guadalcanal. SUMATRA: ANSP 27647–27649 (4) Padang; CAS SU 8342 (1); MNHN A.8026 (75.0). TOKELAU ISLANDS: ANSP 96691 (1) Nukunono Atoll, 100976 (3♀:63.7–77.0) Mekenomo Atoll; USNM uncat. Atafu Is. TONGA ISLANDS: USNM 133869 Vavau Is. VANUATU (NEW HEBRIDES): AMS I.6426 (98.7) Banks Is., I.13846-51 (3♀:62.7–100.3, 5♂:48.2–97.0); CAS SU 24067 (2:33.1–58.9) Malo Is.; BPBM 11493 (♀ 79.7, ♂ 36.8) Efate; FMNH 22580–82 (2♀:93.2–98.8, ♂ 60.8).

DIAGNOSIS

Dorsal spines XII; dark ocellus on opercle; single blue or light spot on each body scale, sometimes crescent-shaped; caudal fin with blue or pale spots; pectoral-fin rays 21

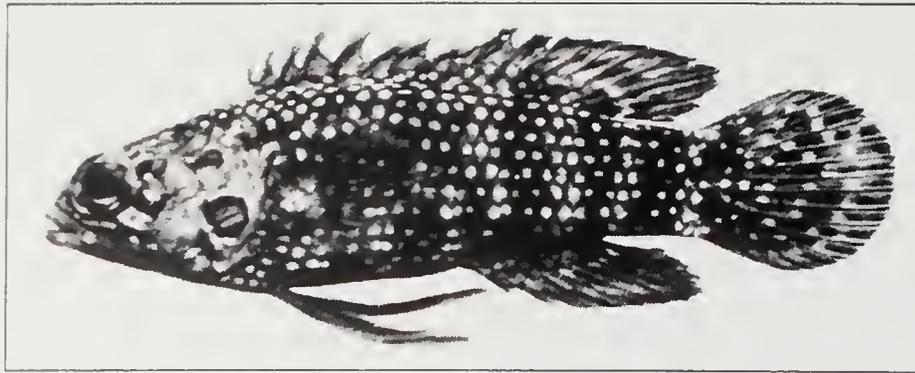


FIG. 15. *Plesiops corallicola*. WAM P.28998-001, 36 mm, Christmas Island, Indian Ocean. From colour slide by G. R. Allen. Appears in colour in Randall, Allen, and Steene (1990:133).

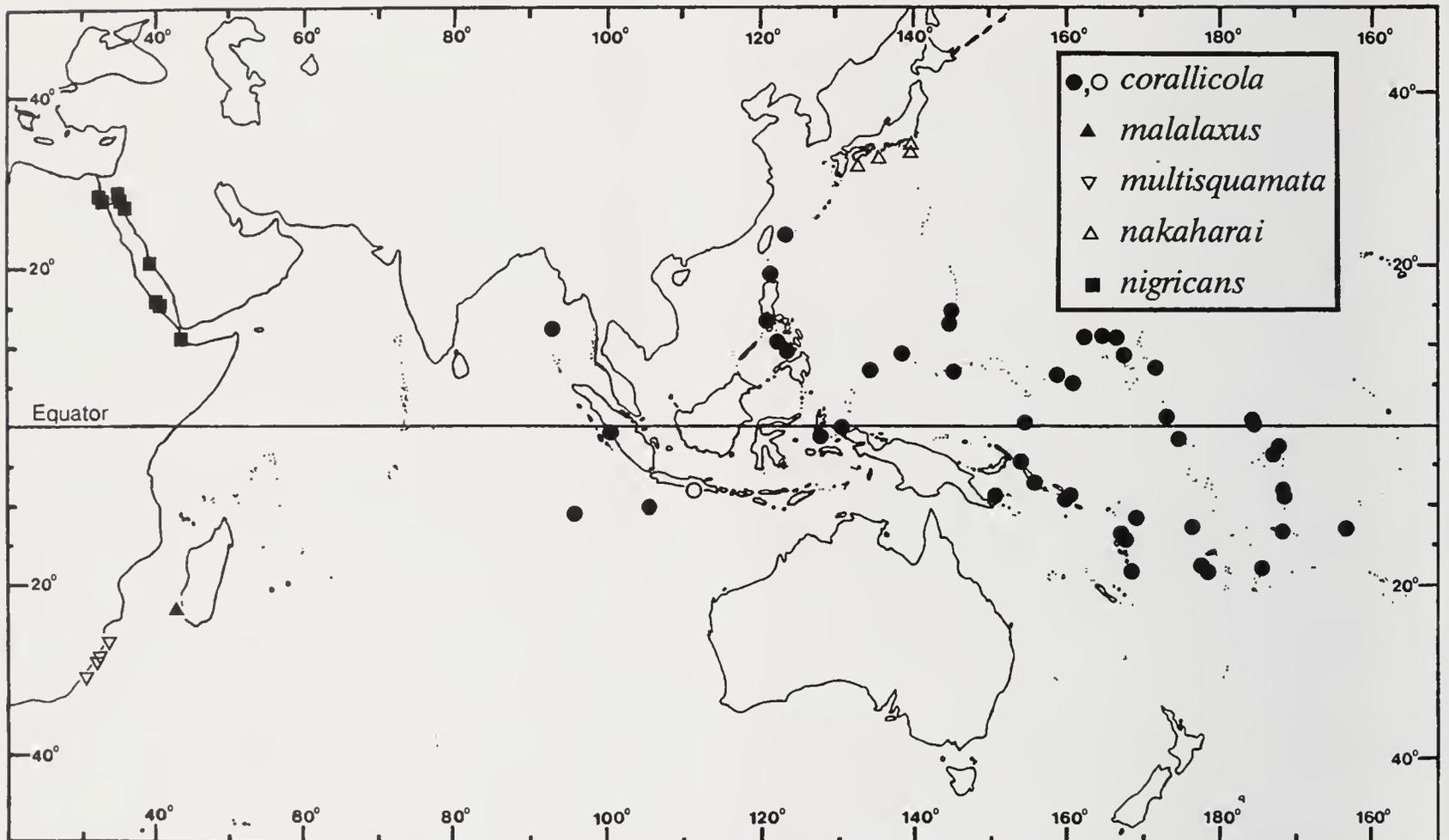


FIG. 16. Distribution of 5 species of *Plesiops*. For *P. corallicola*, closed circles represent localities for material examined by the author, open circles represent reliable literature records.

(20–22); usually 3 or more branches on ventralmost pectoral-fin ray, and a total of usually 25 or more branches on the 6 ventralmost rays; cheek scale rows 4 (4–5), visible as far forward as posterior tip of maxilla; skin bearing pore series posterior to eye and on preopercle not expanded; dentary pore:SL ratio almost always less than 0.5, averaging 0.34, and dentary pores in 3 distinct groupings; suborbital sensory pore series not continuous with that of preopercle or dentary.

DESCRIPTION

Most meristic data based on 155 specimens (11.5–142.6), all morphometric data and remaining meristics based on

52 specimens (16.7–142.6) including types.

Fins. Dorsal-fin spines, rays XII,7 (XII,7; XII–XIII(once),7–8); 5th dorsal-fin ray longest (5th; 5th–6th); anal-fin spines, rays III,8 (III,8); 6th anal-fin ray longest (6th; 6th–7th); pectoral-fin rays 21 left, 22 right (21; 20–22, twice 19); total number of branches on ventral 6 pectoral-fin rays 37 (30–34; 6–54); branches on ventralmost ray 5 left, 2 right (4; 1–7); pectoral fins with ventralmost rays free of membrane to form a fringe, number of free pectoral-fin rays 6 (7; 5–8); pelvic-fin spine, rays I,4; first pelvic-fin ray elongate but relatively short for *Plesiops*, and noticeably thickened, first pelvic-fin ray extends to base of 1st anal-fin spine (2nd ray; 1st

spine—4th ray); 4th pelvic-fin ray branched; principal caudal-fin rays (upper + lower) 10 + 9 (9 + 9; 8–10 + 8–9); procurent caudal-fin rays (upper + lower) 5 + 5 (6 + 5; 5–7 + 5–6).

Gill rakers. Upper + lower 5 + 10 (5 + 10; 3–7 + 6–12); total 15 (14–15; 12–17 (10, 11, and 18 once each)).

Scales. Body scales usually with closed centre, but sometimes open-centred. Lateral-line scales with simple tube, usually without a midposterior lobe on upper line, often, like the lower line, with a midposterior notch. Upper lateral-line scales 19 left, 20 right (19; 18–20, once 21); lower lateral-line scales 13 (14; 12–16, once 10 and 11); midlateral series 24 (24; 23–24, once 25); scale rows above upper lateral line to origin of dorsal fin 3 (3; 3–4, rarely); scale rows below upper lateral line to origin of anal fin 9 (9; 8–9, once 10); predorsal scale rows 8? (7; 6–8, twice 5); cheek scale rows (4; 4–5, once 6); circum-peduncular scales 16; primary anterior pore of each upper lateral-line scale covered by preceding scale, except occasionally the last, especially on the 20th scale; anterior pores of lower lateral-line scales usually uncovered; first ctenoid upper lateral-line scale 14th (14th; 12th–none); first ctenoid scale below upper lateral line 10th (8th; 6th–16th). Anterior body scales cycloid, almost always remaining so above upper lateral line. Below upper lateral line, cycloid scales end at 10th (8th; 6th–16th) scale and extend forward to pectoral-fin base and then ventrally to pelvic-fin base. All scales posterior to this line ctenoid. Cheek scales visible anteriorly to the posterior tip of maxilla.

Cephalic sensory pores. Small but not especially numerous. Dentary pore number varying with SL and ranging from 4–58 (lectotype 26), but generally forming a ratio with SL of < 0.5 ($\bar{x} = 0.34$, range = 0.22–0.56, for SL > 40 mm, lectotype 0.30). Dentary pores arranged in 3 distinct groups, one posterior, one anteriorly, and the other about midway between these 2 groups. Very few or no pores posterior to maxilla; preopercular, dentary and suborbital pore series remaining distinct.

General morphology. As percentage of SL: body depth at anal-fin origin 28 (28; 25–32); body width at pectoral-fin base 18 (18; 12–22); caudal-peduncle length 17 (18; 16–20); caudal-peduncle depth 16 (17; 16–19); predorsal length 35 (36; 34–41); preanal length 70 (65; 62–70); prepelvic length 34 (34; 31–39); dorsal-fin base 51 (54; 48–58); longest dorsal ray 25 (26; 21–33); anal-fin base 20 (21; 18–24); longest anal ray 25 (26; 21–36); pectoral-fin length 22 (25; 22–27); pelvic-fin length 37 (38; 32–42); head length 36 (37; 36–40).

Head. Wide and rounded. Maxilla extending to or beyond posterior margin of orbit. As percentage of HL: snout length 22 (19; 14–23); upper-jaw length 46 (48; 45–54); bony-interorbital width 9 (8; 6–13); posterior

internasal width 14 (15; 13–17); orbital diameter 26 (28; 22–35); head depth at posterior margin of orbit 57 (52; 48–60); head depth at posterior margin of preopercle 67 (67; 58–78); head width at dorsal tip of preopercle 56 (52; 41–60).

Osteology and myology. Vertebrae (abdominal + caudal) 10 + 15 (once 16); dorsal formula 0/0/2/1+1/1 (one specimen with 0//2/1/1+1); epurals 3; epaxial musculature extends onto frontals anterior to sphenotic, lateral muscle bundles in advance of dorsal (medial), meeting in midline in larger specimens; adductor mandibulae with an additional sheet of fibres originating from sphenotic and pterotic as well as usual main body originating from posterior suspensorium.

Colour when fresh. From Myers (1989:pl. 37B). Body background dark grey-brown; each body scale with a single bright blue spot or elongate bar or crescent; each fin-sheath scale also with a bright blue spot; head lighter grey-brown, smaller scales of cheek with 1, and larger scales on opercle with 4 or more small, pale bluish-white spots, except on lower opercle and subopercle where there is an eye-sized dark blue ocellus with a narrow black margin; 4 pupil-sized sky-blue spots not associated with scales, 1 on lower preopercle, 2 on interopercle and 1 on posterior tip of maxilla; cheek with 4 dark spots scattered along its margins, 2 dark spots on dorsolateral head; 3 short, black bars around eye, one posterodorsal, one posterventral, and another from midventral eye running parallel to maxilla and ending at its posterior tip; lips and dentary grey; eye iris blue peripherally, orange directly around pupil; branchiostegal membranes bright blue, branchiostegals appear dark; dorsal fin dark blue-black with a sky-blue basal stripe running along spines becoming a series of discontinuous short slashes running through the membranes of the soft portion of the fin; soft portion of dorsal with a narrow pale margin; anal fin similarly coloured to dorsal, but slashes thicker and running parallel to fin rays; pectoral-fin rays dark, distal 6th of rays and membrane rust-coloured; pelvic fin with dark grey spine, and membranes with blue stripes running parallel to the rays or with a series of short dashes; caudal dark with sky-blue spots and a narrow, pale margin. Small specimens are similarly coloured, and can exhibit barring of darker background (Fig. 15; Randall, Allen, and Steene, 1990:133). As Myers states (1989:113): “This species’ colouration can range from a pale grey with black blotches and blue dots to an almost uniformly black except for the ever-present blue ocellus on the edge of its operculum.” This variability is evident in Figure 13 (c,d, p. 20).

Colour of type material (in ethanol). Body background brown; body, cheek, and opercular scales usually with a white spot, except those on lower opercle where an eye-sized dark brown to black ocellus is present; all fins but pectorals darker than body; caudal, pelvic and soft portion

of dorsal fins with light spots; spinous dorsal fin with light stripe starting at base of first spine and angling upward to end over half-way up the 4th soft ray; a similar stripe on the anal fin.

On other specimens, body background can vary from uniform dark brown to light brown with 4 or 5 evenly spaced dark bands; body scales usually with at least a trace of a central pale spot; head with 3 short stripes around eye, one posterodorsal, one posterventral, and one running from midventral eye above the maxilla and ending at its distal tip, these markings sometimes obscure on dark individuals; occasionally a small dash behind distal tip of maxilla and a dark blotch at the anterior-dorsal opercle; dark ocellus, approximately eye-sized, on ventral opercle and subopercle, present on all specimens above 15 mm SL; branchiostegals usually with dark ventral margin; dorsal and anal fins vary from completely dark to as described in types; caudal always with some pale spots, usually with narrow, pale margin; pectoral fins dark; pelvic fins from uniformly dark to spotted, striped, or with pale chevrons.

DISTRIBUTION AND HABITAT

This species ranges from the Andaman Islands and the west coast of Sumatra and Java, to Cocos-Keeling and Christmas Islands, eastward to the Moluccas, north through the Philippines to the Ryukyus, the southern Mariana Islands, Palau, the Caroline, Marshall, Gilbert, Phoenix, and Tokelau Islands, Samoa, Tonga, Fiji, and back west through the New Hebrides (Vanuatu), Santa Cruz, and Solomons (Fig. 16). Bleeker (1857:479) provides a reliable literature record of Prigi, Java. This species displays a typical Caroline Islands conduit-type distribution (Springer, 1982). It is interesting to note its apparent absence from New Caledonia and the Great Barrier Reef, contrary to some recent faunal compendia (e.g., Randall, Allen, and Steene, 1990:133; Rivaton et al., 1989:61). It is usually collected in less than 3 m of water, often within 1 m of the surface. Myers (1989:113) writes that it is "relatively common on reef flats where it lurks under rocks or in crevices for the small fishes and crustaceans upon which it feeds." X-ray radiographs indicate that gastropods also form an important component of its diet.

COMPARISONS

Plesiops corallicola is the only species of the genus to have an eye-sized ocellus on the ventral opercle and subopercle. This feature is present on all specimens above about 15 mm, and certainly on those above 20 mm. Only 3 other species have pale spots on the body, but none have the opercular ocellus, and they differ in other meristic features: *P. nigricans* has more predorsal scale rows (8–10 vs. 7–8) and more cheek scale rows (6–7 vs. 4–5);

P. multisquamata has higher scale counts in almost all features, for example, upper lateral line (26–30 vs. 19–20), midlateral series (29–33 vs. 24) and scales below upper lateral line (12–13 vs. 8–9); *P. nakaharai* has a much higher dentary pore:SL ratio (average 0.93 vs. 0.34, and ranges do not overlap, 0.61–1.36 vs. 0.22–0.56). Additionally, none of these species are known to be sympatric. It is unlikely that any other species would be confused with *P. corallicola*. The high number of branches on the 6 ventralmost pectoral-fin rays (usually more than 25), low number of pectoral-fin rays (20–22), low dentary pore:SL ratio, and colouration make it distinctive.

BIOLOGICAL REMARKS

Despite the wide range of this species, it exhibits very little geographic variation in the meristic characters surveyed here (e.g., gill raker counts, Table 10). Only number of pectoral-fin rays and dentary pore:SL ratio suggest possible trends. For the former character, the Mariana Islands populations tend to have higher numbers of fin rays than others, although the modal number is the same as that for all populations combined (Table 10). The few Phoenix Island specimens available tend to have slightly fewer pectoral-fin rays (Table 10). Dentary pore:SL ratios are highest, on average, for Cocos-Keeling Islands and Andaman Islands specimens, and lowest in the Gilbert Islands and Phoenix Islands (Table 11). However, the ranges of all other populations at least partially overlap those of these populations. Even the 2 extremes, the low Gilbert Islands and high Cocos-Keeling Islands populations, do not show significantly different correlations between pore number and SL (ANCOVA, $p > 0.05$), although larger sample sizes might alter this conclusion.

Plesiops corallicola appears to breed the year round throughout its range. Gravid females have been found in all months of the year except September and February. Only 1 specimen from each of these months was sexed, and both were male. Of the 385 specimens available, 127 were assigned a sex; 61 were male and 66 were female. The size range of identifiable females was 48.5–124.8 mm, and the smallest gravid female was 58.7 mm; identified males ranged from 18.0–115.3 mm. If sex-changing occurs in this species, it seems unlikely to be size-related (and by inference, age-related). A log likelihood ratio test (G-test) proves to be insignificant ($G = 0.098$, $0.75 < p < 0.90$), which does not permit a rejection of the null hypothesis that the sex ratio is 1:1.

TAXONOMIC REMARKS

Plesiops corallicola has a rather unusual taxonomic history. Apparently this species was collected by van Hasselt who provided a figure identified as *Cirrioptera corallicola*. Bleeker (1853c) lists this name as a synonym in his description of *P. corallicola*, but the name's *icon inedit*

status makes it invalid as such. However, it is interesting that Rüppell (1835:5, translation) mentions as a footnote in his section on *Plesiops* that "Our museum possesses a third kind of *Plesiops*...found in the Java Sea. This kind was collected by von Kuhl [*sic*] and called *Plesiops corallicola* in the Leiden Museum." Thus, the species had been labelled in museums and named in the literature at least 18 years before it was described by Bleeker in 1853!

Bleeker (1853c) described *P. corallicola* from 2 specimens, 116 mm TL and 162 mm TL, from Sumatra. Identifying the specimens that are the Bleeker primary types of this species has proven difficult. Late in his career, Bleeker (1875) synonymized 3 of the 4 species then recognized, *P. corallicola*, *P. coeruleolineatus*, and *P. nigricans*, under the name *P. nigricans*, and relabelled all the specimens, including types, as *P. nigricans*. When the Bleeker collection was auctioned in 1879, it contained specimens labelled only *P. nigricans* and *P. oxycephalus*. The 42 specimens of the former were divided into 5 series within Group III for the auction, with 34 in series A, and 2 in each of series B through E (Hubrecht, 1879). The A series was purchased through the auction by the Rijksmuseum van Natuurlijke Historie in Leiden (RMNH), and the B and E series are reported to have been sent or sold to this same institution at a later date (Whitehead, Boeseman, and Wheeler, 1966). However, only 36 Bleeker *nigricans* specimens are presently identified in the RMNH collection (rather than the expected 38). I have not been successful in locating the remaining 6 of the original 42 specimens. The British Museum is reported to have purchased the C and D collections, but they do not presently have any Bleeker specimens of *Plesiops* (A. Wheeler, pers. comm.). Some species of the C series were purchased for the National Museum of Victoria, but these did not include any *Plesiops* (Dixon and Huxley, 1982). The Muséum Nationale d'Histoire Naturelle in Paris houses three Bleeker specimens of *Plesiops*, all from Sumatra; this makes them potential types of *P. corallicola*. Two of these, MNHN 2974 (60.0 mm TL) and MNHN 2975 (48.0 mm TL), are much too small, and the latter I have reidentified as *P. coeruleolineatus*. The third specimen, MNHN A8026 (102 mm TL) is a closer match to the smaller Bleeker syntype (116 mm TL), but is still too small and shows none of the characteristics of Bleeker type material. Whether or not these 3 specimens were part of the Bleeker specimen auction, or how the Paris museum obtained them is not known.

Among the 36 RMNH Bleeker specimens, 26 are referable to *P. coeruleolineatus* (including the holotype of *P. melas* Bleeker, 1849), so it is possible that the missing 6 specimens might not have any bearing on the identification of the primary types of *P. corallicola*. As noted above, Bleeker (1853c) reported the lengths of the syntypes as 116 mm and 162 mm TL. Presuming that the

types were included in the A series purchased by the RMNH, 6 of the 10 specimens referable to *P. corallicola* are large enough to be candidates as primary types. Only one of these approaches the smaller Bleeker type (114.5 mm TL) and is here designated the lectotype. The largest specimen reaches 153.5 mm TL (25 mm longer than the next largest), and despite not being as close a match as might be desired, is here designated the paralectotype.

ETYMOLOGY

Bleeker (1853c) apparently chose "corallicola" to refer to the habitat of this species, as this name is Latin for "coral dweller."

Plesiops facicavus sp. nov.

Figs. 10, 17, 18; Tables 1–5

Plesiops sp. 2.—Mooi, 1993:286.

TYPE MATERIAL

Holotype. USNM 146471, 46.3, Togian Bay, Togian Island, Sulawesi, "Albatross," 19 Nov. 1909.

Paratype. USNM 315538, 45.8, collected with holotype.

DIAGNOSIS

Anterior of head densely speckled with small (0.5 mm), dark brown spots (Fig. 18); sensory pores on head sparse and very large, especially those of interorbital region (up to 1 mm); only 5 dentary pores, also large (Fig. 18); upper lateral-line scales 18, all but first 2 scales with anterior pore uncovered by preceding scale; predorsal scale rows 10; cheek scale rows 5; pectoral-fin rays 18.

DESCRIPTION

Meristic and morphometric data based on both type specimens, 45.8–46.3 mm.

Fins. Dorsal-fin spines, rays XII,7; 5th dorsal-fin ray longest; anal-fin spines, rays III,8; 5th or 6th anal-fin ray longest; pectoral-fin rays 18, 17 on right side of paratype; ventralmost ray unbranched; total number of branches on ventral 6 pectoral-fin rays 9–11; pectoral fins without fringe, no free pectoral-fin rays; pelvic-fin spine, rays I,4; first pelvic-fin ray about 2.5–3× times as long as 2nd, thin and not particularly thickened (although thicker than other pelvic rays), first pelvic-fin ray extending 2 scales beyond 8th anal-fin ray; 4th pelvic-fin ray branched or unbranched; principal caudal-fin rays (upper + lower) 10 + 9 holotype, 9 + 9? paratype; procurrent caudal-fin rays (upper + lower) 4 + 4 holotype, 5 + 4? paratype.

Gill rakers. Upper + lower 4 + 9 holotype, 4 + 10 left, 4 + 12 right paratype; total 13 holotype, 14 left, 16 right paratype.

Scales. Body scales usually open-centred. Lateral-line

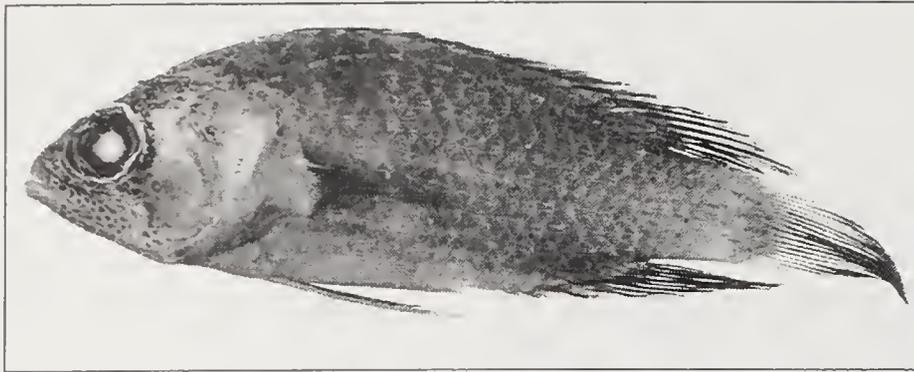


FIG. 17. *Plesiops facicavus* sp. nov. Holotype USNM 146471, 46.3 mm, Sulawesi.

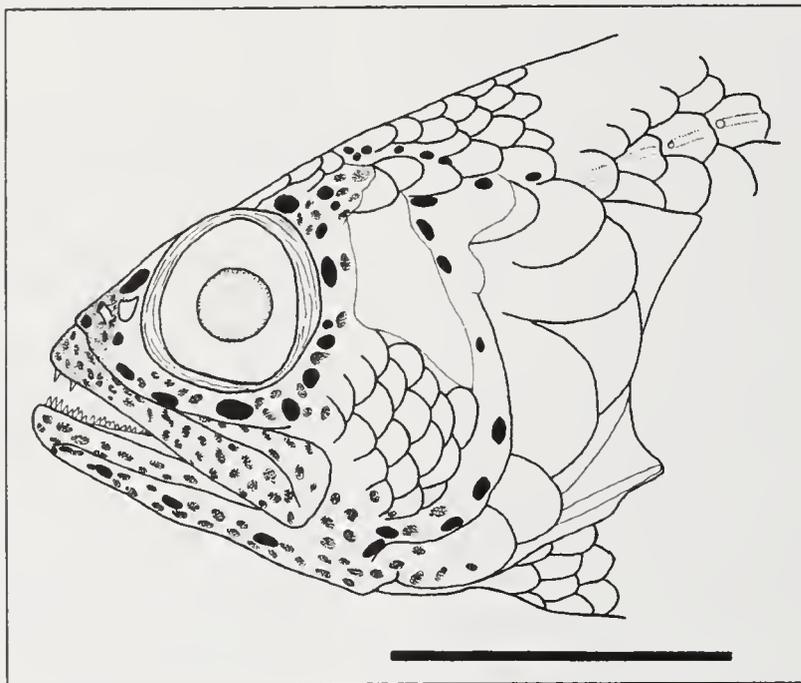


FIG. 18. *Plesiops facicavus*. Lateral view of head of holotype USNM 146471, 46.3 mm. Solid black areas are sensory pores, stippled areas on skin represent darkly pigmented areas. Area on dorsal cheek without scales indicates abraded region on head. Scale bar = 10 mm.

scales with simple tube, without a midposterior lobe on upper line, with a midposterior notch on lower line. Upper lateral-line scales 18; lower lateral-line scales 7, 8; midlateral series 24; scale rows above upper lateral line to origin of dorsal fin 3; scale rows below upper lateral line to origin of anal fin 9; predorsal scale rows 10; cheek scale rows 5; circumpeduncular scales 16; number of upper lateral-line scales with anterior pore not covered by preceding scale 16; anterior pores of lower lateral-line scales uncovered; first ctenoid upper lateral-line scale 10th, 8th; first ctenoid scale below upper lateral-line 6th. Anterior body scales cycloid, remaining so above upper lateral-line. Below upper lateral line, cycloid scales ending at 6th lateral-line scale and extending forward to pectoral-fin base and then ventrally to pelvic-fin base. All scales posterior to this line ctenoid.

Cephalic sensory pores. See Fig. 18. Sparse and relatively large. Dentary pores 5; pores in interorbital region very large (up to 1 mm); no pores posterior to maxilla

linking preopercular to suborbital pore series.

General morphology. As percentage of SL: body depth at anal-fin origin 31; body width at pectoral-fin base 16; caudal-peduncle length 16; caudal-peduncle depth 13; predorsal length 41, 43; preanal length 69, 66; prepelvic length 35, 39; dorsal-fin base 55; longest dorsal-fin ray 27; anal-fin base 20; longest anal-fin ray 27; pectoral-fin length 25, 27; pelvic-fin length 53, 57; head length 40.

Head. Relatively narrow, pointed and long-snouted. Maxilla extending just beyond posterior margin of orbit. As percentage of HL: snout length 20; upper-jaw length 50; bony-interorbital width 8, 9; posterior internasal width 14, 15; orbital diameter 36, 30; head depth at posterior margin of orbit 63; head depth at posterior margin of preopercle 74, 77; head width at dorsal tip of preopercle 47, 51.

Osteology and myology. Dorsal formula 0/0/2/1+1/1; epurals 3; epaxial musculature extends onto frontals anterior to sphenotic, dorsal (medial) muscle bundles in advance of lateral; adductor mandibulae with an addition-

al thin sheet of fibres originating from sphenotic and pterotic as well as usual main body originating from posterior suspensorium.

Colour when fresh. Unknown.

Colour of holotype (in ethanol). See Fig. 17. Body red-brown with faint trace of pale stripes; caudal peduncle with 2 faint dark, elongate spots, one above the other, one being below and the other above the lower lateral line; head pale brown with very short dark bars just posterior to eye, one ventral and one dorsal; interorbital, frontals to expaxial muscle attachment, premaxilla, first 3 suborbitals, maxilla, lower lip, dentary, area between dentaries, ventral portion of cheek, preopercle, and interopercle speckled with numerous, small, dark brown spots (< 1.0 mm); dorsal portion of cheek and opercle unmarked; dorsal fin dark, spines with lighter tips; anal fin dark; caudal fin dark with an interrupted pale crescent; pectoral fins unmarked; pelvic fins with very small and dense pigment spots making them appear brown. Paratype similar to holotype but with a trace of spotting on body.

DISTRIBUTION AND HABITAT

Known from only 2 specimens collected by the "Albatross" Expedition in 1909 in Togian Bay, Togian Island, Sulawesi (Fig. 10, p. 16).

COMPARISONS

Plesiops facicavus is most likely to be confused with *P. cephalotaenia*, *P. gracilis*, or *P. oxycephalus*, whose ranges it overlaps. It differs from these (and all other taxa) in having only 5 large dentary pores (vs. 6 or more), only a few large interorbital dentary pores (vs. more numerous small pores), and a speckled face (vs. no speckles). It also has more upper lateral-line scales with the anterior pore uncovered (16 vs. 11 or fewer). All other species normally have more than 18 pectoral-fin rays and 18 upper lateral-line scales, and only *P. multisquamata* and *P. nigricans* have as many predorsal scale rows (10).

TAXONOMIC REMARKS

These two specimens were listed by Fowler and Bean (1930) as material of *P. nigricans* (non Rüppell), and accompanied by a description which is a hybrid between that of *P. coeruleolineatus* and *P. corallicola*, which certainly does not match these individuals. Inger (1955) reexamined these specimens and considered them a colour variant of *P. oxycephalus*. However, as noted in "Comparisons," these two species are quite different.

ETYMOLOGY

The specific name is a combination of the Latin "facies" meaning "face," and "cavus" meaning "excavated," in reference to the large sensory pores on the head of this species. The name is to be treated as a noun in apposition.

Plesiops genaricus Mooi and Randall, 1991

Figs. 7b, 10, 19, 20b, 21; Tables 1–5

Plesiops sp.—Allen et al., 1976:396 [in part]; Russell, 1983:46.

Plesiops genaricus Mooi and Randall, 1991:384, figs. 3, 5b, 6b, 8–9.

TYPE MATERIAL

Holotype. CAS 13808, ♂ 75.7, Australia, Queensland, One Tree Island, C transect outside lagoon, 6 m, F. H. Talbot, B. B. Collette and party, 26 Nov. 1969.

Paratypes. 253 specimens, 20.5–82.3—AUSTRALIA, Queensland, Great Barrier Reef, CAPRICORN GROUP: AMS I.20464-001, 2♀:58.1–61.5, 3♂:39.2–74.4, One Tree Is., 23°30' S, 152°05' E, 0–1 m, D. F. Hoese and party, 8 Oct. 1972; ANSP 135402, ♂? 34.5, One Tree Is., 3–4 m, 19 Sept. 1968; CAS 67424, 2♀:60.4–61.2, 2♂:41.9–53.0, collected with holotype; BPBM 15941, 4♂:62.8–78.4, One Tree Island, surge channel N side of outer reef, 3–5 m, G. R. Allen, 15 Jan. 1973; LACM 39986-11, 4♀:50.9–57.6, 6♂:44.2–75.8, Heron Is., coral pool, Dec. 1961; ROM 58239, ♀ 76.4, 3♂:63.3–73.2, flat barrier to sand bank 1.6 km NNW of One Tree Is., lagoon side of reef, 0–5 m, V. G. Springer, 25 Nov. 1966; ROM 58240, ♀ 70.9, 14♂:50.6–78.6, 3?:21.4–38.5, Heron Is., outer reef slope, J. H. Choat, 23 Feb. 1967; USNM 274563, 2♀:51.5–58.2, 3♂:69.3–74.5, Heron Is., reef crest pool, J. H. Choat, 13 Feb. 1967; USNM 274570, 18♀:42.0–68.2, 36♂:41.0–72.2, 15?:26.0–40.0, One Tree Is., just above dropoff off reef crest on W side of island, 8–12 m, V. G. Springer, 7 Dec. 1966; USNM 313013, ♂ 69.2, One Tree Is., SW side of island on pie crust coral area, V. G. Springer, 9 Dec. 1966; USNM 274573, 2♀:43.7–49.4, 3♂:58.8–79.0, Heron Is., reef crest pool, J. H. Choat, 14 Feb. 1967; USNM 299024, 2♂:40.8–43.8, Heron Is., reef crest pool, J. H. Choat, 13 Feb. 1967; USNM 299027, 2♀?:58.2–65.2, ? 33.5, Heron Is., reef crest pool, J. H. Choat, 17 May 1966; USNM 299029, 13♀:48.9–66.5, 30♂:40.0–73.7, 6?:34.2–40.0, about 1.6 km from One Tree Is., south reef face, 0–5 m, V. G. Springer et al., 22 Nov. 1966; USNM 299031, 6♀:42.0–53.2, 10♂:35.0–43.6, 12?:30.0–35.0, as USNM 299029; USNM 299034, ♂ 67.0, Heron Is., outer reef slope, J. H. Choat, 3 Feb. 1966; USNM 299035, 4♂:54.2–82.3, 2?:30.0–33.8, Heron Is., reef crest pool, J. H. Choat, 23 Feb. 1967; USNM 299036, 5♀:54.5–69.7, 7♂:43.2–72.2, Heron Is., outer reef slope, J. H. Choat, 23 Feb. 1967; USNM 299037, ♂ 65.0, One Tree Is., 0.8 km NE of island on lagoon side, 0–5 m, V. G. Springer et al., 11 Dec. 1966. AUSTRALIA, Queensland, LIZARD ISLAND: AMS I.19483-026, 13♀:48.5–65.1, 11♂:42.0–69.1, ? 20.5, Sand Cay, windward side of reef flat, 14°38' S, 145°27' E, 1–3 m, Australian Museum party, 27 Nov. 1975.

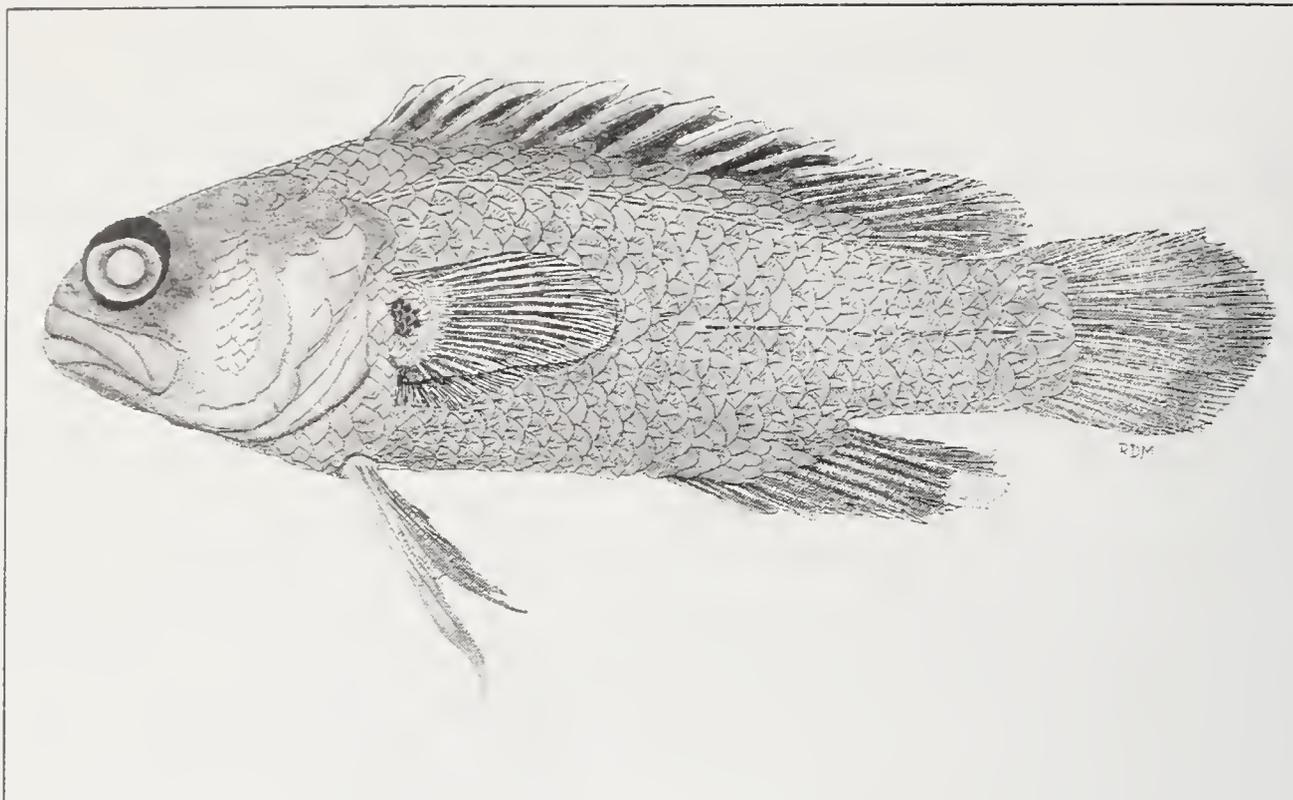


FIG. 19. *Plesiops genaricus*. Holotype CAS 13808, 75.7 mm, Great Barrier Reef. Length of broken left pelvic ray estimated from length of right pelvic ray. From Mooi and Randall (1991:384, fig. 9).

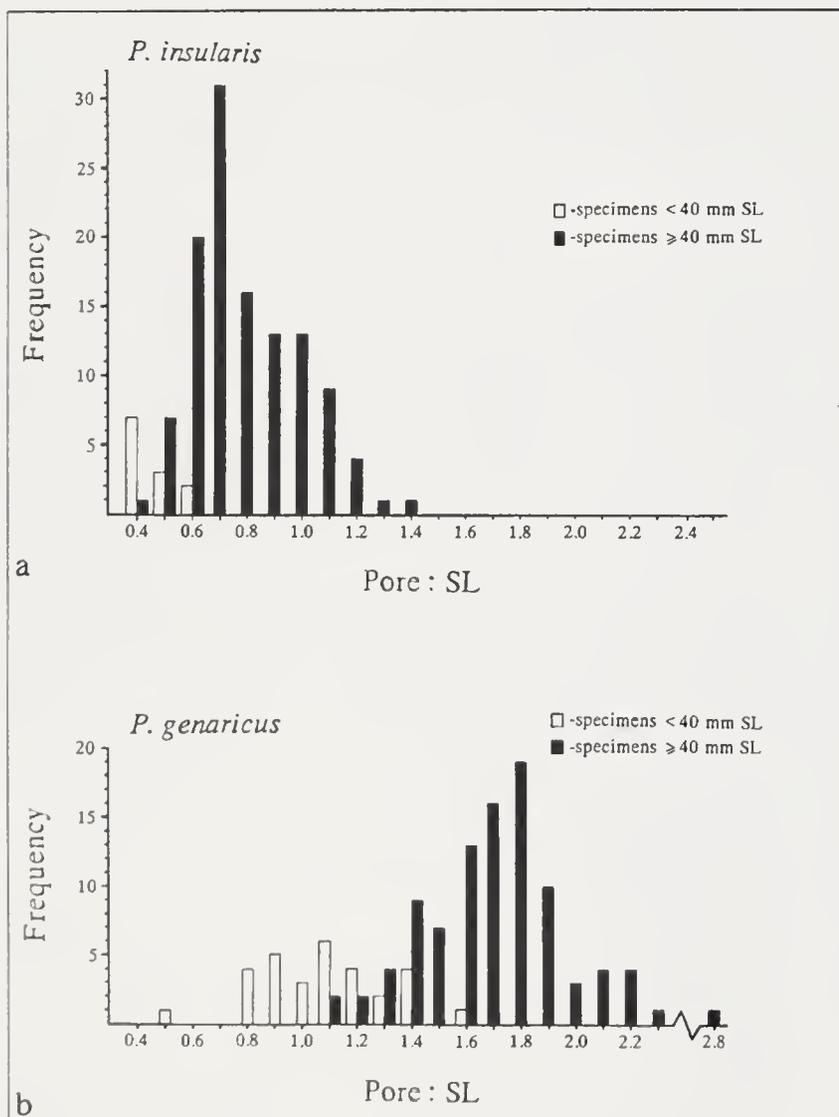


FIG. 20a–b. Frequency of dentary pore:SL ratios in 2 species of *Plesiops*. The frequencies are pooled as classes of ratios centred at intervals of tenths. From Mooi and Randall (1991:381, fig. 6).

- a. *P. insularis*
- b. *P. genaricus*

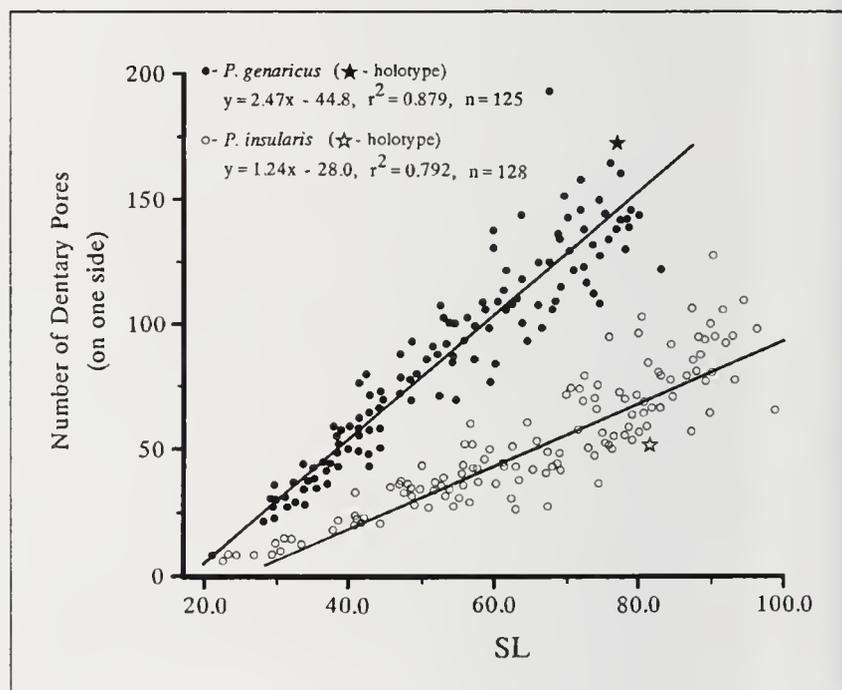


FIG. 21. Number of dentary sensory pores regressed against SL in mm for *Plesiops genaricus* ($n = 125$) and *P. insularis* ($n = 128$). The former species increases the number of pores with respect to SL at almost twice the rate of the latter (slopes significantly different, $F_{1,252} = 699, p < 0.001$). From Mooi and Randall (1991:383, fig. 8).

ADDITIONAL MATERIAL EXAMINED

30 specimens, 35.5–80.0—AUSTRALIA, Queensland: AMS IA.4621 (80.0) North-west Islet, IB.6056 (4:47.0–67.0), IB.6099 (68.0), IB.6230 (2:35.5–48.4), all Swain Reefs, IB.6950 (75.4) Saumarez Reef, I.20770-027 (10:37.0–68.0), I.20770-028 (11:55.0–78.0), both Sir Charles Hardy Is.

DIAGNOSIS

No pale spots on body scales; no opercular or preopercular spots; dorsal-fin spine tips only very slightly paler than remaining fin; scales on pectoral-fin base with dark spot, sometimes absent or obscure; pectoral-fin rays 23 (22–25); cheek scale rows 4 (3–5); skin bearing pore series posterior to eye and on preopercle expanded, limiting visible cheek scales to a narrow area; many sensory pores present immediately posterior to maxilla, resulting in a continuous preopercular, dentary, and suborbital series; dentary pore:SL ratio > 1 on specimens greater than 40.0 mm, averaging 1.8; head wide and round.

DESCRIPTION

Meristic and morphometric data based on 47 of 254 type specimens, 38.5–77.0, except for number of dentary pores based on 125 type specimens, 21.9–82.3.

Fins. Dorsal-fin spines, rays XII,7 (XII,7; XII,6–7); 5th dorsal-fin ray longest (5th; 5th–6th); anal-fin spines, rays III,8; 6th anal-fin ray longest (6th; 5th–7th); pectoral-fin rays 23 (23; 22–25); total number of branches of lower 6 pectoral-fin rays 27 (23; 16–30); branches on ventralmost ray 3 (4; 2–4); pectoral fins with ventralmost rays free of membrane to form a fringe, free pectoral-fin rays 7 (8; 7–9); pelvic-fin spines, rays I,4; first pelvic-fin ray elongate but relatively short for *Plesiops*, and noticeably thickened compared with other rays, first pelvic-fin ray extending to base of 2nd anal-fin ray (1st or 2nd ray; 3rd spine to 5th ray); principal caudal-fin rays (upper + lower) 10 + 8 (9 + 8; 9–10 + 8–10); procurrent caudal-fin rays (upper + lower) 5 + 6 (6 + 6; 4–7 + 4–6).

Gill rakers. Upper + lower 5 + 12 (5 + 13; 4–6 + 11–15); total 17 (18; 15–21).

Scales. Body scales usually open-centred. Lateral-line scales with simple tube, often with a midposterior flap or lobe on upper line, a midposterior notch on lower line. Upper lateral-line scales 20 (20; 19–21); lower lateral-line scales 14 (14; 9–16); midlateral series 24 (24; 24–25); scale rows above upper lateral line to origin of dorsal fin 3 (3; 2–4); scale rows below upper lateral line to origin of anal fin 9 (9; 8–10); predorsal scale rows 7 (7; 6–8); cheek scale rows 3 (4; 3–5); circumpeduncular scales 16 (16; 15–16); primary anterior pore of each upper lateral-line scale covered by preceding scale, except occasionally the last; anterior pores of lower lateral-line scales usually uncovered; first ctenoid upper lateral-line scale 8th (9th;

6th–14th); first ctenoid scale below upper lateral line 5th (5th; 3rd–8th). Anterior body scales cycloid, sometimes remaining so above upper lateral line, but usually becoming ctenoid by 11th (6th–15th, 9th in holotype) upper lateral-line scale. Below upper lateral line, cycloid scales ending at 5th (5th; 3rd–8th) scale and extending forward to pectoral-fin base and then ventrally to pelvic-fin base. All scales posterior to this line ctenoid. Cheek scales not visible as far as posterior end of maxilla (Fig. 7b, p. 10).

Cephalic sensory pores. See Figs. 7b, 20b, 21. Small and numerous. Dentary pore number varying with SL and ranging from 10–190 (holotype 171), but generally forming a ratio with SL of > 1 (\bar{x} = 1.8, range = 1.1–2.8 for SL > 40 mm, holotype 2.3). Many pores present posterior to maxilla which link preopercular and dentary series to suborbital series. Skin bearing pore series posterior to eye and pore series on margin of preopercle very wide, limiting visible cheek scales to a narrow area.

General morphology. As percentage of SL: body depth at anal-fin origin 29 (29; 26–31); body width at pectoral-fin base 21 (19; 15–22); caudal-peduncle length 19 (19; 16–20); caudal-peduncle depth 15 (14; 13–16); predorsal length 38 (38; 36–41); preanal length 65 (65; 62–70); pre-pelvic length 34 (34; 31–39); dorsal-fin base 53 (54; 51–59); longest dorsal-fin ray 20 (20; 16–24); anal-fin base 20 (20; 17–22); longest anal-fin ray 22 (20; 17–25); pectoral-fin length 25 (24; 21–25); pelvic-fin length 42 (40; 36–45); head length 39 (39; 37–44).

Head. Wide and rounded. Maxilla extending to or beyond posterior margin of orbit. As percentage of HL: snout length 20 (17; 15–20); upper-jaw length 46 (48; 44–51); bony-interorbital width 7 (7; 6–9); posterior internasal width 16 (16; 13–19); orbital diameter 30 (31; 27–35); head depth at posterior margin of orbit 56 (56; 51–62); head depth at posterior margin of preopercle 73 (73; 64–80); head width at dorsal tip of preopercle 58 (58; 49–65).

Osteology and myology. Dorsal formula 0/0/2/1+1/1; epurals 3; epaxial musculature extends onto frontals anterior to sphenotic, lateral muscle bundles in advance of dorsal (medial), the latter not reaching frontals; adductor mandibulae with an additional thick sheet of fibres originating from sphenotic and pterotic, as well as usual main body originating from posterior suspensorium.

Colour when fresh. Unknown.

Colour of holotype (in ethanol). See Fig. 19. Body dark sepia; posterior caudal peduncular scales darker than body; dorsal head, suborbital to cheek, and lips very dark; cheek, ventral portion of opercle, subopercle, and interopercle light; branchiostegal membranes pale except for ventral margin which is dark sepia; a black spot on scales of pectoral-fin base; dorsal fin dark, the spine tips slightly paler than rest of spines, the intermembranes black; soft portion of fin also very dark but with a pale margin; anal

fin very dark; caudal fin dark, but paler than other median fins; pectoral fins dark; pelvic fins dusky, first ray with darker tips. On other specimens, body usually dark sepia, but sometimes faded to light brown; posterior caudal peduncle with 2 elongate spots, each mid-way between lower lateral-line and procurrent caudal rays (not visible on dark specimens); 2 dark blotches behind eye, one posterodorsal, the other posteroventral, and a thin dark line running posteriorly from the midventral eye margin parallel to maxilla and ending slightly beyond posterior maxilla; also a dark stripe on maxilla from anterior tip of supra-maxilla extending off maxilla onto lower portion of cheek to ventral margin of preopercle; cheek, ventral part of opercle, subopercle, and interopercle washed with pale yellow; all head colours and patterns often obscure or absent on dark specimens; branchiostegal membranes pale except ventral margin which is sepia; a dark spot on scales of pectoral-fin base, sometimes absent; all median fins dark or dusky, the tips of dorsal spines slightly paler; soft portion of dorsal fin with pale margin; pectoral fins dark; pelvic fins dusky or pale with speckles.

DISTRIBUTION AND HABITAT

Restricted to the Great Barrier Reef, where it is known from only a few scattered localities from Sir Charles Hardy Island and Lizard Island in the north, to Saumarez, Swain, and Capricorn Group reefs in the south (Fig. 10, p. 16). It is expected to be found in the long intervening part of the reef as well. *P. genaricus* is a shallow-water species, generally occurring in less than 5 m of water on coral reef flats.

In Mooi and Randall (1991), a specimen (AMS IA.4621) recorded from North-west Islet, 10°40' S, 142°07' E, was accepted as valid. Such a record, outside of the Great Barrier Reef, is somewhat at odds with the remaining distribution of this species, and that of other Great Barrier Reef endemics. Considering that there is also a North-west Island in the Capricorn Group, this record deserves reappraisal. The specimen was collected by Melbourne Ward in May 1930, and entered into the register of the Australian Museum in July of that year; the latitude and longitude were entered by another hand more recently. Ward had also collected near the Capricorn Group at Rat Island, Port Curtis in May, 1930 (M. McGrouther, pers. comm.). It seems unlikely that Ward would have collected at the northern North-west Islet and in the Capricorn Group, almost 2000 km apart, during the same month. This suggests that the later added latitude and longitude were incorrectly attributed, and that Ward's specimen was collected in the Capricorn Group.

COMPARISONS

Plesiops genaricus can be distinguished from other large members of the genus that have similarly high or higher dentary pore:SL ratios (*P. corallicola*, *P. nigricans*, *P.*

multisquamata, and *P. nakaharai*) by the absence of pale body spots and the absence of opercular or preopercular spots. *P. malalaxus* is quite similar, but does not have fibres of the adductor mandibulae originating from the skull. *P. genaricus* is most similar to *P. insularis*, but they differ by the following characters: *P. genaricus* has a smaller area of visible cheek scales due to an expansion of the skin bearing the postorbital eye and preopercular pore series (Fig. 7, p. 10); its cheek scales are not visible as far anteriorly as the posterior tip of the maxilla (Fig. 7b); its sensory pores are common immediately behind the posterior tip of the maxilla and form a connection between the dentary, preopercular, and suborbital pore series (Fig. 7b); and it usually has a much higher dentary pore:SL ratio (Fig. 20) (frequency distributions significantly different, $t = 147$, $p < 0.001$). The number of dentary sensory pores increases with SL almost twice as rapidly in *P. genaricus* as it does in *P. insularis* (slopes significantly different, $F_{1,252} = 699$, $p < 0.001$) (Fig. 21).

BIOLOGICAL REMARKS

This species displays no sexual dimorphism in colour or size. Of the 212 specimens for which a sex could be determined, 141 were males and 71 were females. This 2:1 male to female ratio is significantly different from 1:1 ($G = 23.6$, $p \ll 0.001$). Because most of the specimens used to determine this ratio are from the same general locality (Capricorn Group, and Heron and One Tree Islands), it seems possible that it reflects a true male-biased ratio. The reason for such a ratio is not readily apparent, as males and females reach comparable sizes (largest female, 76.4 mm; largest male, 82.3 mm). More study of the biology of this species is required before any explanation can be hypothesized. The smallest gravid female was 47.6 mm, and gravid females were found only in October, November, and December collections, although females were identified in only one other month (February).

TAXONOMIC REMARKS

Faunal listings of the fishes of the Great Barrier Reef in Australia frequently include *P. corallicola* (e.g., Goeden, 1974:8; Grant, 1982:254; Russell, 1983:46; Paxton et al., 1989:526; Randall, Allen, and Steene, 1991:133). It is likely that these works or their sources have identified *P. genaricus* as *P. corallicola*. The latter species is not known from continental Australia (Fig. 16, p. 26).

ETYMOLOGY

The specific name is a combination of the Latin words "gena" meaning "cheek," and "rica" meaning "veil," which refers to the expansion of skin on the cheek which covers a large portion of the cheek scales. To be treated as a noun in apposition.

Plesiops gracilis Mooi and Randall, 1991

Figs. 1b, 5, 6, 10, 22; Tables 1–5

Plesiops sp.—Schroeder, 1980:159, fig. 163.

Plesiops gracilis Mooi and Randall, 1991:374, figs. 1–2, pl. IA.—Mooi, 1993:figs. 12b, 19c, 20b.

TYPE MATERIAL

Holotype. BPBM 31410, 54.0, Palau Islands, Auluptagel Is., SE end, E side of T-shaped peninsula, 7°18'50" N, 134°29'52" E, coral and sand, 6–14 m, rotenone, J. E. Randall, H. A. Randall, and R. L. Pyle, 9 July 1986.

Paratypes. 44 specimens, 30.8–70.0—AUSTRALIA: WAM P.27654-027, 2♂:53.0–54.0, Western Australia, Rowley Shoals, Clerke Reef, lagoon 500 m S of Bedwell Island, 17°18' S, 119°22' E, 2–6 m, rotenone, G. R. Allen and P. Berry, 20 July 1982. CAROLINE ISLANDS: CAS 13989, ♀? 32.4, ♂? 47.6, Yap Island, Tomil Harbour. PALAU ISLANDS: BPBM 9732, 2:51.0–52.3, N side of Arumizu Bay, Urur Is., S of Koror, 1.5–15 m, rotenone, P. Helfrich, E. S. Helfman, and party, 8 July 1969; CAS 13985, 4:47.0–60.1, Auluptagel Is., in small coral embayment formed by Auluptagel, Usa and Ryugu Ids., 7°18'47" N, 134°29'22" E, 7.5 m, rotenone, H.H. Dewitt and party, 18 Sept. 1957; CAS 13988, 5:37.2–58.3, Koror Is., small bay on W side of Arappu Pt., 7°19'20" N, 134°30'13" E, 3 m, rotenone, H.A. Fehlmann and party, 23 July 1955; CAS 67419, 2♀:40.0–55.8, ♂ 60.5, N shore of Koror Is., reef bordering eel-grass flat E of Ebadul's Pier, 7°21'03" N, 134°29'19" E, 3 m, R. R. Harry, H. A. Fehlmann, F. M. Bayer, Sumang, and Rikrik, 4 Aug. 1955; CAS 67420, 2♀?:44.2–46.8, 3♂?:44.0–56.5, Ngarahelngael Pass, 320 m N of Imilkolk section of Auluptagel Is., 7°18'51.5" N, 134°29'52" E, 0–15 m, H. H. Dewitt, Tewid, and Sumang, 19 Sept. 1957; CAS 67421, 3♀:45.6–55.0, 5♂:37.1–62.3, between N tip of Auluptagel and Malakal Is., 7°20'12" N, 134°27'50" E, 0–5 m, H. A. Fehlmann, H. H. Dewitt, Sumang, and Tewid, 7 Oct. 1957; CAS 67422, 30.8, Ngarahelngael Pass just about 45 m N of Ngarahelngael part of Auluptagel Is., 7°19'13" N, 134°29'28" E, 12 m, H.A. Fehlmann, H. H. Dewitt, Sumang, Tewid, and Sengich, 9 Oct. 1957; CAS 67423, ♀ 63.9, ? 43.0, cleared and stained, data as for CAS 67421; ROM 56860, 2♂:47.5–57.4, data as for CAS 67420; ROM 56861, ♀ 58.5, ♂ 46.0, data as for CAS 67421. PAPUA NEW GUINEA: AMS I.17089-006, ♀? 37.7, 3♂:41.1–52.5, Madang Harbor, bay in Krankit Is., 5°11' S, 145°50' E, 1.5–8 m, B. B. Collette and party, 30 May 1970. PHILIPPINES: USNM 226939, ♂ 70.0, Palawan, Puerto Princesa City Market, R. E. Schroeder, Sept. 1965; USNM 226940, ♀ 70.0, Palawan, Puerto Princesa City Market, R. E. Schroeder, 27 Sept. 1976.

ADDITIONAL MATERIAL EXAMINED

33 specimens, 16.0–61.6—NEW GUINEA: BPBM 32598 (16.0) Kranket Is.; USNM 313007 (31.5) Batanta Is., 299019 (♂ 40.5), 299025 (22.8), both Kranket Is. PALAU ISLANDS: CAS 13980 (2:46.8–55.0), 13981 (49.3), both Koror Is., 13982 (47.2), 13987 (34.6), 67904 (5:19.0–58.9), all Babelthuap Is., 13983 (3:50.0–61.6), 67906 (2:41.0–57.0), both Auluptagel Is., 13984 (2:26.0–32.0), 13986 (40.7), 67905 (10:41.0–57.0), all Iwayama Bay. PHILIPPINES: USNM 226957 (36.7) Palawan.

DIAGNOSIS

Body and caudal peduncle with about 9 pale stripes running through centre of scales on dark background, sometimes obscure or inconspicuous; cheek and opercle usually pale or yellow; caudal fin often with pale or yellow central band; dentary sensory pores 6 (5–7); a much enlarged pore at anteroventral end of preopercular series; upper lateral-line scales 19 (19–20); number of upper lateral-line scales with anterior pore not covered by preceding scale 10 (5–16); predorsal scale rows 11 (9–11); cheek scale rows 5 (4–5); pectoral-fin rays 18 (17–19), no pectoral-fin rays free of membrane; head and snout pointed.

DESCRIPTION

Meristic and morphometric data based on all type material, 45 specimens, 30.8–70.0.

Fins. Dorsal-fin spines, rays XII,7 (XII,7; XI–XII,7–8); 5th dorsal-fin ray longest (5th; 4th–5th); anal-fin spines, rays III,8; 5th anal-fin ray longest (5th; 5th–7th); pectoral-fin rays 18 (18; 17–19); ventralmost ray unbranched; total number of branches on ventral 6 pectoral-fin rays 10 (11; 8–19); pectoral fins without fringe, no free pectoral-fin rays; pelvic-fin spine, rays I,4; first pelvic-fin ray about twice as long as 2nd, thin and not particularly thickened (although thicker than other pelvic rays), first pelvic-fin ray extending 3 scales beyond 8th ray (just beyond 8th ray; 6th anal-fin ray–1st ventral procurrent ray); 4th pelvic-fin ray usually branched; principal caudal-fin rays (upper + lower) 10 + 9 (10 + 9; 9–11 + 6–10); procurrent caudal-fin rays (upper + lower) 4 + 4 (5 + 5; 4–6 + 3–6).

Gill rakers. Upper + lower 4 + 12 left, 5 + 13 right (5 + 12; 4–6 + 8–14); total 16 left, 18 right (17; 12–20).

Scales. Body scales usually open-centred (but see Fig. 1b, p. 2). Lateral-line scales with simple tube, often with a midposterior lobe on upper line (Fig. 5, p.9), a midposterior notch on lower line. Upper lateral-line scales 19 left, 20 right (19; 19–20); lower lateral-line scales 13 (13; 8–13); midlateral series 24 (24; 23–25); scale rows above upper lateral line to origin of dorsal fin 3 (3; 3–4); scale rows below upper lateral line to origin of anal fin 9 (9; 9–10); predorsal scale rows 10 (11; 9–11); cheek scale rows 5 (5; 4–5); circumpeduncular scales 16 (16; 15–16);

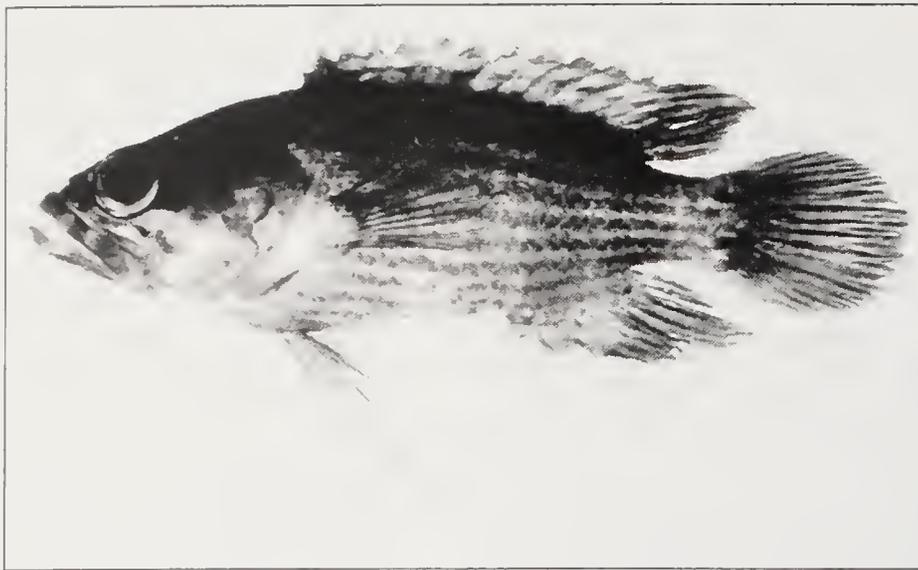


FIG. 22. *Plesiops gracilis*. Holotype BPBM 31410, 54.0 mm, Palau Islands. From a colour slide by J. E. Randall. Appears in colour in Mooi and Randall (1991:pl. IA).

number of upper lateral-line scales with primary anterior pore not covered by preceding scale 12 (10; 5–16) (Fig. 5, p. 9); anterior pore of lower lateral-line scales usually uncovered; first ctenoid upper lateral-line scale 11th (9th; 7th–11th); first ctenoid scale below upper lateral-line 8th (7th; 6th–8th). Anterior body scales cycloid, often remaining so above upper lateral-line, but usually becoming ctenoid by 12th (10th–17th, 17th in holotype) upper lateral-line scale. Below upper lateral line, cycloid scales ending at 7th (6th–8th) lateral-line scale and extending forward to pectoral-fin base and then ventrally to pelvic-fin base. All scales posterior to this line ctenoid.

Cephalic sensory pores. See Fig. 6 (p. 10). Relatively sparse. Dentary pores 5 left, 6 right (6; 5–7, once 9); a much enlarged pore at ventral end of preopercular series; no pores posterior to maxilla linking preopercular to sub-orbital pore series.

General morphology. As percentage of SL: body depth at anal-fin origin 32 (31; 29–35); body width at pectoral-fin base 17 (17; 15–20); caudal-peduncle length 15 (16; 14–20); caudal-peduncle depth 13 (14; 13–15); predorsal length 42 (42; 39–46); preanal length 69 (68; 64–72); pre-pelvic length 38 (38; 35–42); dorsal-fin base 51 (52; 46–69); longest dorsal-fin ray 28 (26; 21–33); anal-fin base 19 (20; 18–22); longest anal-fin ray 29 (27; 20–33); pectoral-fin length 27 (27; 24–31); pelvic-fin length 59 (53; 41–63); head length 42 (42; 40–45).

Head. Relatively narrow, pointed, and long-snouted. Maxilla extending to, or almost to, vertical at posterior margin of orbit. As percentage of HL: snout length 21 (21; 18–25); upper-jaw length 46 (46; 43–50); bony-interorbital width 6 (6; 5–7); posterior internasal width 11 (11; 9–14); orbital diameter 31 (31; 26–37); head depth at posterior margin of orbit 60 (60; 55–66); head depth at posterior margin of preopercle 73 (71; 65–79); head width at dorsal tip of preopercle 45 (45; 39–54).

Osteology and myology. Vertebrae (abdominal + caudal) 10 + 15, holotype 10 + 14; dorsal formula 0/0/2/1+1/1; epurals 2 (3; 2–3); epaxial musculature extends onto frontals anterior to sphenotic, dorsal (medial) muscle bundles in advance of lateral; adductor mandibulae with an additional thin sheet of fibres originating from sphenotic and pterotic as well as main body originating from posterior suspensorium.

Colour when fresh. From slide of holotype, Fig. 22 (Mooi and Randall, 1991:pl. IA). Body background sepia with 9 longitudinal pale stripes through centre of scales, 7 such stripes between bases of anal- and dorsal-fin rays, 5 on caudal peduncle; dorsal head and dorsal-fin sheath darker sepia gradually fading ventrally; scales at caudal-fin base darker than rest of peduncle; posterior caudal peduncle with a dorsal and a ventral elongate spot halfway between lower lateral line and procurrent caudal-fin rays; 2 dark blotches behind eye, one posterodorsal, the other posteroventral, and a longer smudge running from midventral margin of orbit just above maxilla as far as vertical from posterior margin of orbit; trace of smudge from end of maxilla posteroventrally to preopercular edge; scaled portion of cheek and ventral half of opercle copper-yellow; branchiostegal membranes pale except ventralmost which is red-brown with a sky blue margin; maxilla dark with 2 light bands about $\frac{1}{3}$ and $\frac{2}{3}$ from tip of snout respectively; iris of eye blue; dorsal spines and fleshy extensions tipped with yellow-orange; a transparent stripe on each membrane ventral to orange tips except on last spine-first ray membrane; rest of dorsal-fin spines and rays dark with a light median blue stripe from 2nd spine to 3rd ray; anal fin dark with trace of median blue stripe from 1st spine to 3rd ray and a reddish brown stripe distal to this from the 2nd spine to 1st ray; pectoral fins dark; pelvic fins light or transparent with copper-yellow chevrons on membranes between rays making fin appear

yellow, spine and tips of 1st ray dark; caudal fin dark with trace of a red-brown crescent mid-fin.

From colour notes of a very small specimen (BPBM 32598, 16.0 mm, New Guinea), body with 12 narrow, brown body stripes; lips, side of snout and top of head orange; mid-dorsal fin with pale yellow line, and tips of dorsal fin spines red-orange; 2 spots on posterior caudal peduncle, one above the other; red-orange area in caudal.

Colour of holotype (in isopropyl alcohol). Same patterns as in life but no colours apparent. Yellow of fins has gone pale, rest of fins dark. On other specimens body background varying from pale straw yellow in old specimens to dark brown or almost black; stripes can be obvious, often in smaller specimens, to very faint traces on larger and darker individuals; scales just anterior to caudal fin usually dark; posterior caudal peduncle with 2 elongate spots, each midway between lower lateral line and procurrent caudal rays, inconspicuous on dark individuals; blotches behind eye and stripes below as in holotype or more obvious, to absent in dark specimens; presence of yellow cheek and opercle variable, from conspicuous in larger individuals to obscure in smaller ones; lower branchiostegal membranes dark; maxilla usually dark; iris dark but bluish; dorsal fin usually dark, spines with light tips, occasionally a median light stripe visible; anal fin dark; pectoral fins dark; pelvic fins gray or with chevron pattern; caudal fin variable, from completely dark to wide light coloured or yellowish band, the presence of band usually correlated with conspicuously light or yellow cheek patch.

DISTRIBUTION AND HABITAT

Most specimens of this species have been collected in the Palau Islands. The four other localities are Yap, Papua New Guinea, Philippines, and Rowley Shoals off Western Australia (Fig. 10, p. 16). It has not yet been taken in Indonesia, but surely must occur there. This fish has never been collected below 16 m, and has usually been found on reefs in less than 8 m.

COMPARISONS

Plesiops gracilis is most similar to *P. cephalotaenia* Inger, but differs in having fewer dentary sensory pores (5–7 vs. 7–24), more predorsal scale rows (9–11 vs. 6–8), more cheek scale rows (4–5 vs. 3–4), and generally a more pointed head. *P. oxycephalus* Bleeker might be confused with *P. gracilis* because of the cheek and caudal fin colouration, but the body of the former has spots rather than stripes (if a body pattern is present), and differs in other meristic characters, particularly in the number of dentary sensory pores (5–7 in *P. gracilis* vs. 11–40 in *P. oxycephalus*) and the uncovered anterior pores in the upper lateral line (5–16 in *P. gracilis* vs. 0–4 in *P. oxycephalus*). *P. facicavus* also has few dentary pores, but

these are larger in diameter, and the head of this species is spotted, in contrast to *P. gracilis* which has small dentary pores and the typical head pattern of this genus of stripes behind the eye. Otherwise, no other species combines the low number of pectoral-fin rays with such a low number of dentary pores.

BIOLOGICAL REMARKS

Of the 33 individuals for which a sex was determined, 21 were males and 12 were females, although the sex of some individuals was questionable. This ratio is, rather surprisingly, not significantly different from 1:1 ($G = 2.49$, $0.10 < p < 0.25$). Female size ranged from 32.4–70.0 mm, although the 2 specimens smaller than 40.0 mm were only tentatively identified as female. Sex does not appear to be size related, as the 2 largest individuals, both 70.0 mm, represented both sexes. Gravid females were found in collections made in August, September, and October, but the small number of collections available does not permit recognition of a specific breeding period for this species.

This is the only species of *Plesiops* that exhibited any consistent pattern of sexual dimorphism of colour. Specimens were found to exhibit a variety of colour combinations of from broad to no yellow on the cheek, pale striped, dark striped or solid dark body, and from no yellow to a broad yellow subterminal band on the caudal fin. Males were found to have a number of combinations of these colour schemes, but were most often dark-bodied, and had large yellow cheek patches and wide yellow caudal fin bands. Females tended to have very little or no yellow on the cheeks, never had all dark or dark striped bodies, and had much less yellow on the caudal fin.

ETYMOLOGY

The specific name “*gracilis*” is derived from the Latin for “slender,” in reference to the elongate and thin first pelvic-fin ray. It is to be treated as a noun in apposition.

Plesiops insularis Mooi and Randall, 1991

Figs. 2, 7a, 10, 20a, 21, 23; Tables 1–5

Plesiops sp.—Allen et al., 1976:396 [in part]; Kulbicki, Randall, and Riveton, 1994.

Plesiops gracilis Mooi and Randall, 1991:379, figs. 4, 5a, 6a, 7–8, Pl. IB–C.

TYPE MATERIAL

Holotype. BPBM 14762, ♂ 80.5, Lord Howe Island, N. S. W., Australia, reef west of Mt. Lidgbird, 25 m, rotenone, J. E. Randall, G. R. Allen, B. Goldman, B. C. Russell, G. P. Whitley, and D. F. Hoese, 5 Feb. 1973.

Paratypes. 108 specimens, 26.7–98.2—CORAL SEA:

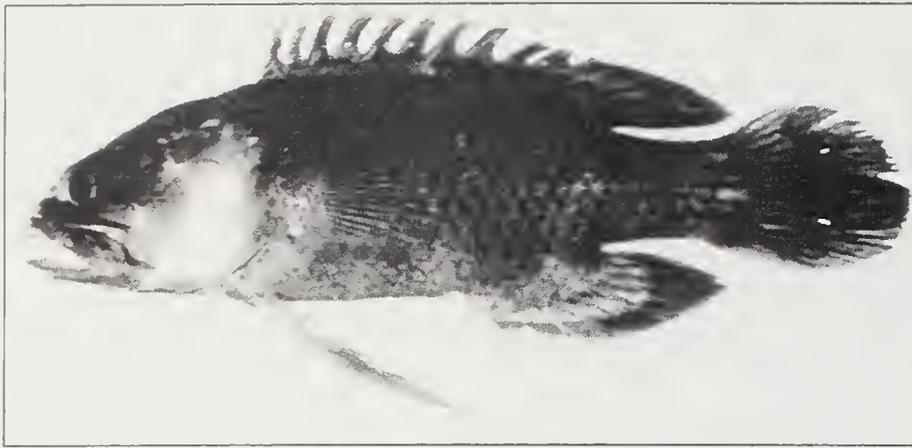


FIG. 23. *Plesiops insularis*. Holotype BPBM 14762, 80.5 mm, Lord Howe Island. From colour slide by J. E. Randall. Appears in colour in Mooi and Randall (1991:pl. IB).

BPBM 33527, ♂ 70.0, Chesterfield Bank, patch reef on SE side of lagoon, 19°53.5' S, 158°28.3' E, 4 m, rotenone, M. L. Kulbicki, J. E. Randall, P. J. Doherty, et al., 19 Aug. 1988. LORD HOWE ISLAND AND VICINITY: AMS I.1482, 80.9, Lord Howe Island, Mr. Etheridge, Nov. 1887; AMS I.17363-004, 6♀:58.7–78.6, 12♂:30.8–98.2, ? 89.1, Lord Howe Island, N.S.W., southern part of lagoon, 31°32' S, 159°04' E, 3–6 m, D. F. Hoese, J. E. Randall, and B. C. Russell, 7 Feb. 1973; AMS I.27142-012, 9♀:45.8–68.5, 8♂:41.0–62.6, 3?:40.8–45.3, Middleton Reef, N.S.W., inside lagoon, 2–3 m, S. Reader, A. C. Gill, and M. Cordell, Dec. 1987; AMS I.27149-006, 3♀:47.5–71.3, 5♂:47.4–80.0, 2?:41.0–53.8, Elizabeth Reef, N.S.W., NE outer slope, 29°54.8' S, 159°2.8' E, 0–10 m, rotenone, S. Reader, A. C. Gill, and M. Cordell, Dec. 1987; BPBM 14828, ♀ 67.1, Lord Howe Island, S of Salmon Beach, 2 m, D. F. Hoese, 9 Feb. 1973; BPBM 14924, ♀ 77.0, Lord Howe Island, North Rock, SE side in 25 m, J. E. Randall, B. C. Russell, and B. Goldman, 24 Feb. 1973; BPBM 33913, 2♀:79.0–80.0, Lord Howe Island, N.S.W., reef W of Mt. Lidgbird, 25 m, rotenone, J. E. Randall, G. R. Allen, B. Goldman, B. C. Russell, G. P. Whitley, and D. F. Hoese, 5 Feb. 1973, collected with holotype; CAS 68316, ♀ 63.5, 2♂:49.8–52.1, as AMS I.27149-006; CAS 68317, 2♂:86.8–87.2, as AMS I.17363-004; LACM 36015-27, ♀ 65.1, ♂ 84.4, Lord Howe Island, off W side of Mt. Lidgbird, Aust. Museum party, 25 Feb. 1973; LACM 36015-28, 2♂:88.6–93.1, Lord Howe Island, near Rabbit Is., Aust. Museum party, 5 Feb. 1973; NMNZ P.11767, ♀ 59.4, 2♂:73.0–90.5, Lord Howe Island; ROM 58237, 3♀:46.7–58.5, 4♂:41.7–65.7, as AMS I.27142-012; ROM 58238, ♂ 89.2, as AMS I.17363-004; USNM 274558, ♀ 74.0, ♂ 57.8, Lord Howe Island, Middle Beach, Aust. Museum party, 11–15 Feb. 1973; USNM 274562, 3:82.7–88.8, Lord Howe Island, N.S.W., lagoon, 31°32' S, 159°04' E, Aust. Museum party, 8 Feb. 1973; WAM P.25650-003, ♀ 71.5, 2♂:84.1–90.0, Lord Howe Island, off W side of Mt. Lidgbird, 31°32' S, 159°04' E, G. R. Allen et al., 5 Feb. 1973. NEW CALEDONIA: BPBM

11433, ♂ 90.7, outside barrier reef off Noumea, 1 km NW of Dumbea Pass, 18 m, rotenone, J. E. and R. D. Randall, P. Fourmanoir, R. Grandperrin, and P. Rual, 14 Aug. 1971 (colour photo); BPBM 33944, ♀ 46.4, lagoon S of Ile Puen, 21°59'15" S, 165°57'45" E, reef in 1–2 m, rotenone, M. L. Kulbicki, J. E. Randall, et al., 24 March 1990 (colour photo); BPBM 33945, ♀ 73.0, outside barrier reef off Tenia Is., 22°01'01" S, 165°55'05" E, reef in 2–4 m, rotenone, M. L. Kulbicki, J. E. Randall, et al., 25 March 1990 (colour photo); BPBM 33946, 2♀:73.0–75.5, 2♂:57.0–80.2, New Caledonia, lagoon near SE end of St. Vincent Pass, 22°02'06" S, 165°57'48" E, reef in 2–4 m, rotenone, M. L. Kulbicki, J. E. Randall, et al., 26 March 1990. NORFOLK ISLAND: AMS I.20271-024, 5♀:62.5–78.8, 13♂:26.7–91.6, Bumbora Beach, tide-pools, 29°04'S, 167°56' E, D. F. Hoese and H. K. Larsen, 22 Sept. 1975.

ADDITIONAL MATERIAL EXAMINED

19 specimens, 23.0–96.3—NORFOLK ISLAND: AMS I.10757 (96.3), I.18497-020 (29.9), I.20268-027 (74.1), both Point Hunter, I.20256-014 (2:32.4–80.0), I.20257-016 (5:38.0–87.0), I.20262-016 (4:23.0–30.6), I.20265-002 (68.3), all Duncombe Bay, I.20264-005 (3:23.9–52.8) Sydney Bay, I.20270-010 (75.0) Philip Is.

DIAGNOSIS

No light spotting on body scales; no opercular or preopercular spots; dorsal-fin spine tips only very slightly paler than remaining fin; scales on base of pectoral fin with a dark spot, sometimes obscure or absent; pectoral-fin rays 23 (21–24); cheek scale rows 5 (4–6), and are visible as far forward as posterior tip of maxilla; skin bearing pore series posterior to eye and on preopercle not expanded; dentary pore:SL ratio generally < 1 but usually > 0.5, averaging 0.76; no or few pores immediately posterior to maxilla, suborbital sensory pore series not continuous with those of preopercle or dentary; head wide and round.

DESCRIPTION

Meristic and morphometric data based on 59 of 109 type specimens, 30.8–98.2, except for number of dentary pores based on 128 specimens, all type material and 19 non-type specimens, 23.0–98.2 mm.

Fins. Dorsal-fin spines, rays XII,7 (XII,7; XII–XIII,6–8); 6th dorsal-fin ray longest (5th; 5th–6th); anal-fin spines, rays III,8 (III,7; III,7–9); 6th anal-fin ray longest (6th; 5th–7th); pectoral rays 23 (23; 21–24); total number of branches on ventral 6 pectoral-fin rays 24 left, 25 right (24; 19–30); branches on ventralmost ray 5 left, 4 right (4; 2–5); pectoral fins with ventralmost rays free of membrane to form a fringe, free pectoral-fin rays 8 left, 9 right (8; 7–9); pelvic-fin spine, rays I,4; first pelvic-fin ray elongate but relatively short for *Plesiops*, and noticeably thickened, first pelvic ray extends to base of 3rd anal-fin ray (2nd ray; 2nd spine–6th ray); 4th pelvic-fin ray branched; principal caudal-fin rays (upper + lower) 10 + 9 (9–10 + 9; 8–10 + 8–9); procurrent caudal-fin rays (upper + lower) 5 + 2 (5–6 + 5; 5–7 + 2–7).

Gill rakers. Upper + lower 5 + 13 (5 + 13; 4–6 + 10–19); total 18 (18; 15–24).

Scales. Body scales usually open-centred. Lateral-line scales with simple tube, often with a midposterior lobe on upper line, a midposterior notch on lower line. Upper lateral-line scales 20 (20; 19–21); lower lateral-line scales 14 (14; 11–17); midlateral series 24 (24; 23–25); scale rows above upper lateral line to origin of dorsal fin 3 (3; 2–4); scale rows below upper lateral line to origin of anal fin 9 (9; 8–10); predorsal scale rows 8 (7; 6–8); cheek scale rows 5 (5; 4–6); circumpeduncular scales 16 (16; 15–16); primary pore of each upper lateral-line scale covered by preceding scale, except occasionally the last; anterior pores of lower lateral-line scales usually uncovered; first ctenoid upper lateral-line scale 12th (12th; 2nd–15th); first ctenoid scale below upper lateral line 6th (5th; 3rd–7th). Anterior body scales cycloid, sometimes remaining so above upper lateral line, but usually becoming ctenoid by 10th (6th–19th, 12th in holotype) upper lateral-line scale. Below upper lateral line, cycloid scales end at 6th (5th; 3rd–7th) scale and extend forward to pectoral-fin base and then ventrally to pelvic-fin base. All scales posterior to this line ctenoid. Cheek scales visible anteriorly to the posterior tip of maxilla (Fig. 7a, p. 10).

Cephalic sensory pores. See Figs. 7a, 20a, 21 (p. 10, 32). Small and numerous. Dentary pore number varying with SL and ranging from 8–127 (holotype 51), but generally forming a ratio with SL of < 1 ($\bar{x} = 0.76$, range = 0.44–1.4, for SL > 40 mm, holotype 0.63). Very few or no pores posterior to maxilla linking preopercular or dentary pore series to suborbital series.

General morphology. As percentage of SL: body depth at anal-fin origin 30 (29; 25–34); body width at pectoral-fin base 19 (20; 17–25); caudal-peduncle length 19 (19;

17–22); caudal-peduncle depth 15 (14; 12–18); predorsal length 40 (38; 35–40); preanal length 64 (66; 62–71); pre-pelvic length 34 (35; 32–42); dorsal-fin base 52 (52; 49–58); longest dorsal-fin ray 21 (22; 19–27); anal-fin base 20 (20; 15–23); longest anal-fin ray 22 (22; 19–27); pectoral-fin length 26 (25; 22–27); pelvic-fin length 40 (41; 36–46); head length 39 (39; 35–41). Smaller individuals have a slightly different overall appearance when compared with larger specimens, seeming to have relatively bigger heads, larger eyes, slimmer bodies, and narrower caudal peduncles.

Head. Wide and rounded. Maxilla extending to or beyond posterior margin of orbit. As percentage of HL: snout length 20 (19; 16–25); upper-jaw length 48 (48; 44–54); bony-interorbital width 10 (8; 6–11); posterior internasal width 15 (16; 13–18); orbital diameter 27 (29; 22–33); head depth at posterior margin of orbit 55 (55; 50–67); head depth at posterior margin of preopercle 75 (73; 62–91); head width at dorsal tip of preopercle 50 (56; 45–67).

Osteology and myology. Dorsal formula 0/0/2/1+1/1 (one specimen with 0/0/2/1/1+1); epurals 3 (rarely 2); epaxial musculature extends onto frontals anterior to sphenotic, lateral muscle bundles in advance of dorsal (medial), the latter not reaching frontals; adductor mandibulae with an additional thick sheet of fibres originating from sphenotic and pterotic, as well as usual main body originating from posterior suspensorium.

Colour when fresh. From slide of holotype, Fig. 23 (Mooi and Randall, 1991:pl. IB). Body and base of median fins dark sepia, body lighter anteroventrally near pelvic-fin base; posterior caudal peduncle with a dorsal and an elongate ventral spot half-way between lower lateral line and procurrent caudal-fin rays, but barely discernible; spot on pectoral-fin base obscure; head dark sepia dorsally; 2 obscure dark blotches behind eye, one posterodorsal and the other posteroventral; a more obvious stripe running from the midventral orbit just above maxilla, another from posterior end of maxilla to preopercular margin; cheek lighter, the opercle, subopercle, interopercle, preopercle, and part of branchiostegal membranes yellow to ochre; iris of eye blue peripherally and orange-red around pupil; dorsal fin with a bright blue stripe from base of 1st spine, angling slowly upward until midlength of 12th spine where horizontal to end at 5th soft ray; above this a red-brown stripe following same pattern; tips of spines gray, rest of soft portion of dorsal fin dark sepia with a white marginal stripe; anal fin with similar pattern to dorsal, but blue from base of 3rd spine back to 7th ray, red-brown only to 5th ray; a white marginal stripe on soft portion of anal fin; caudal fin dark on central rays with yellowish on dorsal and ventral third of fin; pectoral fins dark; pelvic fins pale with yellowish tip on elongate first ray. On other specimens, colour can be

similar to above (e.g., BPBM 11433), or quite different, perhaps due to breeding condition. Specimen BPBM 33945 is generally dark with little or no colour except for eye, as above, and a pale reddish median stripe on dorsal-fin spines and membranes; tips of dorsal-fin spines dark; proximal half or two-thirds of rays and membranes of dorsal, anal, and caudal fins pale; posterior caudal peduncle with 2 elongate spots, each mid-way between lower lateral line and procurent caudal-fin rays.

Colour of holotype (in isopropyl alcohol). Body background light brown; sepia spots on posterior margin of scales; posterior peduncle with 2 elongate spots, each mid-way between lower lateral line and procurent caudal-fin rays; 2 dark blotches behind eye, one posterodorsal, the other posteroventral, and a thin dark line running posteriorly from midventral eye margin parallel to maxilla and ending slightly beyond posterior maxilla; a dark blotch from the posterior end of maxilla to ventral margin of preopercle; cheek, ventral part of opercle, subopercle, and interopercle washed with pale yellow; branchiostegal membranes pale except ventral margin which is sepia; all fins dark, tips of dorsal-fin spines slightly paler; a faint submarginal light stripe through first 3 dorsal-fin rays; a dark spot on scales of pectoral base.

On other specimens, body background varying from pale yellow to dark brown; elongate caudal-peduncular spots variably obvious to obscure; blotches and stripes on head varying from as in holotype, to more obvious or absent in dark individuals; lighter cheek varying from conspicuous in most large individuals to obscure in smaller ones; dorsal fin dark, fleshy spine tips often pale, rays often with a thin white margin; soft portion of anal and dorsal fins sometimes with pale submarginal stripe; pectoral and caudal fins dark; pelvic fins dusky or spotted; pectoral-fin base spot variably obvious or obscure.

DISTRIBUTION AND HABITAT

This species is presently known only from islands in parts of the Coral and Tasman seas. These include Lord Howe Island and the nearby Elizabeth and Middleton reefs, Norfolk Island, New Caledonia, and Chesterfield Bank (Fig. 10, p 16). It has been collected to 25 m, but is found most frequently in shallow lagoons and outer reefs. Allen et al. (1976:396) describe it as being "common in coral outside the lagoon in 2–25 m."

COMPARISONS

Plesiops insularis reaches a relatively large size for the genus, the largest specimen being 98.2 mm. It can be distinguished from other large species by the same characters as those described for *P. genaricus*. *P. insularis* is most similar to *P. genaricus*, particularly in colouration, but differs in the following features: cheek scales visible as far forward as the posterior tip of the maxilla as there

is no expansion of the pored areas on the cheek (Fig. 7a, p. 10); few or no sensory pores immediately posterior to the maxilla (Fig. 7a); a usually lower dentary pore:SL ratio (Fig. 20a) (frequency distributions significantly different, $t = 147$, $p < 0.001$). The number of dentary pores increases with respect to SL at only about half the rate that it does in *P. genaricus* (slopes significantly different, $F_{1,252} = 699$, $p < 0.001$) (Fig. 21). All other species of *Plesiops* have much lower dentary pore:SL ratios, and/or have obviously pale dorsal-fin spine tips.

BIOLOGICAL REMARKS

Of the 98 specimens that were assigned a sex, 37 were females and 61 were males. This sex ratio of 1.65 males for every female is significantly different from a 1:1 ratio ($G = 5.94$, $0.010 < p < 0.025$). However, the largest collection (AMS I.27142-012) was composed of 12 females and 12 males, with 3 specimens undetermined. Whether this species does have a sex ratio skewed towards males requires further investigation. Females ranged in size from 45.8–80.0 mm; gravid females ranged down to 45.8 mm. Males reached 98.0 mm, and seem to reach larger sizes than females. There is some evidence for sexual dimorphism in colouration, as females tend to be lighter coloured, especially on the fin bases, and have less obviously pale cheeks. Some of the smaller males also exhibit this paler colour. Females have been collected in only four months of the year, February, March, September, and December, and gravid females have so far been found in only the latter 2 months.

ETYMOLOGY

The specific name "insularis" is Latin for "of islands," referring to the presently known distribution, being islands in the New Caledonia Basin region. It is to be treated as a noun in apposition.

Plesiops malalaxus sp. nov.

Figs. 16, 24; Tables 1–5

Plesiops sp. 3—Mooi, 1993:286.

Plesiops nigricans (non Rüppell, 1828)(?)—Maugé, 1967:108.

TYPE MATERIAL

Holotype. UMMZ 186072, 96.2, Madagascar, Tuléar, outside barrier reef, 23°S, 44° E, A. L. Maugé and J. E. Bardach, 2–3 Aug. 1964.

Paratypes. 3 specimens, 98.2–110.3—MADAGASCAR: MMNH 71-PE3, 98.2, Tuléar, outer reef slope, spur and groove zone, 6 m, M. L. Harmelin-Vivien, 6 Sept. 1971; ROM 60179, 102.3, Tuléar, outer reef slope, spur and groove zone, 12 m, M. L. Harmelin-Vivien, 7 Nov. 1972;

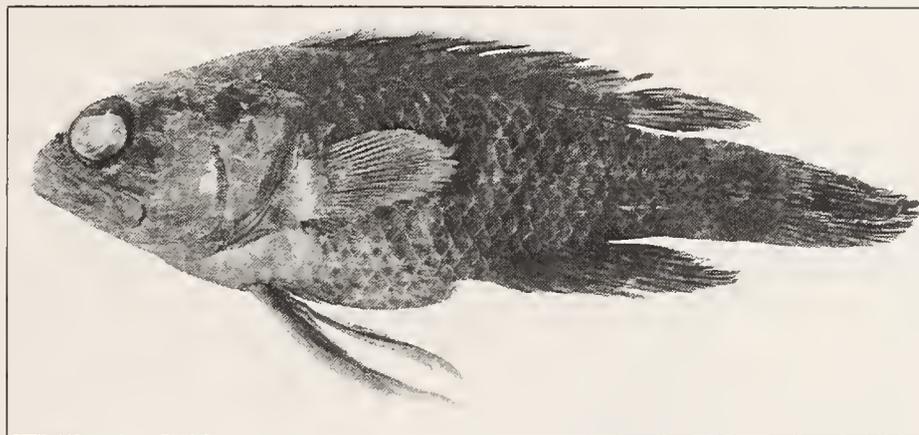


FIG. 24. *Plesiops malalaxus* sp. nov. Holotype UMMZ 186072, 96.2 mm, Madagascar.

USNM 320020, 110.3, Tuléar, reef flat pool, 3 m, M. L. Harmelin-Vivien, 21 Nov. 1969.

DIAGNOSIS

No light spotting on body scales; dorsal-fin spine tips only very slightly paler than remaining fin; no opercular spot; no pale spots on body or median fins; pectoral-fin rays 23 (22–24); total number of branches on lower 6 pectoral-fin rays 30 or more (34–50); sensory pores on head abundant and small, dentary pore:SL ratio of 1.4–2.1, but preopercular, suborbital, and dentary series remain distinct; adductor mandibulae has no fibres originating from the pterotic or sphenotic of the skull; obtains a large size (> 100 mm SL).

DESCRIPTION

Meristic and morphometric data based on all 4 type specimens, 96.2–110.3 mm.

Fins. Dorsal-fin spines, rays XII,7; longest dorsal-fin ray 5th; anal-fin spines, rays III,8; longest anal-fin ray 6th (6th; 5th–6th); pectoral-fin rays 22 left, 23 right (23; 22–24, one specimen with aberrant side with 18); total number of branches of lower 6 pectoral-fin rays 41 left, 37 right (34–50); ventralmost ray branches 5 left, 4 right (5; 4–7); pectoral fins with ventralmost rays free of membrane to form a fringe, free pectoral-fin rays 8 (8; 8–9); pelvic-fin spines, rays I,4; first pelvic-fin ray elongate but relatively short for *Plesiops*, and noticeably thickened, first pelvic-fin ray extends to base of 3rd anal-fin spine or slightly shorter; principal caudal-fin rays (upper + lower) 10 + 9; procurent caudal-fin rays (upper + lower) 5 + 5.

Gill rakers. Upper + lower 5 + 13 left, 5 + 14 right (5 + 14; 5–6 + 12–15); total 18 left, 19 right (19; 17–21).

Scales. Body scales often open-centred. Lateral-line scales with simple tube, no midposterior flap or lobe on upper line, a midposterior notch on lower line. Often small pores present along margins of tube. Upper lateral-line scales 20; lower lateral-line scales 14 (14; 13–14);

midlateral series 24; scales above upper lateral line to origin of dorsal fin 4; scales below upper lateral line to origin of anal fin 9 or 10; predorsal scale rows 6 or 7; cheek scale rows 4; circumpeduncular scales 16; primary anterior pore of each upper lateral-line scale covered by preceding scale; all lower lateral-line scales with anterior pores uncovered; first ctenoid upper lateral-line scale 9th (9th; 8th–9th); first ctenoid scale below upper lateral line 5th (5th; 3rd–5th). Cheek scales visible anteriorly to the posterior tip of maxilla.

Cephalic sensory pores. Small and numerous. Dentary pore number varies with SL and ranges from 145 in the holotype to 210, and forms a ratio with SL of about 1.7 (\bar{x} = 1.7, range = 1.4–2.1, holotype = 1.5). Pores present posterior to maxilla, but preopercular, dentary, and suborbital pore series remain separate and distinct.

General morphology. As percentage of SL: body depth at anal-fin origin 31 (29; 28–31); body width at pectoral-fin base 22 (21; 20–22); caudal-peduncle length 19 (19; 18–19); caudal-peduncle depth 14 (13; 13–14); predorsal length 40 (38; 37–40); preanal length 66 (65; 62–67); pre-pelvic length 35 (35; 33–37); dorsal-fin base 50 (51; 49–53); longest dorsal-fin ray 24 (22; 20–24); anal-fin base 19 (19; 18–20); longest anal-fin ray 23 (22; 21–23); pectoral-fin length 25 (24; 23–25); pelvic-fin length 37 (35; 32–37); head length 42 (40; 39–42).

Head. Rounded. Maxilla extends to or beyond posterior margin of orbit. As percentage of HL: snout length 21; upper-jaw length 48 (49; 48–50); bony-interorbital width 9 (9; 9–10); posterior internasal width 14 (15; 14–16); orbital diameter 28 (27; 26–28); head depth at posterior margin of orbit 56 (57; 56–58); head depth at posterior margin of preopercle 75 (76; 74–79); head width at dorsal tip of preopercle 61 (62; 59–65).

Osteology and myology. Dorsal formula 0/0/2/1+1/1; epurals 3; epaxial musculature extends onto frontals anterior to sphenotic, lateral muscle bundles in advance of dorsal (medial), the latter not reaching frontals; adductor mandibulae with no fibres originating from sphenotic and

pterotic, only a main body originating from the posterior suspensorium.

Colour in life. Unknown.

Colour of holotype (in ethanol). See Fig. 24. Body solid brown, paler on belly, darkest on posterior caudal peduncle; head red-brown with 2 darker brown splotches behind eye, one posterodorsal and one posteroventral, and a thin dark line running posteriorly from the midventral eye margin parallel to maxilla and ending slightly beyond posterior maxilla; head darkest dorsally; branchiostegals dark; dorsal fin dark, tips of dorsal-fin spines pale but dusky; soft portion of dorsal fin dark with a narrow pale margin to 5th ray; anal-fin spines and rays dark with a pale margin to spines continuing to 5th ray; caudal fin black with a very narrow, light terminal margin; pectoral fins dark; pelvic fins dark. Paratypes similar to holotype, but slightly paler, except for USNM 320020 which is much paler. This might be due to their extended preservation in formalin.

DISTRIBUTION AND HABITAT

This species is presently known only from coral reefs near Tuléar, Madagascar (Fig. 16, p. 26). Collection sites are typical for the genus, being tide pools or surge channels in coral to a depth of 12 m.

COMPARISONS

This species is only 1 of 2 which have the primitive condition of the adductor mandibulae with no fibres originating from the skull. Only *P. multisquamata* shares this primitive feature, and this species differs from *P. malalaxus* in having higher scale counts (upper lateral line, 26–30 vs. 20; midlateral series 29–33 vs. 24) and having pale spots on body scales and median fin membranes. The lack of body spots on *P. malalaxus* removes any confusion with *P. corallicola*, *P. nakaharai*, or *P. nigricans*, and its high number of branches on the lower pectoral rays denies confusion with the only 2 sympatric species (*P. mystaxus* and *P. coeruleolineatus*). In shape, it is similar to *P. insularis* (Fig. 23, p.38), but it differs by the adductor mandibulae origin.

ETYMOLOGY

The specific name is a combination of the Latin "mala," meaning "jaw," and "laxus," meaning "loose." It alludes to the maxilla which lacks fibres of the adductor mandibulae attaching it to the skull, which are otherwise present in most species of *Plesiops*. To be treated as a noun in apposition.

Plesiops multisquamata Inger, 1955

Figs. 16, 25; Tables 1–5

Plesiops nigricans (non Rüppell, 1828)—Gilchrist and Thompson, 1911:37; Barnard, 1927:494, pl. XX (fig. 4); Fowler and Bean, 1930:313 [in part]; Fowler, 1935:386; Barnard, 1947:107, pl. 13; Smith, 1952:141, pl. IX; Smith, 1961:186, fig. 410.

Plesiops multisquamata Inger, 1955:264.—Smith and Heemstra, 1986:543, pl. 47.

TYPE MATERIAL

Holotype. Missing. Inger's (1955) description and type designation based on 220 mm TL specimen of Smith (1952:141, pl. IX).

MATERIAL EXAMINED

14 specimens, 44.2–198.0—NATAL, SOUTH AFRICA: ANSP 63831 (♂ 185.0) Durban; BPBM 21774 (♂ 110.7) Kosi Bay; RUSI 723 (198.0) (Smith's second specimen, 1952), 76-16 (3♂:44.2–97.2) Kwazulu, 7827 (193.3) Durban, 26199 (♂ 195.5) Umhloti Pool; USNM 246690 (2♀:123.6–130.7, 3♂:98.6–159.5) Boteler Pt. TRANSKEI, SOUTH AFRICA: RUSI 26198 (♂ 106.6) Bizana.

DIAGNOSIS

Upper lateral-line scales 27 (26–30); scales in midlateral series 32 (29–33); circumpeduncular scales 23 (22–24); scales below upper lateral line to anal-fin base 12 (12–13); larger specimens with head, body and median fins dark, speckled with light-coloured spots.

DESCRIPTION

Meristic and morphometric data based on 14 specimens, 44.2–198.0.

Fins. Dorsal-fin spines, rays (XII,7; XII–XIII,6–7); longest dorsal-fin ray (5th; 5th–6th); anal-fin spines, rays III,8; longest anal-fin ray 6th; pectoral-fin rays (22; 21–23); total number of branches on lower 6 pectoral-fin rays (61–65; 26–85); ventralmost ray with at least 3 branches; pectoral fins with tips of ventral rays free of membrane to form a fringe, free pectoral-fin rays (7; 7–8); pelvic-fin spines, rays I,4; first pelvic-fin ray long and greatly thickened, extending to or beyond anal-fin origin, first pelvic-fin ray extends to 2nd anal-fin ray (1st spine–3rd ray); principal caudal-fin rays 10 + 9; procurrent caudal-fin rays (5 + 3–5).

Gill rakers. Upper + lower (5 + 12; 4–6 + 10–14); total (17; 14–20).

Scales. Body scales with closed centres, except in smallest specimen where *Plesiops* pattern had not yet developed. Lateral-line scales with simple tube, anterior upper lateral-line scales on specimens less than 120 mm SL with 3-lobed posterior edge, posterior upper lateral-

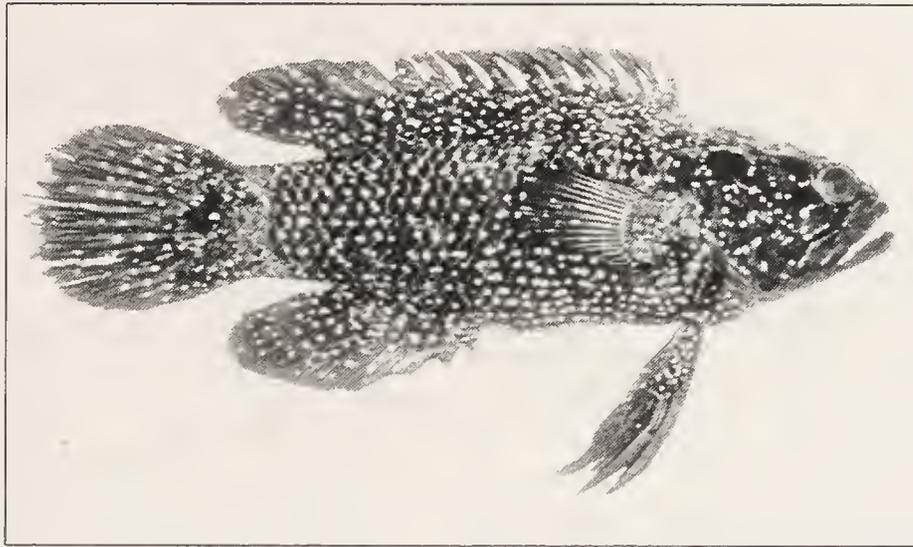


FIG. 25. *Plesiops multisquamata*. BPBM 21774, 110.7 mm, Kosi Bay, South Africa. From colour slide by J. E. Randall.

line scales notched, lower lateral-line scales notched mid-posteriorly, on larger specimens all lateral line scales notched. Upper lateral-line scales (27; 26–30); lower lateral-line scales (15; 13–18); midlateral series (32; 29–33); scales above upper lateral line to origin of dorsal fin (5; 4–5); scales below upper lateral line to origin of anal fin (12; 12–13); predorsal scale rows (10; 8–10); cheek scale rows (6; 5–7); circumpeduncular scales (23; 22–24); primary anterior pore of each upper lateral-line scale covered by preceding scale; all lower lateral-line scales with anterior pores uncovered; first ctenoid upper lateral-line scale (11th; 8th–18th); first ctenoid scale below upper lateral line (6th; 5th–8th). Anterior body scales cycloid, often remaining so above upper lateral-line until 10th (10th; 10th–16th) upper lateral-line scale. Below upper lateral line, cycloid scales end at 6th (6th; 5th–8th) lateral-line scale and extend forward to pectoral base and then ventrally to pelvic base. All scales posterior to this line ctenoid.

Cephalic sensory pores. Small and extremely numerous, all of approximately equal size, number increasing with size of specimen. Dentary pores 28–435, varying with SL, but generally forming a ratio with SL of > 1.0 for specimens over 50 mm ($\bar{x} = 1.86$, range = 0.63–3.0); pores extend past maxilla posteriorly occasionally linking preopercular to suborbital pore series.

General morphology. As percentage of SL: body depth at anal-fin origin (30; 27–34); body width at pectoral-fin base (21; 17–25); caudal-peduncle length (18; 17–20); caudal-peduncle depth (16; 14–18); predorsal length (35; 32–38); preanal length (63; 58–67); prepelvic length (35; 30–42); dorsal-fin base (54; 50–58); longest dorsal-fin ray (21; 19–26); anal-fin base (22; 20–24); longest anal-fin ray (22; 20–27); pectoral-fin length (23; 22–26); pelvic-fin length (36; 32–38); head length (37; 34–39).

Head. Relatively wide and blunt. Preopercular margin fimbriate, resembling serrae, but due to sensory pore

extensions as tubes, becomes more obvious as specimen size increases. Maxilla extends to or beyond vertical at posterior margin of orbit. Bony-interorbital wide, particularly in large specimens. As percentage of head length: snout length (21; 18–25); upper-jaw length (50; 46–54); bony-interorbital width (16; 9–22); posterior internasal width (16; 14–18); orbital diameter (25; 21–30); head depth at posterior margin of orbit (60; 54–67); head depth at posterior margin of preopercle (78; 67–91); head width at dorsal tip of preopercle (57; 49–67).

Osteology and myology. Dorsal formula 0/0/2/1+1/1; epurals 3; epaxial musculature extends onto frontals anterior to sphenotic, lateral muscle bundles in advance of dorsal (medial); adductor mandibulae without additional fibres originating from skull.

Colour when fresh. From Smith and Heemstra (1986:pl. 47, fig. 172.3). Body background dark sepia becoming somewhat lighter ventrally, all body scales with 1–4 small, blue dots. Head dark sepia, lighter on dentary, all of head but upper and lower jaw with small blue dots. Iris of eye brown. All fins brown or dark brown and speckled with small blue spots, although only base of pectoral fin is speckled.

Colour of holotype (in *n*-propyl alcohol). From Smith (1952:143): “Whole of body and fins very dark, almost black, barely lighter on belly. A vague darker area on head at origin of lateral line. Small blue spots, mostly one but sometimes more on each scale, over most of body, head and fins.” Currently, specimen is uniform red-brown with a trace of spotting in caudal. On other specimens (Fig. 25), body uniformly dark, almost black, with 1 or 2 pale small spots on each scale; small specimens with trace of 5–6 wide dark bars on body and spotting, if present, located only ventrally; head usually dark, sometimes lighter ventrally, occasionally with a darker blotch on the dorsal part of opercle at the base of the upper lateral-line; smaller individuals with 2 dark blotches just behind eye,

one posterodorsal and one posteroventral, and a dark, narrow stripe running from the midventral margin of eye along the dorsal border of the maxilla to its distal tip; fins of large specimens dark with small, pale spots; smaller specimens often with spots only on caudal or pelvic fins, sometimes dorsal-fin spines with light tips. Many early writers (particularly Barnard, 1927, 1947) describe this species as having an opercular ocellus or spot because of its misidentification with *P. corallicola*; *P. multisquamata* does not have an opercular ocellus.

DISTRIBUTION AND HABITAT

This species is restricted to the east coast of South Africa, almost all specimens having been collected in Natal (Fig. 16, p. 26). Locality for a J.L.B. Smith specimen is suggested as Bizana, Transkei, but this is not a coastal town. This might refer to the "Bizana Coast", a collecting area sometimes referred to by Smith, and would include the area just south of Natal in the vicinity of Port St. John's in the Transkei (Winterbottom, pers. comm.). The few specimens with complete collection data were caught at depths of 3 m or less, suggesting that it is a shallow water species.

COMPARISONS

This species attains the largest size of any member of the genus, and the high upper lateral-line, midlateral, and circumpeduncular scale counts make it unmistakable. It also has more scales below the upper lateral line (12–13 vs. 8–10) and a generally heavier-bodied appearance.

BIOLOGICAL REMARKS

Two of 12 specimens for which a sex could be determined externally measured 123.6 and 130.7 mm. With such a small sample, no meaningful suggestions can be made pertaining to the breeding biology of this species. In order to determine whether the species are indeed allopatric, more extensive collecting along the east coast of Africa is needed to delimit the complete range of *P. multisquamata* and those of other south African *Plesiops*.

TAXONOMIC REMARKS

Inger (1955:266) described the species without any specimens available to him and stated that the holotype is "220 mm. total length, described by Smith (1952) from Natal and figured in Smith's plate 9." Unfortunately, this specimen cannot be located in the Smith Institute collections (B. Ranchod, pers. comm.). Smith's description refers to 2 specimens, one 220 mm TL designated the holotype by Inger (1955), and one of 245 mm TL. The latter specimen was available as RUSI 723 (198.0 mm SL). According to the label data of this specimen, Inger identified it as the holotype in 1973, although this is clearly in error. The designation of a neotype might be desirable if an exhaustive search cannot locate the smaller Smith (1952) specimen.

ETYMOLOGY

Inger (1955) apparently assigned this name in reference to the relatively high scale counts of this species.

Plesiops mystaxus sp. nov.

Figs. 9, 26; Tables 1–5

Plesiops sp. 4—Mooi, 1993:286.

TYPE MATERIAL

Holotype. ROM 60181, ♀ 54.9, Comores Archipelago, Moheli, reef crest off middle of bay at NE tip of Ouenefou Island 100 m offshore, 12°23'25" S, 43°42'30" E, 0–1 m, rubble and mostly dead coral, calcareous rock, occasional sand patches, rotenone, R. Winterbottom, R. Stobbs, C. Buxton, and W. Holleman, 22 Nov. 1988.

Paratypes. 42 specimens, 12.9–66.1—ARABIAN SEA: BPBM 33953, 2♂:63.0–66.1, 3?:27.0–32.9, Eagle's Retreat, near Miribat, Oman, 16°58'00" N, 54°42'50" E, 6–8 m, rocky bottom, J. E. Randall and J. K. L. Mee, 25 April 1990 (colour photo). COMORES ARCHIPELAGO: ROM 58400, ♀ 35.0, Mayotte, N side of Isle Kakazou adjacent to shore, 12°46'06" S, 45°15'24" E, 0–5 m, rock with sand and rubble, rotenone, R. Winterbottom, C. Buxton, P. Benjamin, W. Holleman, and R. E. Stobbs, 11 Nov. 1988; ROM 60182, 16.2, Mayotte, N coast of Isle Malandzamiayatsini near E tip, 12°40'19"S, 44°03'26.8" E, 0–1 m, 20 m from shore, coral rubble bank with sand channels, rotenone, R. Winterbottom, 16 Nov. 1988; ROM 60183, ♀ 42.0, 6♂:38.2–60.4, ? 17.4, collected with holotype. MADAGASCAR: AMS I.28113-065, ♀ ? 39.6, 3♂:41.1–56.5, Nossi Bé, Andilana Beach 100 m W of hotel, 0.3–2.5 m, 50 m offshore, derris, J. Paxton, B. B. Collette, and D. Cohen, 9 Nov. 1988; MMNH CI-76, 65.5, Tuléar, reef flat pool, M. L. Harmelin-Vivien, 21 Nov. 1969; UMMZ 185567, ♂ 62.5, shallow fringing reef W of Tuléar, J. E. Bardach and A. L. Maugé, 8–9 June 1964. RED SEA: BPBM 18358, ♂ 42.0, Ras Muhammad, S end of Sinai, reef flat at old rock jetty, 27°44' N, 34°15' E, 1 m, rotenone, J. E. Randall, O. Gonahd, and A. Levy, 19 Sept. 1974; TAU P.6391, ♂ 48.6, Nuweiba, Gulf of Aqaba, 28°58' N, 34°38' E, M. Goren, 6 Nov. 1980; USNM 274545, ♂ 35.9, Israel, Strait of Jubal, S end of Sinai Peninsula at Ras Muhammad, 0–10 m, V. G. Springer et al., 26 Sept. 1969; USNM 274546, 2♀:39.3–42.1, ♂ 23.8, NW coast of Gulf of Aqaba, N of Ras Burqa, 0–10 m, V. G. Springer et al., 23 July 1969; USNM 274554, ♀ 43.2, ? 14.9, NW coast of Gulf of Aqaba, reef near road at Marsa Muqabila, 0–2 m, V. G. Springer et al., 29 July 1969; USNM 274555, ♀ ? 29.9, Zubair Is., E. Clark, 30 Sept. 1967; USNM 274557, 2?:12.9–18.2, Ethiopia, 1 km off SW shore of Sciumma Is., 15°32'31" N, 40°00'00" E, 0–7 m, V. G. Springer et

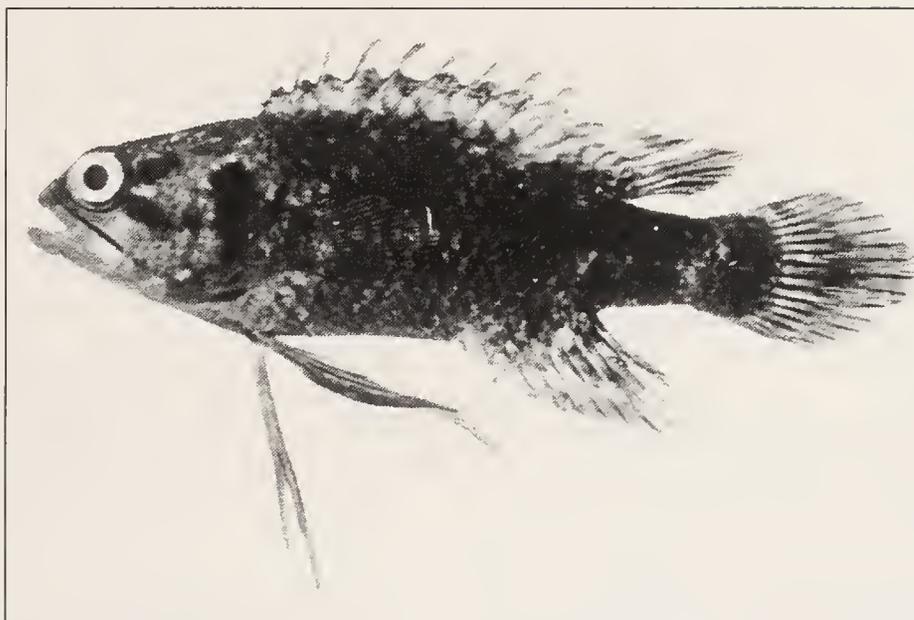


FIG. 26. *Plesiops mystaxus* sp. nov. Holotype ROM 60181, 54.9 mm, Comoro Islands. From colour slide by R. Winterbottom.

al., 9 Aug. 1969; USNM 274559, 2?:18.2–33.7, Ethiopia, Difnein Is., S shore, 16°36' N, 39°20' E, 0–4 m, V. G. Springer et al., 15 Aug. 1969; USNM 313012, 7♂:36.3–53.0, Ethiopia, N end of Isola Delemme just E of Ras Coral, 15°30'30" N, 39°54' E, 0–3 m, V. G. Springer et al., 7 Aug. 1969; USNM 313009, ♂ 53.0, Ethiopia, Massawa, naval base, 0–2 m, V. G. Springer, 12 Aug. 1969.

ADDITIONAL MATERIAL EXAMINED

RED SEA: TAU P.8994 (♂ 27.1) Tiran, Foul Bay South.

DIAGNOSIS

Dark dorsal margin to maxilla; only 2 short dark bars behind eye, one posterodorsal and the other posteroventral; cheek scale rows 3–4; predorsal scale rows 5–7.

DESCRIPTION

Meristic and morphometric data based on 43 type specimens, 12.9–66.1.

Fins. Dorsal-fin spines, rays XII,7; longest dorsal-fin ray 5th; anal-fin spines, rays III,8; longest anal-fin ray 6th; pectoral-fin rays 22 (21: 19–23); total number of branches of lower 6 pectoral-fin rays 21 (15–19; 6–28); ventralmost ray branches 2 (2; 1–4); pectoral fins with ventralmost rays free of membrane to form a fringe, free pectoral-fin rays 9 (9; 7–10); pelvic-fin spines, rays I,4; first pelvic-fin ray elongate and noticeably thickened, first pelvic-fin ray extends to 4th anal-fin ray (4th; 1st–beyond 8th); principal caudal-fin rays (upper + lower) 10 + 9 (10 + 9; 9–10 + 8–10); procurrent caudal-fin rays (upper + lower) 5 + 5 (5 + 5; 5–6 + 4–6).

Gill rakers. Upper + lower 4 + 10 (4 + 10; 3–5 + 8–12); total 14 (14; 11–17).

Scales. Body scales open- or closed-centred. Lateral-

line scales with simple tube, no midposterior fleshy flap or lobe on upper line, a midposterior notch on lower line. Often small pores present along margins of tube. Upper lateral-line scales 19 (rarely 18); lower-lateral scales line 14 (14; 11–15); midlateral series 24, rarely 23; scales above upper lateral line to origin of dorsal fin 3 (3; 2–3); scales below upper lateral line to origin of anal fin 9 (9; 8–9); predorsal scale rows 5 (6; 5–7); cheek scale rows 4 (4; 3–4); circumpeduncular scales 16, rarely 15; primary anterior pore of each upper lateral-line scale covered by preceding scale, except occasionally last scale; all lower lateral-line scales with anterior pores uncovered; first ctenoid upper lateral-line scale 10th (7th–9th; 7th–16th); first ctenoid scale below upper lateral line 5th (5th; 3rd–8th). Anterior body scales cycloid, but becoming ctenoid posteriorly. Cheek scales visible anteriorly to the posterior tip of maxilla.

Cephalic sensory pores. Small and quite numerous. Dentary pore number varies with SL and ranges from 5 to 38 (holotype 25), and forms a ratio with SL of $<< 1$ ($\bar{x} = 0.39$, range = 0.26–0.76, holotype 0.46). Pores present posterior to maxilla, but preopercular, dentary, and suborbital pore series remain separate and distinct.

General morphology. As percentage of SL: body depth at anal-fin origin 31 (30; 27–32); body width at pectoral-fin base 18 (18; 15–21); caudal-peduncle length 21 (19; 16–21); caudal-peduncle depth 13 (15; 13–18); predorsal length 35 (39; 35–45); preanal length 62 (64; 61–70); pre-pelvic length 33 (35; 31–41); dorsal-fin base 54 (54; 51–57); longest dorsal-fin ray 22 (21; 15–31); anal-fin base 21 (20; 17–23); longest anal-fin ray 24 (22; 18–26); pectoral-fin length 25 (26; 22–29); pelvic-fin length 42 (44; 41–51); head length 38 (40; 37–45).

Head. Rounded. Maxilla extends to or beyond posterior margin of orbit. As percentage of HL: snout length 19

(18; 15–20); upper-jaw length 48 (47; 41–52); bony-interorbital width 8 (8; 6–9); posterior internasal width 18 (14; 11–18); orbit diameter 30 (32; 29–37); head depth at posterior margin of orbit 55 (55; 46–63); head depth at posterior margin of preopercle 73 (70; 59–78); head width at dorsal tip of preopercle 55 (53; 41–62).

Osteology and myology. Dorsal formula 0/0/2/1+1/1; epurals 3; epaxial musculature extends onto frontals anterior to sphenotic, lateral muscle bundles in advance of dorsal (medial), the latter not reaching, or just onto frontals; adductor mandibulae with an additional thick sheet of fibres originating from sphenotic and pterotic, as well as main body originating from posterior suspensorium.

Colour when fresh. From slide of holotype, Fig. 26. Body dark sepia, posterior margin of scales darker than anterior portion giving body a spotted appearance; caudal peduncle all dark; head lighter than body with a few scattered pale bluish white spots; 2 dark elongate bars behind eye almost reaching preopercle, one posterodorsal and one posteroventral, each bordered by a blue-white spot at eye; midopercle and subopercle with continuous dark sepia band; branchiostegal membranes dark; maxilla with very dark sepia dorsal margin posteriorly; spines of dorsal fin with orange-red fleshy tips, one half to three-quarters of free membrane pale with a mid dark stripe, rest of spinous portion dark with trace of midfin pale blue stripe; soft portion of dorsal fin dark with pale tips to 5th ray; anal fin dark with wide pale stripe midfin; caudal fin dark with a pale dirty yellow crescent on posterior half of fin; pectoral fins dark, base darker than anterior body; pelvic fins dark, with some paler membranes.

Paratypes: ROM 58400 similar to above but generally paler with trace of 3 body bands and 1 band at end of caudal peduncle; also 4 white spots on preopercle, some on opercle, and flanking bars posterior to eye; pale portion of free spinous membranes with more pigment, so not as pale as holotype. ROM 60182, a very small specimen (16.2 mm), similar but all pigment in individual melanophores, and no orange tips to spinous portion of dorsal fin.

Colour of holotype (in ethanol). As above, but all colours have disappeared. Red tips to dorsal fin pale, blue-white head spots no longer present. Paratypes similar to holotype, differing in the following ways: body often much darker, almost black; head markings not always as obvious except for dark dorsal margin of maxilla; Comores specimens with noticeably paler head dorsally, not found on specimens from other localities except one from Madagascar.

DISTRIBUTION AND HABITAT

Occurs from Tuléar, Madagascar, through the Comores, and into the Red Sea and Gulf of Aqaba, as well as the

Arabian Sea off Oman (Fig. 9, p. 13). It has been collected only as deep as 8 m.

COMPARISONS

This species can be distinguished from all other members of *Plesiops* by the dark dorsal margin of the maxilla and lack of a third stripe running from the midventral margin of the eye just dorsal to the maxilla (Fig. 26). It also tends to have fewer predorsal scale rows than other species found in its range. Colouration and counts are most similar to *P. coeruleolineatus*, but the present species has XII dorsal spines rather than XI, and a dorsal formula of 0/0/2/1+1/1 which *P. coeruleolineatus* never exhibits.

BIOLOGICAL REMARKS

Of the 26 specimens that were assignable to a sex, 18 were male and 8 were female. This 2.25:1 ratio is barely significantly different from 1:1 ($G = 3.96$, $p < 0.05$). Larger collections from single populations are needed to verify this difference.

ETYMOLOGY

The latinized “mystaxus” is derived from the Greek “mystax,” which means moustache, alluding to the unique dark dorsal margin of the maxilla. It is to be treated as a noun in apposition.

Plesiops nakaharai Tanaka, 1917

Figs. 16, 27; Tables 1–5

Plesiops nakaharæ Tanaka, 1917:199.

Pharopteryx nakaharæ—Tanaka, 1918 (1st ed.), 1935 (2nd ed.):497, pl. 137 (fig. 383).

Plesiops nigricans (non Rüppell, 1828)—Fowler and Bean, 1930:313 [in part].

Plesiops oxycephalus—Aoyagi, 1941:429 [in part]; Aoyagi, 1943:92 [in part].

Plesiops corallicola—Inger, 1955:266 [in part].

Plesiops nakaharæ—Sano et al., 1984:12, pl. 6a,b; Masuda et al., 1984:140, pl. 126J; Masuda and Allen, 1987:136.

TYPE MATERIAL

Holotype. ZUMT 8128, 101.8, Shima or Kii, central Japan, Kosaku Nakahara, collection date unknown.

ADDITIONAL MATERIAL EXAMINED

10 specimens, 73.2–107.4—JAPAN: BPBM 18988 (76.6) Miyake-Jima; FUMT-P 1516 (98.8), 3423 (96.6), 21085 (99.4) all Nachi-Katsuura, Kii Peninsula; IORD 80-167 (107.4), 80-168 (100.6) both Futo, Izu Peninsula; YCM-P 12278 (78.1), 12741 (106.9) both Futo, Izu Peninsula; ZUMT 18923 (102.6) Okinoshima, 42795 (73.2) Hachijo Is.

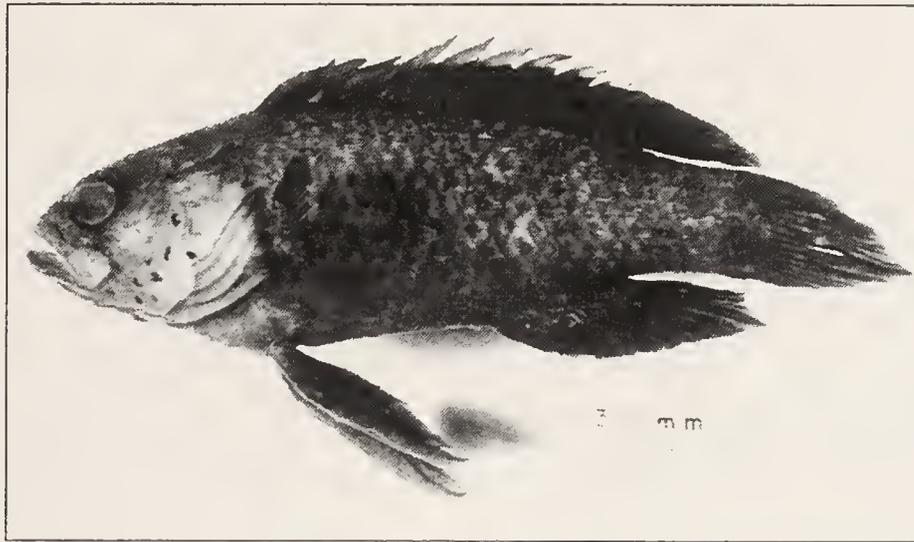


FIG. 27. *Plesiops nakaharai*. IORD 80-167, 107.4 mm, Izu Peninsula, Japan. From a colour slide of a preserved specimen by H. Kishimoto.

DIAGNOSIS

Light central spot on body scales; no large dark ocellus on opercle, but sometimes a small spot on ventral part of opercle; 4 or 5 dark spots, much smaller than eye diameter, on preopercle; no pale spots on caudal fin; pectoral-fin rays 21–22; more than 35 branches in total on ventral 6 pectoral-fin rays; sensory pores on head abundant and small, dentary pore:SL ratio of almost 1.

DESCRIPTION

Meristic and morphometric data based on 11 specimens, 73.2–107.4 mm.

Fins. Dorsal-fin spines, rays XII,7; longest dorsal-fin ray 5th (5th; 5th–6th); anal-fin spines, rays III,8; longest anal-fin ray 6th; pectoral-fin rays 21 (22; 21–22); total number of branches of lower 6 pectoral-fin rays 48 left, 45 right (48; 43–53); ventralmost ray branches 7 (8; 4–8); pectoral fins with ventralmost rays free of membrane to form a fringe, free pectoral-fin rays 8 (8; 7–9); pelvic-fin spines, rays I,4; first pelvic-fin ray elongate but relatively short for *Plesiops*, and noticeably thickened, first pelvic-fin ray extends to 3rd anal-fin spine (2nd ray; 1st spine–3rd ray); principal caudal-fin rays (upper + lower) 9 + 8 (9 + 9; 9–10 + 8–9); procurrent caudal-fin rays (upper + lower) 5 + 5 (5 + 4; 5–6 + 4–6).

Gill rakers. Upper + lower 3 + 9 left, 4 + 10 right, (5 + 9; 3–6 + 8–12); total 12 left, 14 right (14; 12–17).

Scales. Body scales open- or closed-centred. Lateral-line scales with simple tube, no midposterior flap or lobe on upper line, a midposterior notch on lower line. Often small pores present along margins of tube. Upper lateral-line scales 20 (20; 19–23); lower lateral-line scales 13 (13; 12–14); midlateral series 24 (one with 25); scales above upper lateral-line to origin of dorsal fin 4 left, 3 right (3; 3–4); scales below upper lateral-line to origin of anal fin 9 (9; 8–10); predorsal scale rows 7 (7; 6–8); cheek scale rows 4 (4; 4–5); circumpeduncular scales 16;

primary anterior pore of each upper lateral-line scale covered by preceding scale, except occasionally on the last 1 or 2 scales; all lower lateral-line scales with anterior pores uncovered; first ctenoid upper lateral-line scale 9th (13th; 7th–14th); first ctenoid scale below upper lateral line 3rd (3rd; 2nd–4th). Cheek scales visible anteriorly to the posterior tip of maxilla.

Cephalic sensory pores. Small and numerous. Dentary pore number varies with SL and ranges from 48 to 145, but forms a ratio with SL of ≈ 1 ($\bar{x} = 0.93$, range = 0.61–1.36). Pores present posterior to maxilla, but preopercular, dentary, and suborbital pore series remain separate and distinct.

General morphology. As percentage of SL: body depth at anal-fin origin 28 (30; 27–32); body width at pectoral-fin base 22 (22; 20–24); caudal-peduncle length 19 (19; 18–20); caudal-peduncle depth 16 (16; 14–17); predorsal length 36 (36; 34–37); preanal length 67 (65; 62–68); pre-pelvic length 37 (36; 33–37); dorsal-fin base 51 (53; 51–56); longest dorsal-fin ray 21 (23; 21–26); anal-fin base 25 (21; 18–25); longest anal-fin ray 27 (24; 21–27); pectoral-fin length 25 (26; 24–29); pelvic-fin length 37 (38; 33–42); head length 36 (38; 36–40).

Head. Rounded. Maxilla extends to or anterior to posterior margin of orbit. As percentage of HL: snout length 22 (22; 18–25); upper-jaw length 48 (47; 45–49); bony-interorbital width 12 (11; 9–13); posterior internasal width 17 (17; 15–18); orbital diameter 28 (28; 26–29); head depth at posterior margin of orbit 63 (57; 51–63); head depth at posterior margin of preopercle 76 (73; 66–78); head width at dorsal tip of preopercle 63 (62; 54–69).

Osteology and myology. Dorsal formula 0/0/2/1+1/1; epurals 3; epaxial musculature extends onto frontals anterior to sphenotic, lateral muscle bundles in advance of dorsal (medial), the latter not reaching frontals; adductor mandibulae with an additional thick sheet of fibres originating from sphenotic and pterotic, as well as main body

originating from posterior suspensorium.

Colour when fresh. From Masuda et al. (1984:pl. 126J). Body dark with trace of 5-6 dark bars, scales with pale spot, described as white but appears bluish in figure; head dark, mottled with pale blue spots from about $\frac{1}{4}$ pupil diameter up to pupil diameter in size; branchiostegal membranes dark, ventralmost membrane intense blue; dorsal fin dark with pale bluish median stripe running from base of first spine to 4th ray; spine tips perhaps paler; soft portion of dorsal with narrow, pale margin; anal fin dark with median bluish stripe from base of first spine to 4th ray; pale margin on soft portion of anal fin; caudal fin dark with no pale spots; pectoral fin dark; pelvic fin dark; eye iris blue peripherally and red around pupil. A photograph of a specimen identified as a juvenile of this species by H. Masuda is similar except that the body scales have no pale or blue spots, dorsal-fin spine tips are not pale, and caudal fin margin is yellow. However, no voucher for this specimen exists, and identification could not be confirmed.

Colour of holotype (in ethanol). Body solid brown or sepia; body scales with dark margins and dark bases, giving hint of originally pale centres; head dark, especially dorsally; 4 evenly spaced, dark, preopercular spots, smaller than pupil; 1 dark spot each on anterior part of interopercle and subopercle; ventralmost branchiostegal very dark; dorsal fin dark sepia except for tips of last 6 spines and pale margin to soft portion of fin; anal fin dark with pale margin to soft portion; caudal fin dark; pectoral and pelvic fins also dark. Other specimens similar to holotype (e.g., Fig. 27), but differing in some features such as: body scales with dark posterior margin and paler anterior crescent; head with 2 dark bars behind eye, one posterodorsal and one posteroventral, and a thin dark line running posteriorly from the midventral eye margin parallel to maxilla and ending slightly beyond posterior tip of maxilla; up to 5 dark, evenly spaced spots on preopercle, 1 on lower opercle, 2 on anterior part of subopercle, 1 on interopercle, and 3 spots on posterior margin of cheek, all smaller than pupil diameter; dorsal spines sometimes with pale tips, 1 specimen with a lighter stripe running from base of first spine to middle of last spine; almost always pale margin to soft portion of dorsal fin; both anal and caudal fins dark with pale margins; pelvic fins often spotted or with dark chevron pattern.

DISTRIBUTION AND HABITAT

This species is presently known only from the eastern coast of central Japan, from the Izu Islands to Kochi (Fig. 16, p. 26). The holotype was obtained from a fishmonger at Tomita, Prov. Ise, and probably collected off Prov. Shima or off Kii. The latter locality has provided additional specimens recently.

COMPARISONS

This species is most similar to the apparently allopatric *P. corallicola*, and is best differentiated by the absence of the large opercular ocellus characteristic of the latter, and by the lack of pale spots in the caudal fin. *P. nakaharai* also has more dentary pores and a higher dentary pore:SL ratio than *P. corallicola* (0.93 vs. 0.34). *P. multisquamata* and *P. nigricans* might be confused with *P. nakaharai*, but can be distinguished by a variety of meristic characters (Tables 1-5). *P. multisquamata* has a much higher upper lateral-line scale count (26-30 vs. 19-23), midlateral scale series count (29-33 vs. 24-25), and uniquely high circumpeduncular scale count (22-24 vs. 16). *P. nigricans* has a higher number of cheek scale rows (6-7 vs. 4-5), predorsal scale rows (8-10 vs. 6-8), and has pale spots in the caudal fin. *P. malalaxus* differs in colouration and does not have fibres of the adductor mandibulae originating from the skull. No other species reaches the high number of pectoral-fin ray branches that *P. malalaxus* and *P. nakaharai* otherwise share.

TAXONOMIC REMARKS

The original spelling of the species name *nakaharæ* and subsequent spelling as *nakaharæ* has been emended here to *nakaharai*, following Article 31a(ii) of the International Code of Zoological Nomenclature. As noted below in "Etymology," Tanaka was clearly naming this species after a man named Nakahara, without first Latinizing his name. Hence, *nakaharæ* is an incorrect original spelling, and the correct spelling is *nakaharai*.

ETYMOLOGY

This species was "named for Mr. Nakahara, who was fortunate enough to obtain this rare species" (Tanaka, 1918, 1935:500).

Plesiops nigricans (Rüppell, 1828)

Figs. 16, 28; Tables 1-5

Pharopteryx nigricans Rüppell, 1828:15, pl. 4 (fig. 2).

Pharopterix nigricans—Rüppell, 1830:37.

Plesiops nigricans—Rüppell, 1835:5; Günther, 1861:363; Klunzinger, 1871:517; Bleeker, 1876:322 [in part]; Inger, 1955:262, fig. 3d; Randall, 1983:61; Dor, 1984:107; Sano et al., 1984:15.

TYPE MATERIAL

Lectotype. SMF 1779, 108.1, Red Sea, Mohila [identified as Al-Muwaylih, Saudi Arabia, 27°41' N, 35°27' E (F. Krupp, pers. comm.)], E. Rüppell, 1828.

Paralectotype. SMF 9502, 93.5, label data as for lectotype.

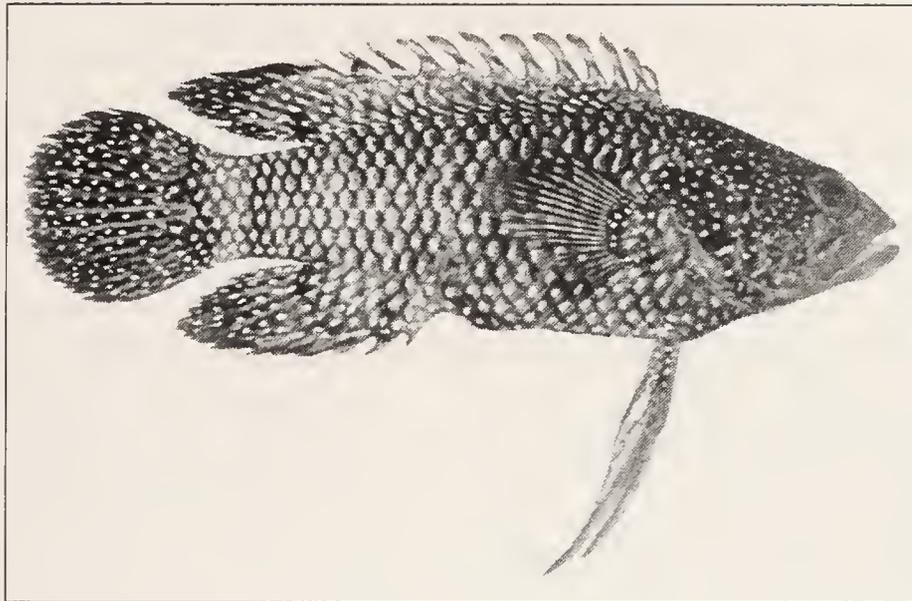


FIG. 28. *Plesiops nigricans*. BPBM 18253, 94.9 mm, Gulf of Aqaba, Red Sea. From colour slide by J. E. Randall. Appears in colour in Randall (1983:61).

ADDITIONAL MATERIAL EXAMINED

25 specimens, 29.5–117.5—RED SEA AND GULF OF ADEN: BPBM 18253 (♀ 94.9) Elat; MNHN 1895-172 (67.0) Djibouti; TAU P.5504 (2♂:53.7–65.6) Ras Atantur, P.6643 (♀? 65.4) Ras Garra, P.6879 (♀ 101.0, ♂ 88.4) Ras Garra, P.9092 (2♂:32.6–34.3) Shurat el Manqata; USNM 147530 (♂ 34.0) Jidda, 274564 (♀ 80.1) Ghardaqa, 274565 (3♀?:66.1–88.7) Hurghada, 274566 (68.3) Massawa, 274567 (♀? 117.5 mm, ♂ 29.5 mm) Sinai Peninsula, 274568 (♀? 68.3) Ghardaqa, 274569 (6?:59.4–77.1) Isola Delemme, 274577 (♂ 117.5).

DIAGNOSIS

Body and peduncular scales dark with blue, white or pale central spots becoming crescent-shaped dorsally; nape, cheek, and opercular scales also with small pale spots; soft rays of all fins except pectorals spotted; no ocellus on opercle; cheek scale rows 6–7 (rarely 5); predorsal scale rows 9–10 (rarely 7–8).

DESCRIPTION

Meristic and morphometric data based on 26 specimens, 29.5–117.5 mm SL. When data missing from lectotype, paralectotype data substituted.

Fins. Dorsal-fin spines, rays XII,7 (XII,7; XI–XII,7–8); longest dorsal-fin ray 5th (5th; 4th–6th); anal-fin spines, rays III,8 (8; 7–9); longest anal-fin ray 6th (6th; 5th–6th); pectoral-fin rays 21 left, 19 right (21; 19–22); total number of branches of lower 6 pectoral-fin rays 31 (31–35; 12–60); ventralmost ray with 4 (4; 2–6); pectoral fins with tips of ventral rays free of membrane forming a fringe, free pectoral-fin rays (5–8); pelvic-fin spines, rays I,4; first pelvic fin ray very long and thickened, first pelvic-fin ray extends to 2nd anal-fin ray (1st anal ray; 1st anal spine–5th anal ray); principal caudal-fin

rays (upper + lower) 10 + 9 (10 + 9; 9–10 + 9); procurrent caudal-fin rays (upper + lower) 5 + 5 (5 + 5; 4–6 + 4–5).

Gill rakers. Upper + lower 5 + 11 (5 + 13; 4–7 + 11–14); total 16 (18; 16–20).

Scales. Body scales usually open-centred. Lateral-line scales with simple tube, rarely with a midposterior flap or lobe on upper line (usually only on small specimens), a midposterior notch on lower line. Upper lateral-line scales 19 (20; 19–21) (although reported as 23 on Rüppell's 1828 fig. 2 by Smith, 1952, and Inger, 1955, I count only 21; Rüppell's (1828) fig. 2 not accurate because it has about 30 midlateral scales, 33 according to Smith, 1952, but only 23 or 25 on the actual lectotype and paralectotype); lower lateral-line scales 11? lectotype, 16 right, 14 left on paralectotype (14; 10–16); midlateral series 23? lectotype, 24 left and 25 right on paralectotype (24; 23–25); scales above upper lateral line to origin of dorsal fin 4 (4; 3–5); scales below upper lateral line to origin of anal fin 9 (9; 8–10); predorsal scale rows 9? lectotype, 10 paralectotype (10; 7–10); cheek scale rows appear crowded, 6 (6; 5–7); circumpeduncular scales 16; primary anterior pore of each upper lateral-line scale uncovered by preceding scale, except rarely last 1 or 2; all lower lateral-line scales with anterior pores uncovered; first ctenoid upper lateral-line scale 9th (8th–15th); first ctenoid scale below upper lateral line 6th (7th; 5th–11th). Anterior body scales cycloid, occasionally remaining so above upper lateral line, but usually becoming ctenoid by 6th–17th upper lateral-line scale. Below upper lateral line, cycloid scales end at 6th (7th; 5th–11th) lateral-line scale and extend forward to pectoral base and then ventrally to pelvic base. All scales posterior to this line ctenoid.

Cephalic sensory pores. Numerous and present as small pores only. Dentary pore number varying with SL, ranging from 10 to 110 (36? lectotype, 60? paralecto-

type), dentary pore:SL ratio usually between 0.5 and 1.0 (\bar{x} = 0.59, range 0.33–0.94, lectotype 0.33, paralectotype 0.64); no enlarged pore at ventral end of preopercular series; no pores posterior to maxilla linking preopercular to suborbital pore series.

General morphology. As percentage of SL: body depth at anal fin origin 29 (29; 25–35); body width at pectoral-fin base 19 (19; 15–25); caudal-peduncle length 17 (18; 16–20); caudal-peduncle depth 16 (15; 14–18); predorsal length 40 (40; 37–43); preanal length 63 (66; 63–71); pre-pelvic length 36 (36; 30–47); dorsal-fin base 56 (53; 48–59); longest dorsal-fin ray 24 (24; 18–28); anal-fin base 21 (20; 18–22); longest anal-fin ray 24 (24; 20–26); pectoral-fin length 25 (25; 21–29); pelvic-fin length 40 (40; 29–46); head length 40 (40; 37–43).

Head. Rounded. Maxilla extends to, or beyond, vertical at posterior margin of orbit. As percentage of HL: snout length 20 (19; 17–22); upper-jaw length 48 (47; 44–49); bony-interorbital width 9 (8; 5–14); posterior internasal width 16 (14; 12–22); orbital diameter 26 (28; 23–32); head depth at posterior margin of orbit 61 (58; 53–66); head depth at posterior margin of preopercle 73 (71; 65–79); head width at dorsal tip of preopercle 52 (52; 44–62).

Osteology and myology. Dorsal formula 0/0/2/1+1/1; epurals 3 (rarely 2); epaxial musculature extends onto frontals anterior to sphenotic, lateral muscle bundles in advance of dorsal (medial); adductor mandibulae with an additional sheet of fibres originating from sphenotic and pterotic as well as main body originating from posterior suspensorium.

Colour when fresh. From slide of BPBM 18253, Fig. 28 (also Randall, 1983:61). Body background sepia, each body scale with a pale bluish-white central spot or crescent; head dark sepia dorsally, paler ventrally, with white spots smaller than those of body, and often 2 or more per scale, especially on opercle and cheek; trace of dark markings behind eye; maxilla with a dark stripe posteriorly, running close to, but not along, the dorsal margin, also some scattered pale spots; iris of eye red adjacent to pupil and blue peripherally; dorsal fin darker than body, spine tips somewhat paler than rest of fin; membrane of soft portion of dorsal fin with pale spots; anal and caudal fins both darker than body with pale spots; all sheath scales with pale central mark or spot; scales of pectoral-fin base with pale spots, fin dark; pelvic fin sepia with small pale spots on membranes.

Colour of lectotype (in ethanol). Faded to a beige-brown with only a trace of light spots still visible. Paralectotype straw yellow becoming a dirty brown dorsally, especially on predorsal area, rays of dorsal, anal, pelvics, and caudal fins with lighter spots. On other specimens, body background black, dark grey, or sepia; scales with white or pale central spots becoming crescent-

shaped dorsally; small specimens with up to 6 dark brown bands which are wider than the intervening light brown bands, scales usually have light centres; head scales on nape, cheek, and opercle also have small light central spots; eye on small specimens followed by 2 dark blotches, one posterodorsal and one posteroventral; soft portion of dorsal and anal fins, pelvic fins, and caudal fin dark with white or pale spots, on older preserved specimens and on small individuals, often only caudal is spotted; dorsal spines sometimes with paler tips.

DISTRIBUTION AND HABITAT

This species is apparently restricted to the waters of the Red Sea and Gulf of Aden (Fig. 16, p. 26). It is not known to have been collected below 9 m.

COMPARISONS

Plesiops nigricans is 1 of only 3 species of *Plesiops* to have pale spots on the caudal fin membranes. The other 2 species are *P. multisquamata* and *P. corallicola*. The first of these is distinguishable from *P. nigricans* by its higher upper lateral-line scale counts (26–30 vs. 19–21) and higher midlateral series scale counts (29–33 vs. 23–25). *P. corallicola* always possesses an opercular ocellus, which is absent from all other species of the genus. Other than by colouration, *P. nigricans* differs from all other congeners by its higher number of cheek scale rows (6–7 vs. 5 or fewer).

BIOLOGICAL REMARKS

This species was particularly difficult to sex externally, although some males and females could be definitely identified. The 2 largest specimens, both 117.5 mm, represented both sexes. The smallest female identified was 65.4 mm.

TAXONOMIC REMARKS

The name *nigricans* has been applied indiscriminantly to almost every species of *Plesiops* described before 1955. When Bleeker (1875) synonymized all species of the genus except *P. oxycephalus* under the name *P. nigricans*, problems arose from the amalgamation of descriptions that belonged to different species. Almost no report of the occurrence of a member of the genus was associated with a good description, and the descriptions that were given were often taken from previous literature rather than from the specimens at hand (e.g., Barnard, 1927 used Day's, 1875 figure of *P. corallicola* in his own work for what is now recognized as *P. multisquamata*, which he referred to as *P. nigricans*!). Any worker referring to specimens collected outside of the Red Sea as *P. nigricans* is not discussing this species, and is most likely referring to *P. corallicola*. In the synonymy provided above, literature records of "*P. nigricans*" outside of the Red Sea are omit-

ted, and are included only under the appropriate species, rather than listing them as here as "in part."

Rüppell (1828) described the species based on 3 specimens, but in his hand-written catalogue, he mentions only 2; the third one had probably been sent as an exchange specimen to another museum (F. Krupp, pers. comm.).

ETYMOLOGY

Unknown, but Rüppell (1828) was apparently referring to the dark colour of this species.

Plesiops oxycephalus Bleeker, 1855

Figs. 10, 29; Tables 1–5

Plesiops oxycephalus Bleeker, 1855:320.—Günther, 1861:364; Bleeker, 1865:275(second set); Bleeker, 1875:29, Tab. II (fig. 1); Bleeker, 1875–8:vol. 9, pl. 389 (fig. 7); Vaillant, 1889:57; Boulenger, 1895:341; Fowler, 1928:188; Weber and de Beaufort, 1929:377; Fowler and Bean, 1930:316; Aoyagi, 1941:429; Aoyagi, 1943:92; Smith, 1952:140, 143; Inger, 1955:274, figs. 1c,3b; Masuda et al., 1984:141, pl. 126K; Sano et al., 1984:19, pl. 7c.

Plesiops nigricans (non Rüppell, 1828)—Fowler, 1928:188 [in part].

Plesiops oxycephalus okinawaensis Aoyagi, 1941:429.—Aoyagi, 1943:92.

TYPE MATERIAL

Lectotype. RMNH 6353, 74.2, Indonesia, Batu Archipelago, just west of Sumatra, approx. 0°30' S, 99° E, P. Bleeker, February 1855.

Paralectotype. RMNH 32451, 66.5, collected with lectotype.

ADDITIONAL MATERIAL EXAMINED

47 specimens, 33.8–72.8—INDONESIA: ANSP 157399 (♂? 59.9) Pulo Bai, Sumatra; MNHN A.8065 (70.0) Moluccas; RMNH 32452 (55.4) Ambon; USNM 162719 (♀? 41.8, 2♂:33.9–35.0), 169721 (2♀:47.8–48.7, ♂ 48.5), both Tomahu Is., Bouro. JAPAN: FUMT-P 4332 (5:42.5–67.3) Okinawa; IORD 76-774 (♂ 54.1), 76-816 (♂ 33.8), S. Ryukyu Is.; NSMT P19655 (48.0) Okinawa; YCM-P 6883 (5:46.3–72.2) Okinawa Is. (probable type specimens of *P. oxycephalus okinawaensis* Aoyagi, 1941). PALAU ISLANDS: CAS GVF 1868 (3♀:40.8–63.8, ♂ 60.6) Malakel Passage, GVF 1830 (2♂:68.8–70.1) Raeldil reef. PAPUA NEW GUINEA: AMS I.16671-075 (2♀:58.9–69.0) Madang Harbor; CAS 65915 (2:48.4–72.3) Little Pig Is.; USNM 275700 (2♂:60.3–63.8), 245699 (♂ 46.0), both from Bagabag Is. PHILIPPINES: USNM 146461 (♀? 55.2) Pangasinan Is., 274575 (3♀:49.3–54.7, 4♂:48.8–72.8), Palawan, 274576

(♂ 64.2) Palawan. SOLOMON ISLANDS: CAS SU 25385 (♂? 65.3) Tenibuli. VANUATA (NEW HEBRIDES): FMNH 22583 (♂ 66.7) Efate Is. VIETNAM: CAS 67842 (71.9) Khanh Hoa Prov.

DIAGNOSIS

Body with dark spots, either in bars or scattered, not present on dark specimens; cheek and opercle usually washed with yellow (pale in preserved specimens); caudal fin usually with yellow or pale crescentic band; predorsal scale rows 9–11, usually 9–10; cheek scale rows usually 5, sometimes 4; rarely more than 25 branches in total on lower 6 pectoral-fin rays; dentary pore:SL ratio averaging 0.40, number of dentary pores ranging from 11 to 40.

DESCRIPTION

Meristic and morphometric data based on 46 specimens, 33.8–74.2 mm.

Fins. Dorsal-fin spines, rays XII,7; longest dorsal-fin ray (5th; 4th–5th); anal-fin spines, rays III,8 (7–9); longest anal-fin ray (5th; 5th–6th); pectoral-fin rays 20 (20; 19–21); total number of branches of lower 6 pectoral-fin rays 16 (14–18; 12–27); ventralmost ray 2 branches (2; 1–2); pectoral fins with tips of ventral rays free of membrane to form fringe, ventral 3–6 pectoral-fin rays free; pelvic-fin spines, rays I,4; first pelvic ray long and thickened, first pelvic-fin ray extends to 4th or 5th anal-fin ray (3rd; 3rd anal spine–beyond 8th ray); principal caudal-fin rays (upper + lower) 10 + 9 (10 + 9; 9–11 + 8–10); procurrent caudal-fin rays (upper + lower) 5 + 5 (5 + 5; 4–6 + 4–6).

Gill rakers. Upper + lower 6 + 10 (5 + 10; 4–6 + 8–14); total 16 (16; 12–20).

Scales. Body scales open- or closed-centred. Lateral-line scales with simple tube, often with a midposterior flap or lobe on upper line, a midposterior notch on lower line. Upper lateral-line scales 19 (19; 18–21); lower lateral line scales 12 (12; 9–15); midlateral series 24 (24; 23–25); scales above upper lateral line to origin of dorsal fin 4 (4; 3–4); scales below upper lateral line to origin of anal fin 9 (9; 8–10); predorsal scale rows 9 (9; 9–11); cheek scale rows 5 (5; 4–5); circumpeduncular scales 16; primary anterior pore of each upper lateral-line scale covered by preceding scale except on last (1; 0–2, rarely 3); all lower lateral-line scales with anterior pores uncovered; first ctenoid upper lateral-line scale 9th (10th; 7th–13th); first ctenoid scale below upper lateral line 6th (7th; 5th–10th). Anterior body scales cycloid, sometimes remaining so above upper lateral line, but usually becoming ctenoid by 13th (8th–17th) upper lateral-line scale. Below upper lateral line, cycloid scales end at 7th (5th–10th) lateral-line scale and extend forward to pectoral base and then ventrally to pelvic base. All scales posterior to this line ctenoid.

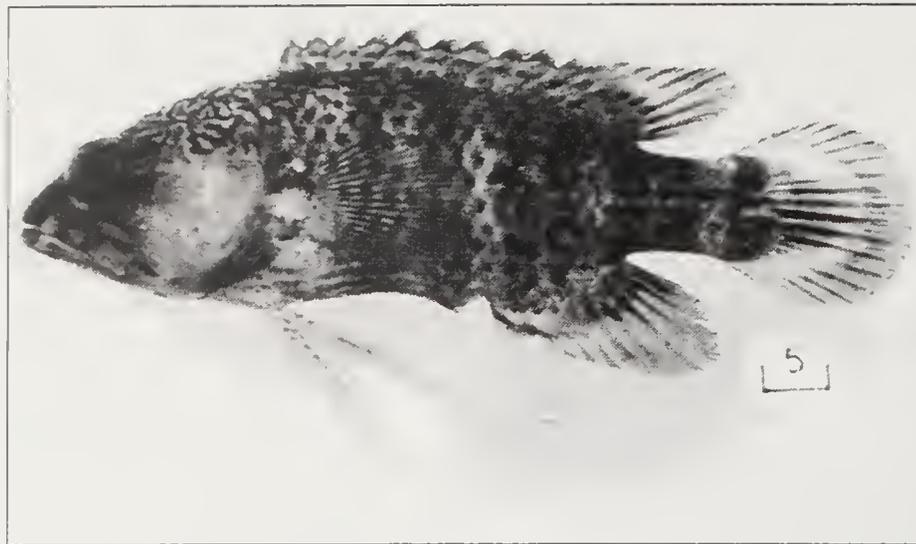


FIG. 29. *Plesiops oxycephalus*. IORD 76-774, ♂, 54.1 mm, Ryukyu Islands. From colour photograph by H. Kishimoto. Appears in colour in Masuda et al. (1984:pl. 126K).

Cephalic sensory pores. Relatively sparse. Dentary pore number ranges from 11 to 40 (lectotype 25), generally found in three groupings; dentary pore:SL ratio ranges from 0.21–0.60 (\bar{x} = 0.38, lectotype = 0.34); no pores posterior to maxilla linking preopercular to suborbital pore series.

General morphology. As percentage of SL: body depth at anal fin origin 30 (30; 28–32); body width at pectoral-fin base 18 (19; 15–22); caudal-peduncle length 18, 19 (18; 16–22); caudal-peduncle depth 15 (14; 12–16); pre-dorsal length 41 (42; 38–45); preanal length 67 (67; 60–71); prepelvic length 38 (36; 34–39); dorsal base 54 (52; 47–56); longest dorsal-fin ray (22; 17–27); anal-fin base 18 (18; 16–21); longest anal-fin ray (22; 19–26); pectoral-fin length (26; 22–30); pelvic-fin length (44; 39–51); head length 41 (42; 36–44).

Head. Appears somewhat narrow, pointed and long-snouted. Maxilla extends to or usually beyond a vertical at posterior orbital margin. Bony interorbital narrow. As percentage of HL: snout length 21 (21; 18–24); upper-jaw length 49 (49; 46–51); bony-interorbital width 8 (7; 5–10); posterior internasal width 14 (12; 10–17); orbital diameter 28 (30; 27–35); head depth at posterior margin of orbit 64 (60; 53–65); head depth at posterior margin of preopercle 78 (74; 66–78); head width at dorsal tip of preopercle 50 (51; 43–56).

Osteology and myology. Dorsal formula 0/0/2/1+1/1; epurals 3 (3; 2–3); cpaxial musculature extends onto frontals anterior to sphenotic, dorsal (medial) muscle bundles in advance of lateral; adductor mandibulae with an additional thin sheet of fibres originating from sphenotic and pterotic as well as main body originating from posterior suspensorium.

Colour when fresh. From slide of IORD 76-774, Fig. 29 (Masuda et al., 1984:pl. 126K). Body background pale grey with darker spots on scales, these spots being close

enough together intermittently to form 6 roughly equally spaced bands, 4 on the body and 2 on the caudal peduncle; a 7th band occurs at the caudal-fin base; head dorsally with elongated spots producing a mottled or almost dendritic pattern down to level of dorsal margin of eye, dorsal preopercle, and opercle; opercle, subopercle, and cheek orange, the latter with a few scattered small dark spots; 2 dark bars behind eye, one posterodorsal and one posteroventral, but short, being truncated by orange of cheek; a narrow dark stripe running from midventral margin of eye as far as posterior end of maxilla; maxilla alternately dark and pale banded, 3 bands of each; branchiostegals dark; dorsal fin dark with blue stripe running from base of first spine to median of 4th ray; dorsal-fin spine tips pale, most proximally white, and most distally bright yellow; anal fin dark at base and bluish medially on spines to distally on rays; caudal fin dark with a central orange crescentic band; pectoral fins dark; pelvic fins bright yellow proximally with chevron-shaped dark markings, distally pale yellow; iris of eye blue peripherally and red directly around pupil.

This description closely matches the original colour description by Bleeker (1855), although he noted that on one of the types the crescentic band is interrupted medially.

Colour of type material (in ethanol). All colour at least somewhat faded. Body background straw yellow, a hint of dark body spotting; obviously lighter tips to dorsal-fin spines; all fin rays darker than body; pale crescentic band on caudal fin, one quarter length of fin from distal tip. On other specimens, body background varies from pale straw yellow to dark brown; body often spotted, with evenly spaced or less uniform chocolate brown pigment found on inner scale sheaths in about 8 bands, about 16 spots per band, not visible on dark individuals; some individuals with pale background body colour and 7–8 dark bands with darker spots within the bands themselves; preopercle

occasionally with 4 small spots equidistant from each other; posterior caudal peduncle with 2 elongate spots, each mid-way between lower lateral line and procurrent caudal-fin rays, inconspicuous on dark individuals; 2 blotches behind eye, one posterodorsal and the other posteroventral; line running from ventral margin of orbit just above maxilla to its distal tip or just beyond; cheek and opercle yellowish; nape just above opercle and cheek with dark brown dendritic pattern; maxilla occasionally with 2 or 3 evenly spaced dark bars; all head colour inconspicuous on darker individuals; dorsal fin usually dark, spines with light tips, occasionally 1 or 2 median darker stripes on dorsal-fin spines and 1 on dorsal-fin rays; anal fin dark, sometimes becoming lighter towards ray tips; pectoral fins dark or light; pelvic fins gray or pale with chevron stripes or spots; caudal fin dark with a light-coloured or yellowish crescentic band through the middle or distal half of fin, the band occasionally interrupted medially, and occasionally inconspicuous.

DISTRIBUTION AND HABITAT

South and west from the Ryukyu Islands to the western coast of Sumatra, then east through the Solomon Islands and Vanuatu (Fig. 10, p. 16). It has been collected in stations from 0–15 m, but is usually found in water shallower than 3 m on reefs or in tide pools. Russell (1983) reports a doubtful record for this species on the Great Barrier Reef based on a colour transparency. Rivaton et al. (1989) provides a listing for New Caledonia. I have seen no specimens from either of these localities.

COMPARISONS

This species is most similar to *P. gracilis*, *P. cephalotaenia*, and *P. facicavus*. It is distinguished from all 3 species by the presence of spots on the body rather than stripes (when a pattern is present), and many fewer upper lateral-line scales with the primary anterior pore uncovered (0–3 vs. 5–16, rarely only 3 or 4 in *P. cephalotaenia*). Inger (1955) listed the specimens that I have now described as *P. facicavus* as *P. oxycephalus*, but the former has only a few, greatly enlarged head sensory pores and has a spotted pattern over the anterior head, whereas the latter has more numerous, small head sensory pores and has a dendritic colour pattern restricted to the nape. *P. oxycephalus* does tend to have more dentary sensory pores than the other 2 similar species as well (mean dentary pore:SL ratio of 0.38 vs. 0.26 in *P. cephalotaenia* and well below 0.20 in *P. gracilis*). All other species of the genus have fewer predorsal scale rows (except *P. nigricans* and *P. multisquamata* which have white spots on the body scales and fin membranes) and usually more pectoral-fin rays. Colour is also very different in *P. oxycephalus* from other members of the genus.

BIOLOGICAL REMARKS

Of the 28 specimens identified as to sex, 16 were males and 12 were females. This is not significantly different from a 1:1 sex ratio ($G = 0.57$, $0.25 < p < 0.50$). Specimens of both sexes had yellow cheeks and opercles and a yellow crescent in the caudal fin. Body colour varied from dark and spotted to light and spotted. Only males exhibited the dark background colouration, but many other males had light bodies. Females consistently had a pale body background. Gravid females were found in April, May, and December collections; February was the only other month for which females were identified, and only 1 specimen was available. Size of females ranged from 40.8–63.8 mm, and the largest male identified was 72.8 mm.

ETYMOLOGY

Bleeker (1855) named this species for the narrow and pointed head of this species, hence the Greek “oxys” for sharp or acute, and “kephalos” for head.

Plesiops polydactylus sp. nov.

Figs. 9, 30; Tables 1–5

TYPE MATERIAL

Holotype. USNM 242117, 45.8, NW side of Naviti Island, Fiji, 17°06' S, 177°13' E, 80–100', V. G. Springer et al., May 28, 1982.

Paratypes. Eight specimens, 23.2–42.6—CAS 79532 (39.3); MPM 31022 (38.1); ROM 66146 (38.1); USNM 324960 (5:23.2–42.6). All specimens collected with holotype.

DIAGNOSIS

Dorsal fin spines XI, only 1 supernumerary spine on first dorsal pterygiophore; pectoral-fin rays 26–28; cheek scale rows 3–4; predorsal scale rows 5–6; no pale spots on scales; no opercular ocellus; no dark stripe along dorsal margin of maxilla; dentary pores 9–21, dentary pore:SL ratio of 0.5 or less, averaging 0.41; total gill rakers 13–18, 4–5 gill rakers on upper arch, 9–13 on lower arch.

DESCRIPTION

Meristic and morphometric data based on 9 specimens, 23.2–45.8 mm.

Fins. Dorsal-fin spines, rays XI,7; 5th dorsal-fin ray longest; anal-fin spines, rays III,8; 6th anal-fin ray longest; pectoral-fin rays 26 left, 27 right (26; 26–28); total number of branches on ventral 6 pectoral-fin rays 12; branches on ventralmost ray 2; pectoral fins probably with ventralmost rays free of membrane, but difficult to determine, number of free pectoral-fin rays undetermined; pelvic-fin spine, rays I,4; first pelvic-fin ray elongate and noticeably thickened, first pelvic-fin ray extends to base

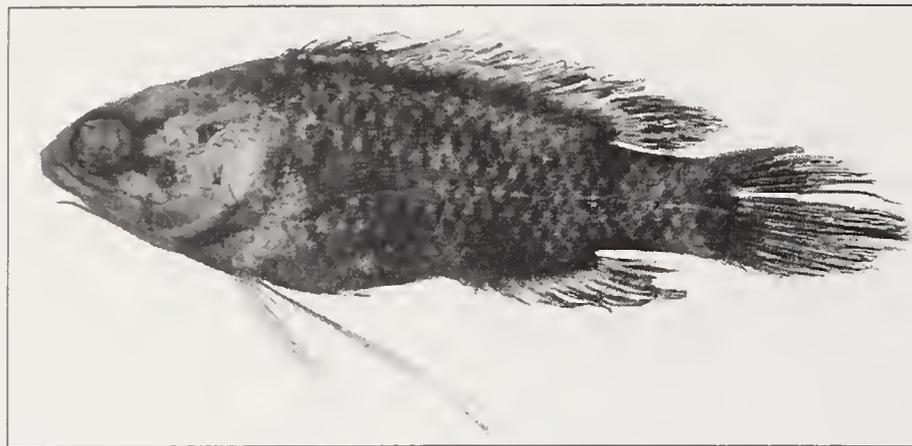


FIG. 30. *Plesiops polydactylus* sp. nov. Holotype USNM 242117, 45.8 mm, Fiji.

of 4th anal-fin ray (4th ray; 4th–6th ray); 4th pelvic-fin ray branched, except in smallest specimen; principal caudal-fin rays (upper + lower) 10 + 9 (10 + 9; 9–10 + 8–9); procurent caudal-fin rays (upper + lower) 5 + 5 (5 + 5; 5–6 + 4–6).

Gill rakers. Upper + lower 4 + 11 left, 5 + 10 right (4–5 + 9–13); total 15 (15; 13–18).

Scales. Body scales open- or closed-centred. Lateral-line scales with simple tube, often with a midposterior lobe on upper line, a midposterior notch on lower line. Upper lateral-line scales 19 (19; 18–19); lower lateral-line scales 11 left, 13 right (12; 9–13); midlateral series 24 (24; 23–24); scales above upper lateral line to origin of dorsal fin 2 left, 3 right (2; 2–3); scale rows below upper lateral line to origin of anal fin 8 (8; 7–9); predorsal scale rows 5 (5; 5–6); cheek scale rows 3 (3; 3–4); circumpectuncular scales 16; primary anterior pore of each upper lateral-line scale covered by preceding scale, except occasionally the last; anterior pores of lower lateral-line scales usually uncovered; first ctenoid upper lateral-line scale 7th (9th; 6th–10th). Anterior body scales cycloid, remaining so above upper lateral line until the 11th to 15th upper lateral-line scale. Below upper lateral line, cycloid scales end at 4th (4th; 3rd–6th) scale and extend forward to pectoral base and then ventrally to pelvic-fin base. All scales posterior to this line ctenoid. Cheek scales visible anteriorly to the posterior tip of maxilla.

Cephalic sensory pores. Small and sparse. Dentary pore number varies with SL and ranges from 9–21 (holotype 18), but always forming a ratio with SL of < 1 (\bar{x} = 0.44, range = 0.39–0.49, for SL > 40 mm, holotype 0.49). No pores posterior to maxilla linking preopercular or dentary pore series to suborbital series.

General morphology. As percentage of SL: body depth at anal-fin origin 29 (28; 26–30); body width at pectoral-fin base 18 (18; 15–20); caudal-peduncle length 18 (19; 18–20); caudal-peduncle depth 14 (14; 13–14); predorsal length 38 (39; 38–41); preanal length 63 (65; 63–69); pre-pelvic length 34 (35; 34–38); dorsal-fin base 52 (52; 51–53); longest dorsal ray 21 (21; 18–23); anal-fin base

23 (22; 21–23); longest anal ray 22 (21; 18–24); pectoral-fin length 24 (24; 22–25); pelvic-fin length 47 (45; 43–47); head length 39 (40; 38–42).

Head. Rounded. Maxilla extending to or beyond posterior margin of orbit. As percentage of HL: snout length 19 (18; 15–22); upper-jaw length 48 (46; 44–49); bony-interorbital width 8 (7; 6–8); posterior internasal width 15 (13; 12–16); orbital diameter 31 (32; 31–35); head depth at posterior margin of orbit 56 (57; 54–59); head depth at posterior margin of preopercle 72 (67; 61–72); head width at dorsal tip of preopercle 55 (52; 46–55).

Osteology and myology. Dorsal formula 0/0/1/1+1/1; epurals 3; epaxial musculature extends onto frontals anterior to sphenotic, lateral muscle bundles in advance of dorsal (medial); adductor mandibulae with an additional sheet of fibres originating from sphenotic and pterotic as well as usual main body originating from posterior suspensorium.

Colour when fresh. Unknown.

Colour of holotype (in ethanol). See Fig. 30. Body dark sepia with 4 indistinct lighter brown bars, one directly behind the pectoral-fin base, one at the anterior anal-fin base, one at the caudal peduncle base, and another at the base of the caudal-fin rays; scales have a darker base giving the body a spotted appearance; head sepia, darker dorsally, with 2 black blotches behind eye, one posterodorsal, one posteroventral; dorsal fin dusky, spines with pale tips, posterior spines and all rays with a median pale stripe; anal fin dark with a median pale stripe; caudal dark; pectoral fins dark; pelvic fins pale with small sepia spots. Other specimens much as holotype with body barring variably distinct or indistinct, 1 specimen with dusky dorsal-fin spine tips. It is likely that this species can be barred or unbarred, as in *P. coeruleolineatus*.

DISTRIBUTION AND HABITAT

This species is only known from the type locality, Naviti Island, just northwest of Viti Levu (Fig. 9, p. 13). The collection was obtained at an unusually deep site for most *Plesiops* species, at 17 m and 25–30 m. This is compared

to the most similar species, *P. coeruleolineatus*, which is usually found in water shallower than 3 m, although a very few collections are reported below 20 m.

COMPARISONS

Plesiops polydactylus is 1 of only 2 species of the genus having 11 dorsal spines as a result of having only 1 supernumerary spine on the first pterygiophore. It is differentiated from the other species, *P. coeruleolineatus*, by its higher number of pectoral-fin rays (26–28 vs. 19–23, rarely 24), higher number of gill rakers on the first arch (4–5 + 9–13 = 13–18, usually 15 vs. 3–4, rarely 5 or 6 + 7–10, rarely 11 = 10–14, rarely 15, usually 11–12), fewer predorsal scale rows (5–6 vs. 7–8, rarely 5 or 6), and fewer cheek scale rows (3–4 vs 4–6) (Tables 1, 3, 4). The 11 dorsal spines should differentiate *P. polydactylus* from all other *Plesiops* species. Its high pectoral-fin ray count also excludes confusion with all but 2 species, *P. auritus* and *P. thysanopterus*. *P. auritus* differs from the current species in having a dark spot of about eye diameter on the dorsal portion of the opercle and a higher dentary pore:SL ratio ($\bar{x} = 0.76$ vs. $\bar{x} = 0.41$) (Table 5), as well as having 12 dorsal spines with 2 as supernumerary spines on the first pterygiophore. The few specimens of *P. thysanopterus* available are much darker than *P. polydactylus*, pectoral-fin ray counts are higher (28–30 vs. 26–28), and the dentary pore:SL ratio is much higher ($\bar{x} = 1.1$ vs. $\bar{x} = 0.41$), in addition to its having 12 dorsal spines with 2 being supernumerary on the first pterygiophore.

BIOLOGICAL REMARKS

This species is very similar to *P. coeruleolineatus*. It is possible that it is a meristically aberrant population of the latter species, but this seems unlikely considering the constancy of meristics of *P. coeruleolineatus* throughout its wide range. The occurrence of a species of *Plesiops* endemic to Fiji mirrors the situation noted for many other taxonomic groups: *Meiacanthus ovalauensis* (Günther, 1880) of the Nemophini (Smith-Vaniz, 1987); *Ecsenius fijiensis* Springer, 1988 and *E. pardus* Springer, 1988 of the Salariini (Springer, 1988); and *Siganus uspi* Gawel and Woodland, 1974 of the Siganidae (Woodland, 1990). This will be further discussed later in the paper.

Of the 7 specimens for which sex could be determined, 6 were male (including the holotype) (32.2–45.8 mm) and 1 was female (36.7 mm). The sample size precluded statistical tests regarding sex ratio.

ETYMOLOGY

The specific name is a combination of the Greek “polys,” meaning “many,” and “daktylos,” meaning finger. It refers to the high number of pectoral-fin rays that characterize this species. To be treated as a noun in apposition.

Plesiops thysanopterus sp. nov.

Figs. 9, 31, 32; Tables 1–5

Plesiops sp. 5—Mooi, 1993:286.

TYPE MATERIAL

Holotype. ANSP 157386, ♂ 63.4, Sumatra, Pulo Boenta, off Achen Head, surge channel in coral reef, 5°33'10" N, 95°09'03" E, 2–12 feet, Te Vega Cruise A, Sta. 93, Field No. TEV-93, 20 Nov. 1963.

Paratypes. 2 specimens, 37.8–52.2—SUMATRA: ROM 60178, ♀ (gravid) 52.2, collected with holotype; USNM 315537, ♂ 37.8, collected with holotype.

DIAGNOSIS

No light spotting on body scales; dorsal spine tips only very slightly paler than remaining fin; pectoral-fin rays 29 (28–30); last free pectoral-fin ray 14 (14–15); cheek scale rows 4; predorsal scale rows 5 (5–6); sensory pores on head abundant and small, dentary pore:SL ratio of about 1.1, but preopercular, suborbital, and dentary series remain distinct.

DESCRIPTION

Meristic and morphometric data based on the 3 type specimens, 37.8–63.4 mm.

Fins. Dorsal-fin spines, rays XII,7; longest dorsal-fin ray 5th; anal-fin spines, rays III,8; longest anal-fin ray 6th; pectoral-fin rays 30 (29; 28–30); total number of branches of lower 6 pectoral-fin rays 15 left, 16 right (16; 13–18); ventralmost ray branches 2 left, 3 right (2; 2–3); pectoral fins with ventralmost rays free of membrane to form a fringe, free pectoral-fin rays 15 (14; 14–15); pelvic-fin spines, rays I,4; first pelvic-fin ray elongate but relatively short for *Plesiops*, and noticeably thickened, first pelvic-fin ray extends to 2nd or 3rd anal-fin ray; principal caudal-fin rays (upper + lower) 10 + 9 (9 + 9; 9–10 + 9); procurrent caudal-fin rays (upper + lower) 5 + 5 (6 + 5; 5–6 + 5).

Gill rakers. Upper + lower 4 + 8 (4 + 9; 3–4 + 8–10); total 13 (13; 12–14).

Scales. Body scales always closed-centred. Lateral-line scales with simple tube, no midposterior fleshy flap or lobe on upper line, a midposterior notch on lower line. Often small pores present along margins of tube. Upper lateral-line scales 19; lower lateral-line scales 14 (14; 14–16); midlateral series 24; scales above upper lateral line to origin of dorsal fin 3; scales below upper lateral line to origin to origin of anal fin 9; predorsal scale rows 5 (5; 5–6); cheek scale rows 4; circumpeduncular scales 16; primary anterior pore of each upper lateral-line scale covered by preceding scale; all lower lateral-line scales with anterior pores uncovered; first ctenoid upper lateral-line scale 8th (8th; 4th–8th); first ctenoid scale below

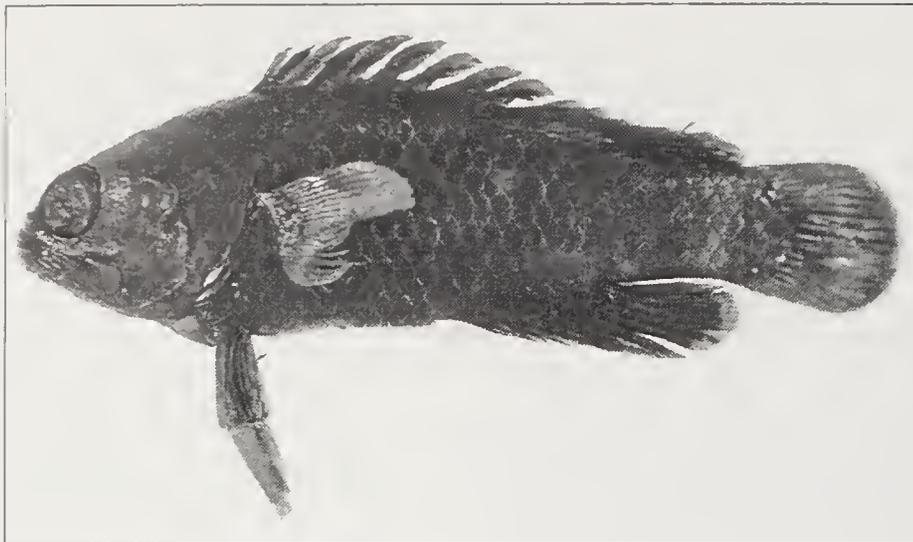


FIG. 31. *Plesiops thysanopterus* sp. nov. Holotype ANSP 157386, ♂, 63.4 mm, Sumatra. From negative by S. Schaefer.

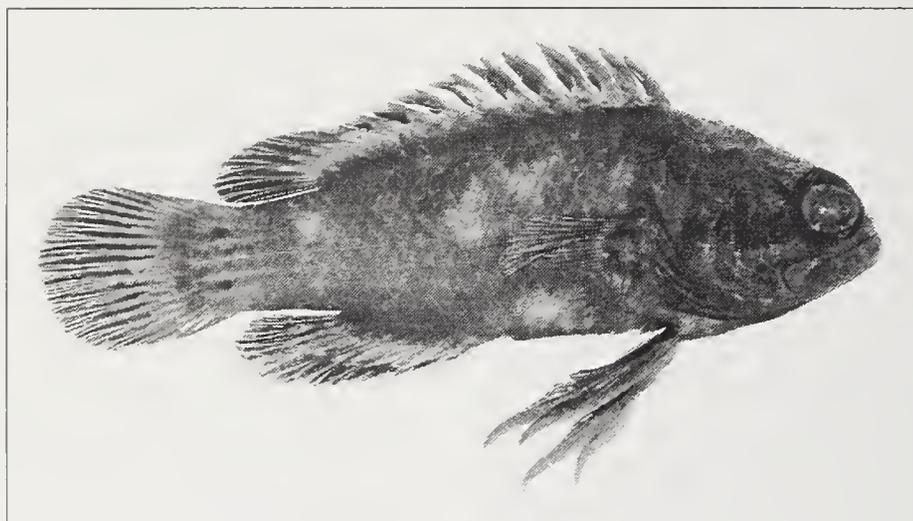


FIG. 32. *Plesiops thysanopterus* sp. nov. Paratype USNM 315537, ♂, 37.8 mm, Sumatra.

upper lateral-line 2nd (3rd; 2nd–5th). Anterior body scales cycloid, but becoming ctenoid further anteriorly than in most other members of the genus, i.e., ahead of the pectoral- and pelvic-fin bases. Cheek scales visible anteriorly to the posterior tip of maxilla.

Cephalic sensory pores. Small and numerous. Dentary pore number varies with SL and ranges from 40 to 69 (holotype 68), but forms a ratio with SL of ≈ 1 ($\bar{x} = 1.1$, range = 1.06–1.13, holotype 1.07). Pores present posterior to maxilla, but preopercular, dentary, and suborbital pore series remain separate and distinct.

General morphology. As percentage of SL: body depth at anal-fin origin 29 (29; 28–30); body width at pectoral-fin base 20 (17; 16–20); caudal-peduncle length 20 (20; 20–21); caudal-peduncle depth 15 (15; 14–15); predorsal length 38 (38; 37–39); preanal length 60 (60; 60–61); pre-pelvic length 32 (33; 32–36); dorsal-fin base 52 (52; 52–53); longest dorsal-fin ray 20 (20; 19–21); anal-fin base 22 (21; 20–22); longest anal-fin ray 20; pectoral-fin length 23 (23; 21–24); pelvic-fin length 36 (36; 36–37); head length 38 (39; 38–39).

Head. Rounded. Maxilla extends to or beyond posteri-

or margin of orbit. As percentage of HL: snout length 18 (18; 18–19); upper-jaw length 49 (47; 44–49); bony-interorbital width 8 (8; 7–8); posterior internasal width 16; orbital diameter 29 (31; 29–33); head depth at posterior margin of orbit 58 (58; 57–59); head depth at posterior margin of preopercle 76 (74; 73–76); head width at dorsal tip of preopercle 58 (56; 52–58).

Osteology and myology. Dorsal formula 0/0/2/1+1/1; epurals 3; epaxial musculature extends onto frontals anterior to sphenotic, lateral muscle bundles in advance of dorsal (medial), the latter not reaching frontals; adductor mandibulae with an additional thick sheet of fibres originating from sphenotic and pterotic, as well as main body originating from posterior suspensorium.

Colour in life. Unknown.

Colour of holotype (in ethanol). See Fig. 31. Body solid brown or sepia; posterior caudal peduncle with hint of 4 dark spots in line with end of hypural plates, 2 above and 2 below lower lateral line; dorsal part of head very dark brown, almost black, cheeks and ventral part of head as body; very slight trace of 2 dark splotches behind eye, one posterodorsal and one posteroventral, and a thin dark

line running posteriorly from the midventral eye margin parallel to maxilla and ending slightly beyond posterior tip of maxilla; a single small spot (1 mm) on ventral portion of opercle, and posterior margin of opercle dark; branchiostegal membranes dark, particularly ventrally; no spot on scales of pectoral-fin base; dorsal fin dark, tips of dorsal spines slightly paler brown; anal-fin spines and rays dark; caudal fin with a very narrow, light terminal band; pectoral fins grey-brown; pelvic fins brown with a few evenly spaced spots on fin membrane. Paratypes similar to holotype (Fig. 32), differing in the following ways: 2 or 4 caudal peduncular spots more distinct; head splotches and stripes more distinct, with an additional small dark marking just posterior to end of maxilla; no opercular spot; smallest paratype with a light stripe midfin on dorsal and anal; larger specimen with a noticeably darker margin to dorsal-fin spine membranes.

DISTRIBUTION AND HABITAT

This species is presently known only from the northern tip of Sumatra (Fig. 9, p.13). Its collection site is typical for the genus, being a surge channel in a coral reef at 1–4 m.

COMPARISONS

This species can be distinguished from all other members of the genus with 12 dorsal-fin spines by its high number of pectoral-fin rays (28–30 vs. 27 or fewer) and few predorsal scale rows (5–6 vs. 6 or more) (Tables 2, 4). It is most similar meristically to *P. auritus*, but lacks the dorsal opercular. In general body shape and colour (preserved) it most closely resembles *P. genaricus*, but the high number of pectoral-fin rays easily distinguishes it. *P. thysanopterus* and *P. polydactylus* have similarly high pectoral-fin ray counts (28–30 vs. 26–28), but the latter has only 11 dorsal-fin spines and 1 supernumerary spine on the first pterygiophore (vs. XII and 2), as well as a lower dentary sensory pore:SL ratio (\bar{x} = 0.44 vs. \bar{x} = 1.1) (Table 5).

ETYMOLOGY

The specific name is a combination of the Greek “thysanos,” meaning “tassled” or “a fringe,” and “pteryx,” meaning “fin.” It alludes to the pectoral fin which has a relatively high number of free, branched rays. To be treated as a noun in apposition.

Plesiops verecundus sp. nov.

Figs. 9, 33; Tables 1–6, 12–14

Plesiops n. sp.—Mooi, 1990:table 2, fig. 5b.

Plesiops sp. 6—Mooi, 1993:286.

Plesiops cephalotaenia—Russell, 1983:45.

Plesiops coeruleolineatus (non Rüppell, 1835)—Burgess and Axelrod, 1975:1480.

TYPE MATERIAL

Holotype. ROM 60208, ♂? 83.8, Fiji, Great Astrolabe Reef, Dravuni Is., Kandavu, marginal subtidal area just S of black rock 300 m S of village on W side, 18°45'52" S, 178°31'13" E, 0–2 m, 0–50 m offshore, R. Winterbottom, A. Emery, F. Emery, T. Emery, J. Payne, and R. McKinnon, 27 March 1983.

Paratypes. 57 specimens, 19.2–94.5—FIJI: AMS I.18361-024, ♂ 94.5, Laucala Bay, Suva, fringing reef E side of Nukulau Is., B. Carlson and B. Goldman, 7 March 1974; ANSP 157384, ♀ 44.8, 5♂:33.0–77.6 mm, ? 30.4, Mbulia Is., SW shore, 18°50'30" S, 178°32'10" E, 4–6 m offshore, 1–3 m, Te Vega Cr. 1, 28 Aug. 1963; ANSP 157387, ♀ 60.9, Viti Levu, reef S of Univ. of South Pacific, Nukumbutho Pass, Lauthala Bay, Suva, 18°08' S, 178°25' E, 2–3 m, W. Smith-Vaniz, B. Carlson, and P. Colin, 15 April 1974; ANSP 157391, 4♂:43.1–71.2, ? 24.4, North Vuro Is., Great Astrolabe Reef, outer reef, 18°52' S, 178°30'30" E, Te Vega Cr. No. 7, 8 May 1965; ANSP 157402, 2♀:59.0–67.6, ♂ 65.0, 2?:29.3–29.5, Great Astrolabe Reef, 18°52' S, 178°30'30" E, Te Vega Cr. 7, 8 May 1965; CAS 72677, ♂ 73.2, Vomo Is., reef at middle of W shore, Vomo Is. is 10–12 mi. NW of Lautaka, Viti Levu Is., 17°29'45" S, 177°15'30" E, 1–6 m, M. R. Brittan and 1 Fijian, 4 Aug. 1959; ROM 46746, 3♀?:47.6–77.6, 5♂:37.2–67.5, 2?:25.1–25.4, Great Astrolabe Reef, Dravuni Is., shallow reef 300 m S of Univ. of South Pacific Research Station, 18°45'52" S, 178°31'13" E, 0.5–2.5 m, 50–100 m offshore, channelled reef with undercut platform, R. Winterbottom, A. R. Emery, F. Emery, and R. McKinnon, 20 March 1983; ROM 46747, ♀ 65.8, 17♂:35.6–86.5, 5?:20.9–25.0, Great Astrolabe Reef, E pt. of Dravuni Is., Kandavu, 18°45'15" S, 178°31'59" E, 0.5–3 m, 0–150 m offshore, coral and algae on boulders in wave swash, A. Emery, R. Winterbottom, J. Payne, T. Emery, and R. McKinnon, 23 March 1983; ROM 46748, ♂ 73.3, 4?:19.2–25.8, collected with holotype; USNM 243989, ♂ 32.6, reef NNE of Malamala Is. which is E of Malolo Is., 17°44' S, 177°17' E, 0–8 m, V. G. Springer et al., 25 May 1982.

ADDITIONAL MATERIAL EXAMINED

436 specimens, 12.8–80.0—AUSTRALIA: Great Barrier Reef: AMS I.15681-043 (6♀:40.3–59.8, 7♂:58.3–74.9, ? 35.8), I.18267-001 (2♂:40.5–61.2), both One Tree Is., I.19444-052 (3♀:33.4–42.1, 2♂:39.6–49.0, 3?:12.8–19.8), I.19483-026 (5♀:36.7–45.0, 2♂:48.8–53.0, ? 30.4), both Lizard Is., I.19641-001 (2?:22.7–25.0) Tantabiddi Creek, I.20770-025 (♀ 49.5, 2♂:53.2–58.4, 2?:37.1–40.6), I.20770-120 (♂ 55.7, 4?:33.8–37.2), both Sir Charles Hardy Is., I.26745-003 (♂ 39.4), I.26746-010 (♀ 41.3), both Ashmore Reef; BPBM 11495 (♀ 60.8) Heron Is.; CAS 67574 (6♀:39.0–57.9, 11♂:37.6–73.0) One Tree Is.; MNHN 1978-582 (3:32.7–52.0); ROM 39285 (♀ 51.0, ♂



FIG. 33. *Plesiops verecundus* sp. nov. Holotype ROM 60208, 83.8 mm, Fiji. From colour slide by R. Winterbottom.

31.5) Lizard Is.; USNM 274550 (5 ♀:45.0–68.0, 9 ♂:50.0–72.3), USNM 274571 (♀ 61.2, 2 ♂:59.3–67.9), One Tree Is.; WAM P.25819-015 (3 ♂:41.9–61.6, ? 22.8) South Muiron Is., WYPO26631/008 (♀ 59.9, 5 ♂:43.5–52.6, 2?:26.5–31.2) North West Cape. INDONESIA: ANSP 166922 (6 ♀:37.5–50.0, 2 ♂:39.1–56.1) Mentawai Is.; BPBM 26740 (♂ 34.8) Bonebetang Is., Sulawesi; USNM 245694 (♀ 48.2) Borear Is., 313022 (♀ 54.2, ♂ 35.1) Bawean Is. JAPAN: BPBM 7395 (2 ♀:52.2–52.7, 3 ♂:44.5–58.6, ? 42.4) Ryukyu Is. NEW CALEDONIA: BPBM 2711 (2:72.2–77.8); MNHN 1980-722 (♀ 60.7, 2 ♂:40.1–78.9), 1980-796 (2 ♂:58.4–60.0), 1980-882 (♀ 53.7, 2 ♂:50.4–73.0), 1980-883 (♂ 49.5). PAPUA NEW GUINEA: AMS I. 16671-042 (2 ♂:43.0–54.1) Madang Harbor; CAS 65920 (4:43.0–56.2), 65923 (53.3), 65924 (3:49.2–52.1), 65925 (64.8); USNM 245693 (♀ 60.4) Port Moresby, 245695 (2 ♀:42.2–43.0, 3 ♂:37.2–43.6) Wewak, 313006 (2 ♀:43.0–52.0, 5 ♂:48.9–62.2) Umboi Is., 245701 (5 ♀:48.1–57.9, 11 ♂:41.3–66.1, 2?:28.4–30.2) Louisade Arch., 295546 (3 ♂:38.6–56.8, ? 30.0) Bagabag Is., 295547 (♂ 35.2) New Ireland, 295551 (♂ 58.2) Madang Harbor. PHILIPPINES: CAS GVF 1598 (4 ♀:31.1–43.2, ♂ 36.6, 3?:20.7–27.5) Dumaguete; USNM 232051 (♀ 46.3) Pangasinan, 313024 (96 ♀:26.0–35.3, 125 ♂:24.0–48.0, 27?:13.0–25.0 + many < 25 mm) Cuyo Is. SOLOMONS: USNM 274553 (2 ♂:56.2–58.3) Guadalcanal. TAIWAN: BPBM 23342 (♀ 47.6, 3 ♂:46.4–72.2) Truan Fan Shih, 274551 (5 ♀:42.4–72.0, 9 ♂:48.0–80.0) Ch'uan-Fan-Shih, 278136 (♂ 42.2) Chin-Chiao-Wan, 295537 (6 ♀:46.5–67.8, ♂ 51.1) Ch'uan-Fan-Shih, 295541 (76.5) K'en Ting, 295548 (♂ 38.7) Ch'uan-Fan-Shih. VANUATU (NEW HEBRIDES): ANSP 91595 (25.4); USNM 274994 (55.2), 295536 (♂ 41.6), 295552 (32.1), 295553 (♂ 54.9), Espiritu Santo. VIETNAM: CAS 57653 (♀ 49.7) Hon Lon of Nhatrang

Bay, 57655 (♂ 66.4) Cua Be and Mui Dongba, 72676 (9 ♂?:31.9–66.1) Cu Lao Hon, 67845 (♀ 49.9) Hon Mieu of Nhatrang Bay.

DIAGNOSIS

Twelve dorsal-fin spines, all with obviously light tips when in ethanol, bright red in life; no spots in membranes of anal, dorsal or in caudal fin; no dark dorsal margin to maxilla; no ocellus on opercle; pectoral-fin rays 20–23, rarely 24; predorsal scale rows usually 7–8, rarely 6; more than 10 dentary pores in specimens more than 30 mm, mean dentary pore:SL ratio averaging 0.58; anterior pores of upper lateral line covered, except occasionally the last; adductor mandibula A₁ section with some fibres originating from the skull.

DESCRIPTION

Morphometric data based on 121 specimens, meristic data based on 206 specimens, except for pectoral-fin counts based on 220 specimens, gill raker counts based on 258 specimens, and number of dentary pores based on 276 specimens, 19.2–94.5.

Fins. Dorsal-fin spines, rays XII,7; longest dorsal-fin ray 5th; anal-fin spines, rays III,8; longest anal-fin ray 6th; pectoral-fin rays 21 (22; 20–23, rarely 24, one specimen with 19) (number of rays varies somewhat with locality, see Biological Remarks); total number of branches of lower 6 pectoral-fin rays 17 (12; 11–22); ventral-most ray branches 2 (2; 1–2, very rarely 3); pectoral fins with ventralmost rays free of membrane to form a fringe, free pectoral-fin rays 9 (8; 7–10); pelvic-fin spines, rays I,4; first pelvic-fin ray elongate but relatively short for *Plesiops*, and noticeably thickened, first pelvic-fin ray extends to 4th anal-fin ray (3rd; 1st–8th); principal caudal-fin rays (upper + lower) 10 + 9 (9 + 8; 9–10 + 8–9);

procurent caudal-fin rays (upper + lower) 5 + 5 (6 + 6; 4–6 + 4–6).

Gill rakers. Upper + lower 5 + 10 (5 + 10; 3–6 + 7–14); total 15 left, 16 right (15; 11–18).

Scales. Body scales often open-centred. Lateral-line scales with simple tube, with or without a midposterior flap or lobe on upper line, a midposterior notch on lower line. Often small pores present along margins of tube. Upper lateral-line scales 20 (19; 18–20); lower lateral-line scales 14 (14; 10–16); midlateral series 24 (24; rarely 23 or 25); scales above upper lateral line to origin of dorsal fin 3 (3; 2–4); scales below upper lateral line to origin of anal fin 9 (9; 8–9, very rarely 7 or 10); predorsal scale rows 8 (7; 6–8, very rarely 9); cheek scale rows 4 (4; 3–5, rarely 6); circumpeduncular scales 16; primary anterior pore of each upper lateral-line scale covered by preceding scale, except occasionally on last scale; all lower lateral-line scales with anterior pores uncovered; first ctenoid upper lateral-line scale 11th (9th; 6th–14th); first ctenoid scale below upper lateral line 8th (5th; 5th–9th). Cheek scales not visible anteriorly to the posterior tip of maxilla.

Cephalic sensory pores. Always small, but number varies with SL and locality, see Biological Remarks. Dentary pore number ranges from 7 to 115 (holotype 28), and forms a ratio with SL of usually < 1 ($\bar{x} = 0.57$, range = 0.25–1.76, holotype 0.33). (The extreme ratios occur in populations from Taiwan ($\bar{x} = 0.86$, range = 0.57–1.76) and New Caledonia ($\bar{x} = 0.32$, range = 0.25–0.42). Table 14 shows the means and ranges for all localities.) Pores present posterior to maxilla, but preopercular, dentary, and suborbital pore series remain separate and distinct.

General morphology. As percentage of SL: body depth at anal-fin origin 30 (29; 21–32); body width at pectoral-fin base 22 (18; 13–24); caudal-peduncle length 17 (19; 17–23); caudal-peduncle depth 15 (14; 13–16); predorsal length 39 (40; 35–44); preanal length 69 (66; 62–70); pre-pelvic length 40 (36; 32–46); dorsal-fin base 52 (52; 43–56); longest dorsal-fin ray 24 (21; 17–30); anal-fin base 17 (19; 16–25); longest anal-fin ray 23 (22; 15–30); pectoral-fin length 25 (26; 22–30); pelvic-fin length 45 (43; 31–49); head length 40 (39; 37–44).

Head. Rounded. Maxilla extends to or beyond posterior margin of orbit. As percentage of HL: snout length 22 (19; 15–23); upper-jaw length 46 (47; 42–50); bony-interorbital width 8 (7; 4–10); posterior internasal width 13 (14; 10–17); orbital diameter 26 (31; 26–37); head depth at posterior margin of orbit 61 (56; 50–65); head depth at posterior margin of preopercle 75 (71; 63–83); head width at dorsal tip of preopercle 63 (55; 42–63).

Osteology and myology. Dorsal formula 0/0/2/1+1/1; epurals 3, rarely 2; epaxial musculature extends onto frontals anterior to sphenotic, lateral muscle bundles in advance of dorsal (medial), the latter not reaching

frontals; in large specimens (ROM 46747, 87.7 mm) lateral bundles meet in midline; adductor mandibulae with an additional thick sheet of fibres originating from sphenotic and pterotic, as well as main body originating from posterior suspensorium.

Colour when fresh. From slide of holotype, Fig. 33. Body sepia, fin-sheath scales entirely dark, body scales with darker posterior margins than anterior portions creating a spotted or reticulated pattern; nape dark; dorsal portion of head dark with pale mottling; behind eye are a posterodorsal and a posteroventral short, dark bar; thin, dark stripe running from midventral margin of eye parallel and adjacent to maxilla but extending 2 scale rows beyond posterior tip of maxilla; maxilla generally dusky with 2 pale spots; inter- and subopercle and branchiostegal membranes orange-yellow, except for ventralmost branchiostegal which has a bright blue margin; eye with outer ring of iris blue, and inner ring around pupil orange-red; spinous portion of dorsal fin pale ventrally, some sheath scales without pigment, then a pale medial blue stripe, dark membrane above this, followed by a pigmentless stripe; tips of dorsal-fin spines orange-red; soft portion of dorsal fin pale basally and darker distally in equal widths; pale blue stripe continuing from spines through dark portion to 5th ray; pale tips on first 5 rays; anal fin like soft dorsal with blue stripe in dark portion of fin through spine membranes and first 5 rays; hint of rusty colour in top third of anal fin to 4th ray; caudal fin with pale basal membrane but dark rays, then dark band with dark rays, followed by a yellow crescent in both rays and membranes in third quarter of fin; posterior quarter of caudal fin dark with some rusty red; pectoral fins dark; pelvic fins pale grey with sepia chevrons. Other colour photo available of specimen from the Great Barrier Reef (ROM 39285, 51 mm) is similar but generally darker in all areas, and therefore lacking the spotted or reticulated appearance of the body, and has bright red tips to dorsal spines. Colour photo of a specimen from Marau, Solomon Islands, in Burgess and Axelrod (1975:1480), has a brown body with dark posterior margins to the scales giving a slight reticulated appearance. Head as holotype, dorsal fin as Australian specimen.

Colour of holotype (in ethanol). Colours essentially as described above, but reds have become pale and blues have become dark. Paratypes similar to holotype, but several are quite dark obscuring details on head and body. Older specimens often red-brown rather than dark sepia. Some specimens with 4 to 5 equally spaced, dark spots on preopercle. Pale base to anal and dorsal fins often absent. Pale tips to dorsal fin sometimes dusky, especially on smaller specimens. Other specimens: Great Barrier Reef individuals similar to paratypic Fiji material, but reticulation on body usually obscured by darker colour, and pale dorsal-fin spine tips often more obvious and perhaps

slightly more extensive. Specimens from western Australia are paler with 4-5 caudal peduncle spots arranged one above the other. Taiwanese individuals are similar to those of the Great Barrier Reef except dorsal-fin spine tips are often quite dusky, though still obviously paler than the rest of the fin. All other localities are much like Fijian type material. Paler specimens show traces of caudal peduncular spots, usually 2, one above and one below the lower lateral line. Individuals from each locality have an all-dark caudal fin with no pale crescent visible and occasionally a dark spot on base of the pectoral fin.

DISTRIBUTION AND HABITAT

This species has spotty records ranging from the west coast of Sumatra, through the Malay Archipelago, the Philippines and north to Taiwan and the southern Ryukyu Islands. It also occurs off the west and north coasts of Australia and the Great Barrier Reef, and extends its range eastwards from the north coast of Papua New Guinea through the Solomons, New Hebrides, New Caledonia, and Fiji (Fig. 9, p. 13). There is considerable variation in meristic characters among localities, and these are discussed below (see Biological Remarks). The species is reported from depths of up to 30 m, but is generally found in 3 m or less of water on coral reefs and in surge channels.

COMPARISONS

Typical specimens of *P. verecundus* are notable for the bright red (in life) or obviously pale tips (preserved) to the dorsal-fin spines, but this feature does not necessarily differentiate it from other species. Within its range, *P. coeruleolineatus*, *P. polydactylus* and *P. oxycephalus* can have pale tips to the dorsal-fin spines. The first 2 species are immediately identifiable by their XI,7 dorsal fin count and single supernumerary spine on the first pterygiophore of the dorsal fin (vs. XII,7 and 2 supernumerary spines in *P. verecundus*). A comparison of specimens of *P. coeruleolineatus* and *P. verecundus* from the same collection site is made in Table 6. *P. oxycephalus* usually has a higher predorsal scale count (9-10 vs. 7-8), a lower pectoral-fin ray count (19-21 vs. 20-23), usually a pale body with scattered dark spots (vs. usually dark or uniformly patterned), and has the dorsal epaxial musculature in advance of the lateral (vs. lateral in advance of the dorsal). Other taxa have distinctive features that make it unlikely that *P. verecundus* would be confused with them. This species is distinguished from other members of the genus by characters that it lacks rather than those that it has.

BIOLOGICAL REMARKS

The apparently disjunct distribution of this species might suggest collecting deficiencies. It displays considerable variation in its meristic characters, both within and between populations, particularly when compared with

other members of this genus, which tend to be quite conservative. The Great Barrier Reef population has from 3 to 6 cheek scale rows, and at a few localities pectoral-fin ray counts vary by as much as 4 or 5 rays (Table 12). The Fijian population exhibits the lowest mode of pectoral-fin ray count compared to all other populations, and Taiwan has the highest. Little variation occurs in gill raker number (Table 13). Dentary sensory pore:SL ratio shows a great deal of variation among populations (Table 14). There appears to be 3 main groupings of populations according to dentary pore number: Taiwan with the highest number; Great Barrier Reef, Japan, Papua New Guinea, Vietnam, and Sumatra in an intermediate group; and Fiji, New Caledonia, Vanuatu, and western Australian populations with the lowest values. The 3 groups are significantly different from one another, but show no significant differences among localities within each group (pair-wise ANCOVA, $p < 0.01$). The only exception to this is the Philippines population which is intermediate between the low and middle groups. The variation among populations might be an indication that more than one species is represented in the specimens examined, although most characters that differentiate the populations intergrade over the range. Because of the ambiguity, I have restricted type specimens to a single locality (Fiji), but have kept the populations as a single species. This should help maintain taxonomic stability in the event that molecular or other data suggest the populations at different localities deserve separate species status.

Of the total of 438 specimens for which a sex was determined, 265 were males and 173 were females. This is highly significantly different from a 1:1 ratio ($G = 19.4$, $p < 0.001$). However, individual collections varied greatly in the ratios they provided, from 17:1 in favour of males to 6:1 in favour of females. The largest collection sampled (USNM 295533, Philippines) had 125 males and 96 females identifiable, which is just insignificantly different from 1:1 ($G = 3.82$, $p > 0.05$). It is difficult to determine whether sex ratios produced from collections from different times of the year and from different localities is a reasonable reflection of reality. Breeding cycles and behaviour might introduce collection bias and greatly influence estimates of male:female sex ratios.

The smallest gravid female was 31.1 mm, and females ranged in size from 31.1-72.2 mm. Males reached 94.5 mm, although maximum lengths of between 65 and 80 mm were more common.

ETYMOLOGY

The specific epithet "verecundus" is derived from the Latin "verecund" which means "unassuming," in reference to the lack of distinguishing or obvious features that make it different from other species in *Plesiops*. To be treated as a noun in apposition.

Phylogeny of the Genus *Plesiops*

The presentation of characters follows the notation found in Figure 34. Each node of the cladogram is designated by a letter; characters are assigned a number and are found below the node to which they refer. Homoplastic characters are indicated by asterisks and appear below each node where the homoplasy is evident; characters with apparent reversals to a condition similar to that of the plesiomorphic state are marked by "r." Characters considered to be composed of more than one derived state have sequential states in the series and are given a secondary number (e.g., if character 3 consists of two derived states

in sequence, these are 3.1 and 3.2). This permits tracing of character evolution on the cladogram as well as providing a convenient system for denoting evidence for a given node. Immediate outgroups are the non-plesiopine plesiopids as in Figure 4 (p. 6). Table 15 provides character state distributions for *Plesiops* and two sequential outgroups.

Autapomorphies of individual species are not included here. In most cases, autapomorphies can be found in the diagnoses of the species descriptions. Some nodes of the cladogram are not well-supported, and these portions of the cladogram will be further investigated in the discussion.

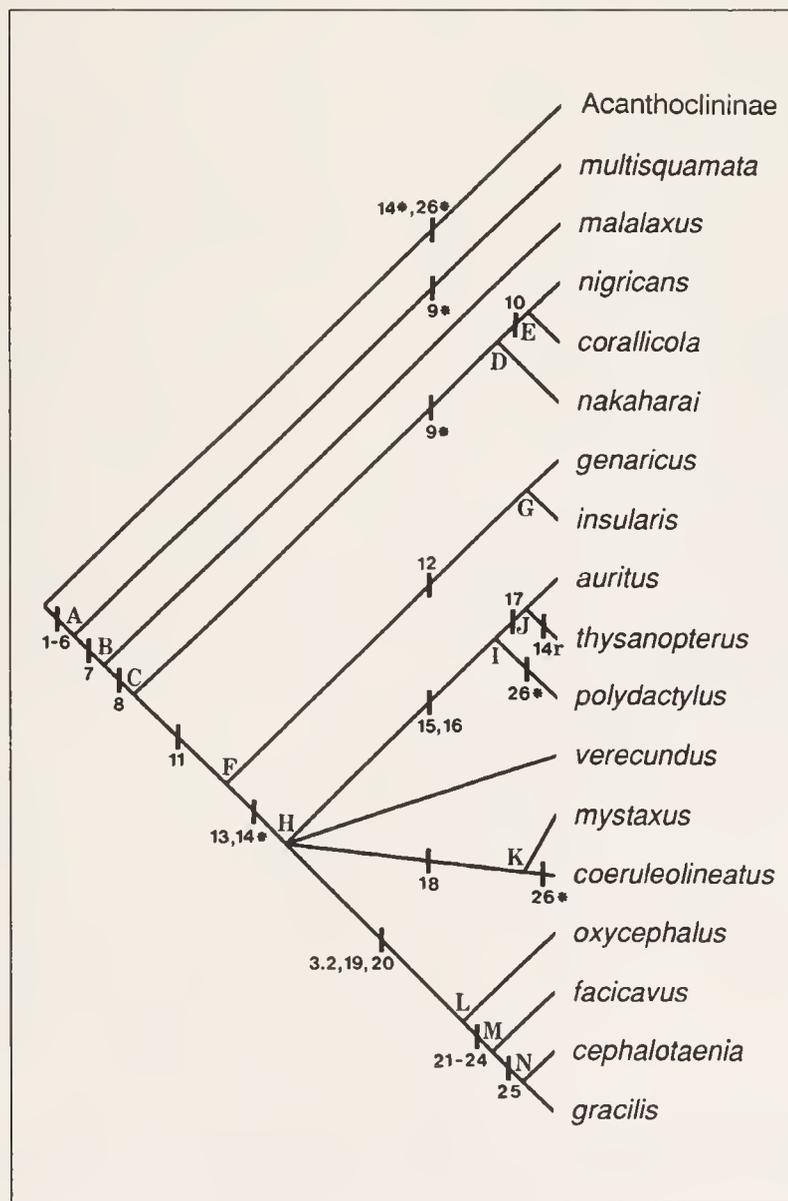


FIG. 34. Cladogram of the genus *Plesiops*. Nodes are lettered A to N. Characters supporting that node are numbered at vertical bars. Characters marked by an asterisk are homoplastic, those by "r" are apparent reversals to a condition similar to the plesiomorphic state. Node letter and character number identify clades and characters which are described in the text.

Character Analysis

Node A: Characters 1, 2, 3.1, 4-6

1. Scales with distinct centres.

Plesiomorphy. All immediate outgroups possess at least some ctenoid scales, all of which are typical for lower percoids, having concentric annuli from the centre outwards, and radii in the anterior fields only (Fig. 1a, p. 2).

Apomorphy. All species of *Plesiops* possess ctenoid body scales that have distinct centres where annuli are absent and have radii extending into all or almost all fields, including the posterior ones (Fig. 1b,c ; p. 2).

Homoplasies. None. As mentioned in the generic description, a number of species of Pseudochromidae exhibit a similar scale morphology, including the pseudoplesiopines *Pseudoplesiops rosae*, *P. typus*, and an undescribed species (A. C. Gill, pers. comm.), and probably all species of congrogadines. However, the conditions in these species are isolated instances and the taxa are derived members of the Pseudochromidae, implying that these are nonhomologous derivations. Allen and Randall (1985:186) report that *Steeneichthys* Allen and Randall, 1985 has "scales with distinct centres and radiating lines," but I cannot find such scales on the holotype, paratypes, or other specimens.

2. Cleithral hook well-developed.

Plesiomorphy. All immediate outgroups have small cleithral projections, sometimes hook-shaped, but never well-developed (Fig. 35c).

Apomorphy. All plesiopines have a well-developed, robust cleithral hook (Fig. 35a,b).

Homoplasies. None. Other lower percoids, such as pseudochromids, possess cleithral projections that could be described as hooks, but they are never robust. Blennioids also have cleithral hooks, but these usually turn medially into the body rather than following the general outline of the cleithrum, and are often short and squared off rather than long and pointed. The difference in shape and orientation of these hooks, as well as the obviously distant relationship of blennioids to *Plesiops*, indicates that these cleithral hooks are not homologous.

3.1. Pelvic iliac process well-developed.

Plesiomorphy. In all plesiopids other than the Plesiopinae and its sister group, the Acanthoclininae, the pelvic iliac process is present as a small bump or protuberance, occasionally reaching a size large enough to deserve the term "process" (Fig. 36a). Basal acanthoclinines have a more obviously produced iliac process, but it remains relatively small (Fig. 36b).

Apomorphy. The plesiopines all possess very well-

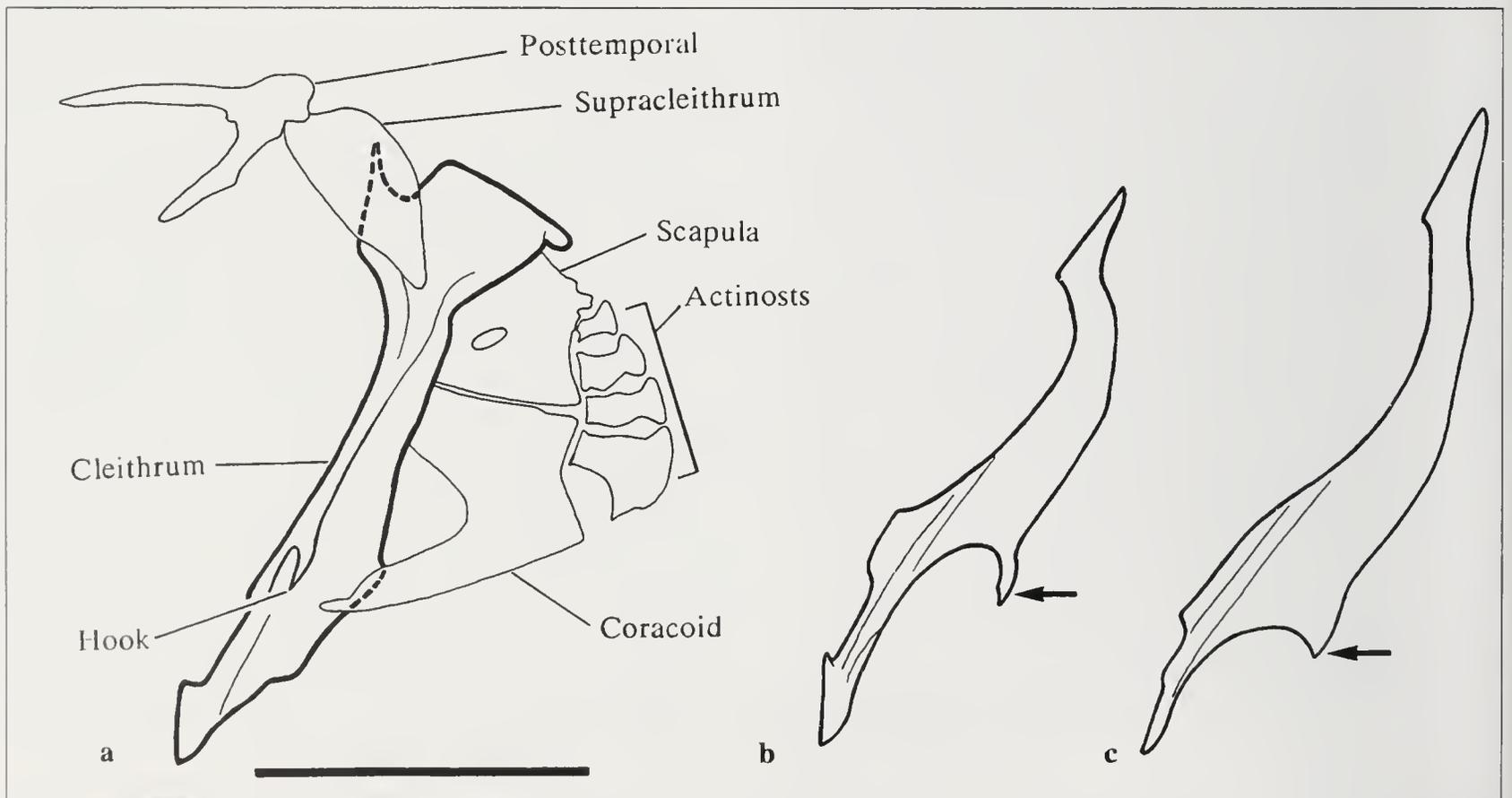


FIG. 35a-c. Cleithral morphology of 2 plesiopids. Cleithrum in bold. Dotted lines are cleithrum under overlying element. Scale bar = 5 mm.

a. *Plesiops coeruleolineatus*, ROM 776CS, 50.0 mm. Lateral view of left pectoral girdle.

b. *P. coeruleolineatus*, ROM 776CS, 50.0 mm. Anterior view of left cleithrum. Arrow indicates cleithral hook.

c. *Paraplesiops poweri*, USNM 274568, 47.8 mm. Anterior view of left cleithrum. Arrow indicates cleithral process.

developed iliac processes, much larger and more produced than other members of the family (Fig. 36c).

Homoplasies. None. Some percoid groups have iliac processes (e.g., Opistognathidae), as do some other perciforms (Trachinoidei), but these processes are different shapes than those found in the Plesiopidae, and the groups are too distantly related to affect homology determination.

4. Extensor proprius pelvicius with lateral and medial muscle fibres.

Plesiomorphy. In all basal percoids and all immediate outgroups except the acanthoclinines, the extensor proprius is composed of one main muscle bundle originating laterally from the basipterygium or fascia of the adductor profundus (Fig. 37a). It inserts onto the medial pelvic rays (the number varies between taxa). In the acanthoclinines, the extensor proprius muscle is absent—the rays that the muscle normally inserts onto are also absent in this taxon.

Apomorphy. All ingroup members have an extensor proprius consisting of two separate muscle bodies, one

originating laterally from fascia of the adductor profundus and arrector dorsalis, and the other originating medially from the medial pelvic girdle surface and closely overlying the adductor profundus (Fig. 37b). The lateral fibres insert onto the second and third rays, and the medial fibres insert onto the third and fourth rays. In at least some species, the lateral and medial fibres to the third ray share the same tendon, but no fibres are shared between the lateral and medial muscle bodies.

Homoplasies. None.

Remarks. Acanthoclinines do not have an extensor proprius, but because all other plesiopids possess one, the common ancestor of plesiopines and acanthoclinines must also have had one (Fig. 4, p. 6). We cannot know whether the ancestral condition of these two taxa was the primitive one of *Fraudella* Whitley, 1935 and other plesiopids, or the derived state of plesiopines. This being the case, it is possible that the derived state presented here as evidence for monophyly of *Plesiops* is actually a more general character of an acanthoclinine/plesiopine common ancestor.

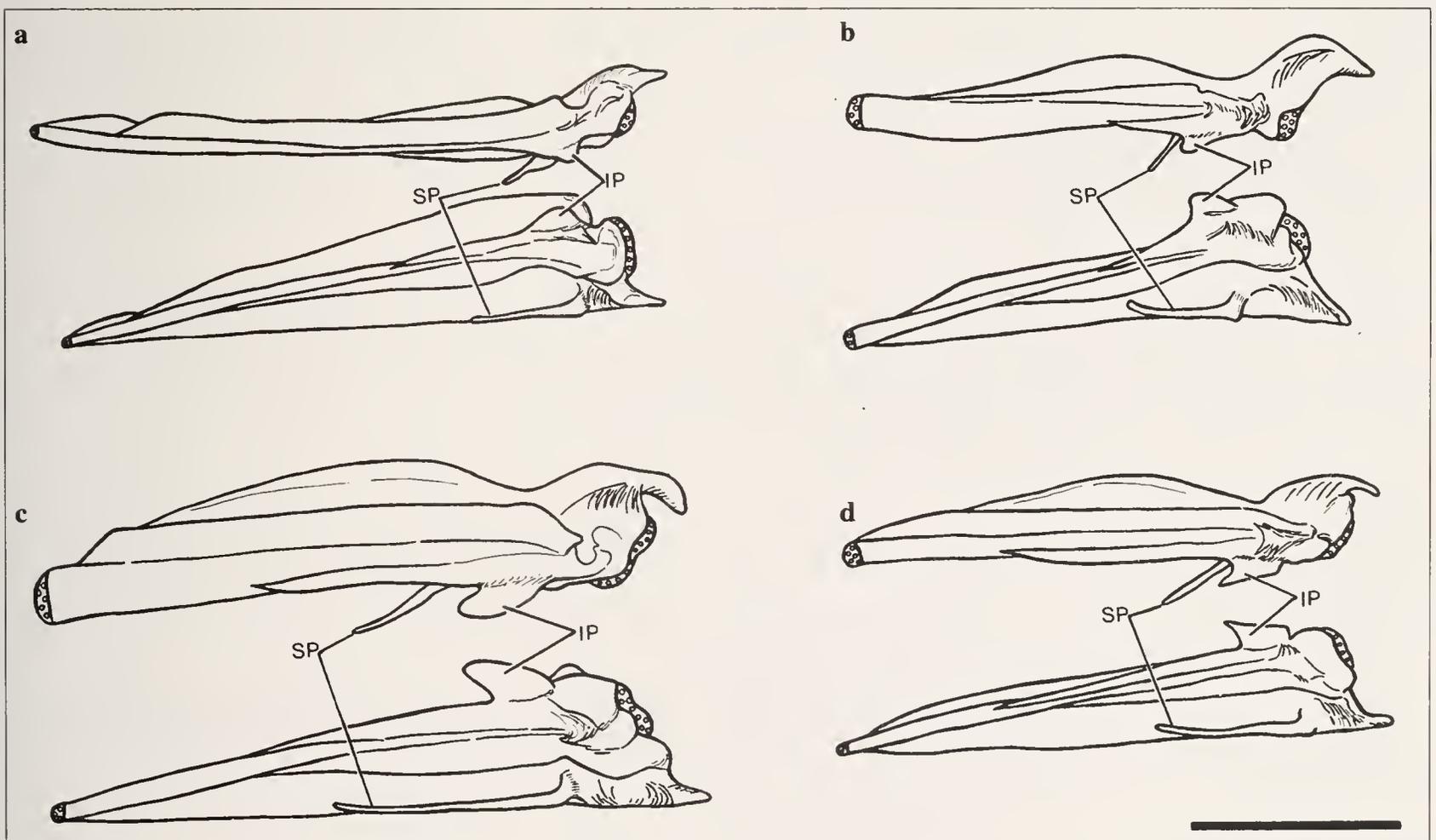


FIG. 36a–d. Pelvic girdles of 4 species of plesiopid. Top figure in each is a left lateral view, bottom figure is ventral view of the left side. Anterior to left. Pelvic spine and rays removed. Small open circles represent cartilage. IP = iliac process, SP = subpelvic process. Scale bar = 2 mm.

a. *Assessor macneilli*, USNM 269466, 47.5 mm. Note the small iliac process.

b. *Acanthoclinus fuscus*, NMNZ P.14719, 61.3 mm. Iliac process obvious but not large.

c. *Plesiops coeruleolineatus*, ROM 776CS, 46.0 mm. Note the large iliac process.

d. *P. gracilis*, CAS 67423, 41.8 mm. Iliac process modified to have a flat distal surface and a pronounced anterior point.

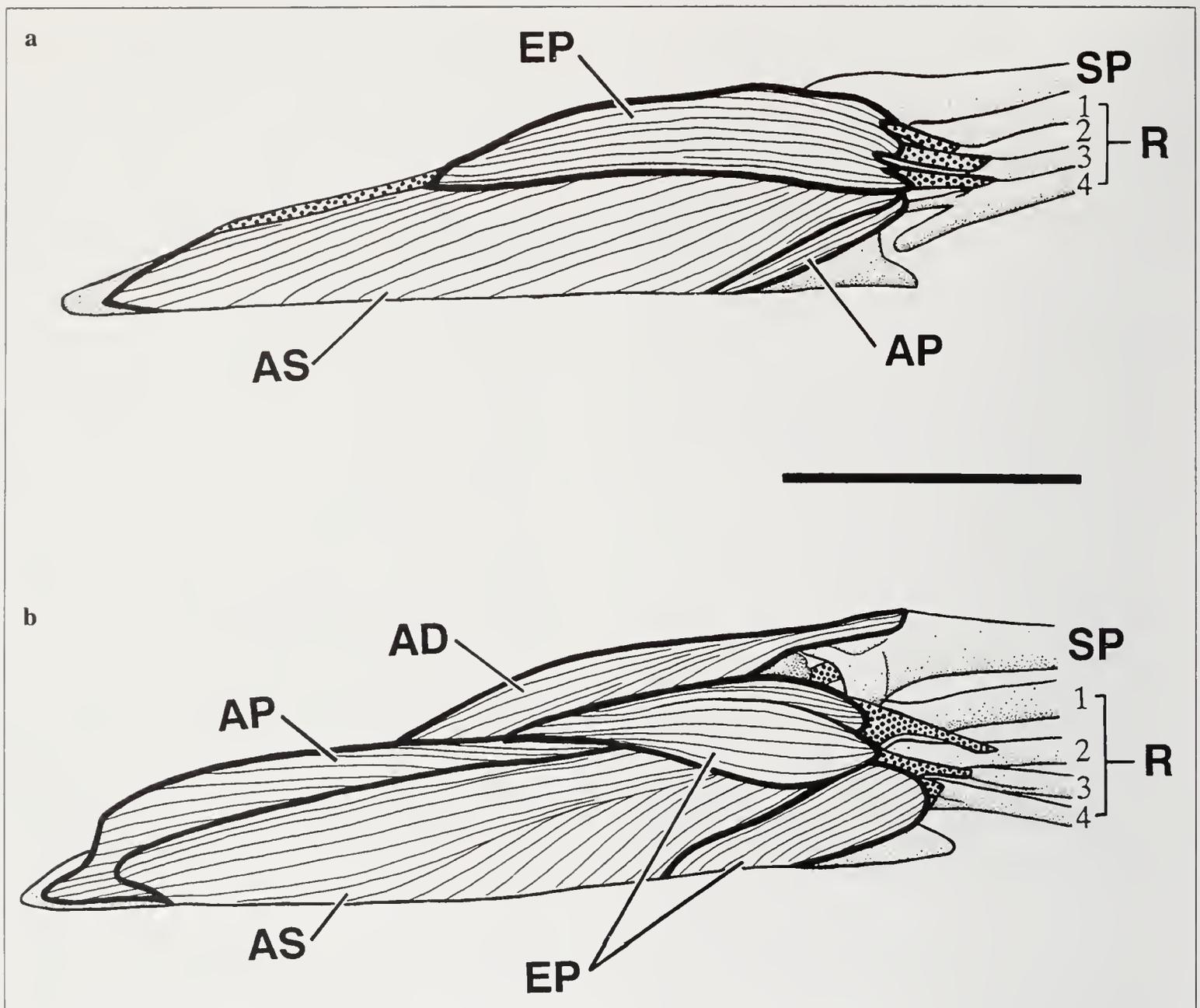


FIG. 37a-b. Dorsal pelvic musculature of 2 plesiopids. Anterior to left. Bold lines demarcate muscles, black dots represent tendons, stipple represents bone. AD = arrector dorsalis, AP = adductor profundus, AS = adductor superficialis, EP = extensor proprius, R = rays, SP = spine. Scale bar = 5 mm.

a. *Paraplesiops poweri*, USNM 274579, 95.0 mm.

b. *Plesiops corallicola*, ANSP 122597, 90.0 mm.

5. Parapophysis of 10th vertebra in contact with first anal pterygiophore.

Plesiomorphy. None of the immediate outgroups have the parapophysis of the 10th vertebra in contact with the first anal pterygiophore. Most genera have the first anal pterygiophore most closely associated with the haemal spine of the 11th vertebra (Fig. 38a).

Apomorphy. The parapophysis of the 10th vertebra is in contact with the first anal pterygiophore, often, although not consistently, with a posteriorly-directed bend in order to effect articulation (Fig. 38b,c).

Homoplasies. None. Some distant outgroups, such as the serranid epinepheline *Cephalopholis* Bloch and Schneider, 1801 and the grammistine *Pseudogramma* Bleeker, 1875, also have the first anal pterygiophore articulating with the 10th vertebra, but the morphology of this

articulation is different, and hence nonhomologous. Additionally, this taxon is too distantly related to alter the polarity of this feature.

6. Eggs oblong bearing numerous filaments arising from buttonlike knobs surrounding the micropyle.

Plesiomorphy. All immediate outgroups have spherical eggs with filaments arising from modified attachment structures scattered over the entire egg surface (Mooi, 1990).

Apomorphy. All species of *Plesiops* for which eggs have been examined (5) have oblong eggs bearing filaments arising in pairs from buttonlike knobs surrounding the micropylar region (Mooi, 1990:fig. 5a,b).

Homoplasies. None. A few percoid families outside of the Plesiopidae do have eggs with filaments surround-

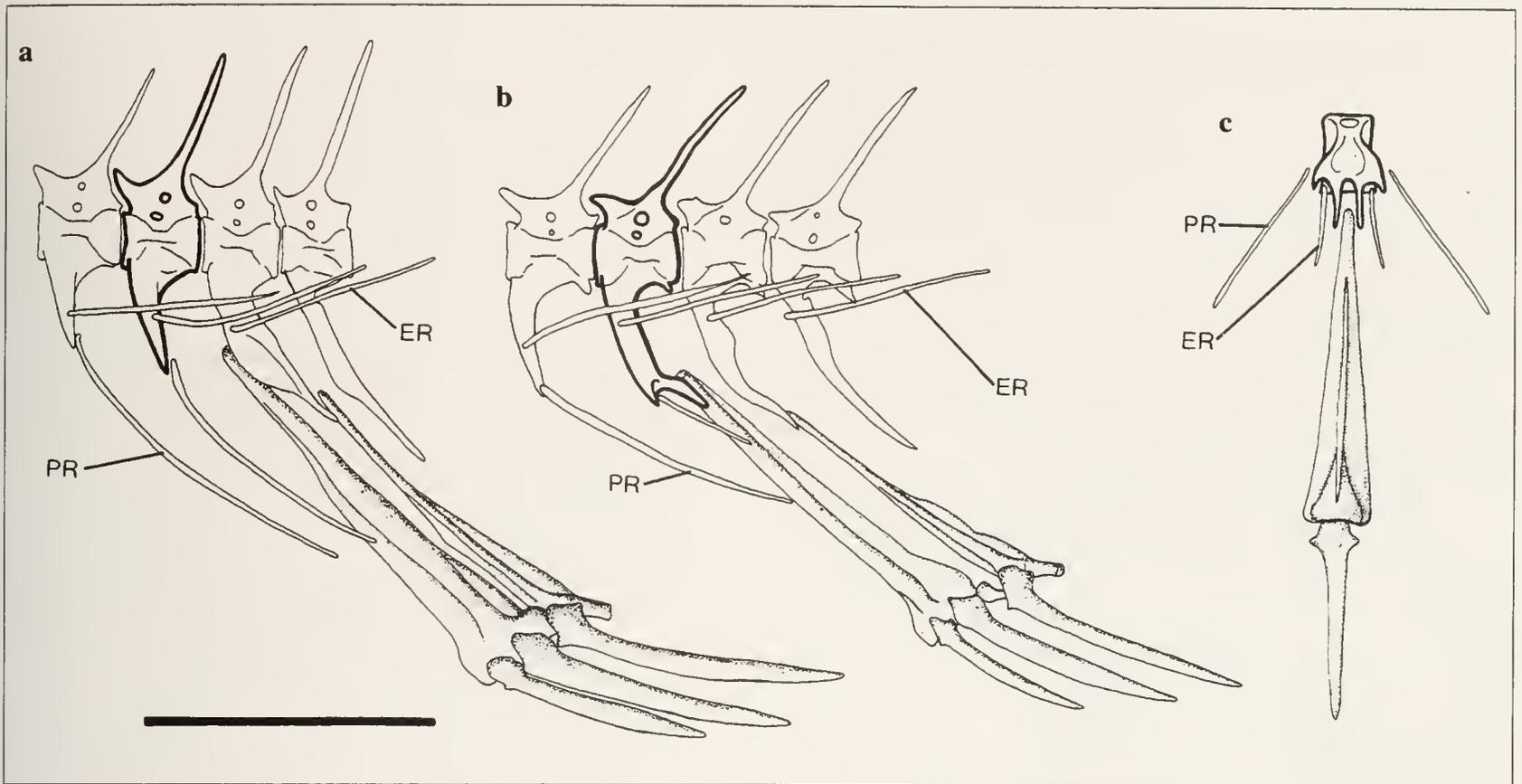


FIG. 38a-c. Articulation of the first anal-fin pterygiophore with the vertebrae in 2 plesiopids. Tenth vertebra in bold. First and second anal-fin pterygiophore and spines stippled. ER = epineural rib, PR = pleural rib. Scale bar = 5 mm.

a. *Paraplesiops poweri*, USNM 274578, 47.8 mm. Lateral view. Note that first anal-fin pterygiophore articulates with haemal spine of 11th vertebra.

b. *Plesiops coeruleolineatus*, ROM 776CS, 46.0 mm. Lateral view. First anal-fin pterygiophore articulates with modified 10th vertebral parapophysis.

c. *P. coeruleolineatus*, ROM 776CS, 46.0 mm. Ventral view. Tenth vertebra and first anal-fin pterygiophore and spine. Note the modified parapophysial articulation.

ing the micropylar region. These include: the Opistognathidae which differ by having spherical eggs and filaments without expanded bases attaching individually to the chorion (Mooi, 1990); the Grammatidae which are very similar except for the possession of spherical eggs and additional knobs without filaments (at least in *Gramma* Poey, 1868) scattered over the egg surface (Mooi, 1990); and the Pomacentridae with a very similar egg structure in some species (Mooi, 1990; Stiassny and Mezey, 1993). However, most of these groups, as noted, have some structural difference or arrangement that suggests nonhomology with the structure of the eggs of *Plesiops*. Additionally, if *Plesiops* is related to other plesiopids as shown in Fig. 4 (p. 6), global parsimony indicates that any similar egg structure to that of *Plesiops* outside of this group must be nonhomologous.

Node B: Character 7

7. Reduced number of body scales.

Plesiomorphy. *Plesiops multisquamata* and the sister-group Acanthoclininae have numerous body scales, the midlateral series in excess of 28 scales, at least for the

basal species of the sister group. *Fraudella* also has a high number of body scales (35-38).

Apomorphy. All species of *Plesiops* except *P. multisquamata* have a reduced number of body scales of 23-25 scales in the midlateral series.

Homoplasies. Although not homoplastic when the primary and secondary outgroups are the only consideration, the other taxa within the Plesiopidae display a wide variety of body scale counts. *Paraplesiops* Bleeker, 1875 and *Trachinops* Günther, 1861 both have higher numbers of body scales than those species above Node B, but *Assessor* Whitley, 1935, *Calloplesiops* Fowler and Bean, 1930, and *Steeneichthys* have scale counts similar to those of the proposed derived *Plesiops* species. Global parsimony suggests that a high number of scales is primitive for the family and for *Plesiops*.

Node C: Character 8

8. A₁ section of adductor mandibulae with dorsal portion originating from sphenotic and pterotic of cranium.

Plesiomorphy. None of the immediate outgroups nor the two *Plesiops* species below Node C have any fibres of

the adductor mandibulae originating from the cranium (Fig. 39a). They have a typical primitive condition where the A_1 portion originates mostly from the dorsal part of the preopercle with some fibres from the hyomandibula.

Apomorphy. All *Plesiops* species above Node C have a sheet of A_1 muscle fibres originating from the sphenotic and pterotic bones of the cranium, as well as maintaining the primitive origin of fibres from the preopercle and hyomandibula (Fig. 39b).

Homoplasies. None. Some distant outgroups within the percoid assemblage have a similar though apparently nonhomologous condition, as the taxa are too distantly related to postulate common ancestry, and the entire arrangement of adductor mandibulae musculature has

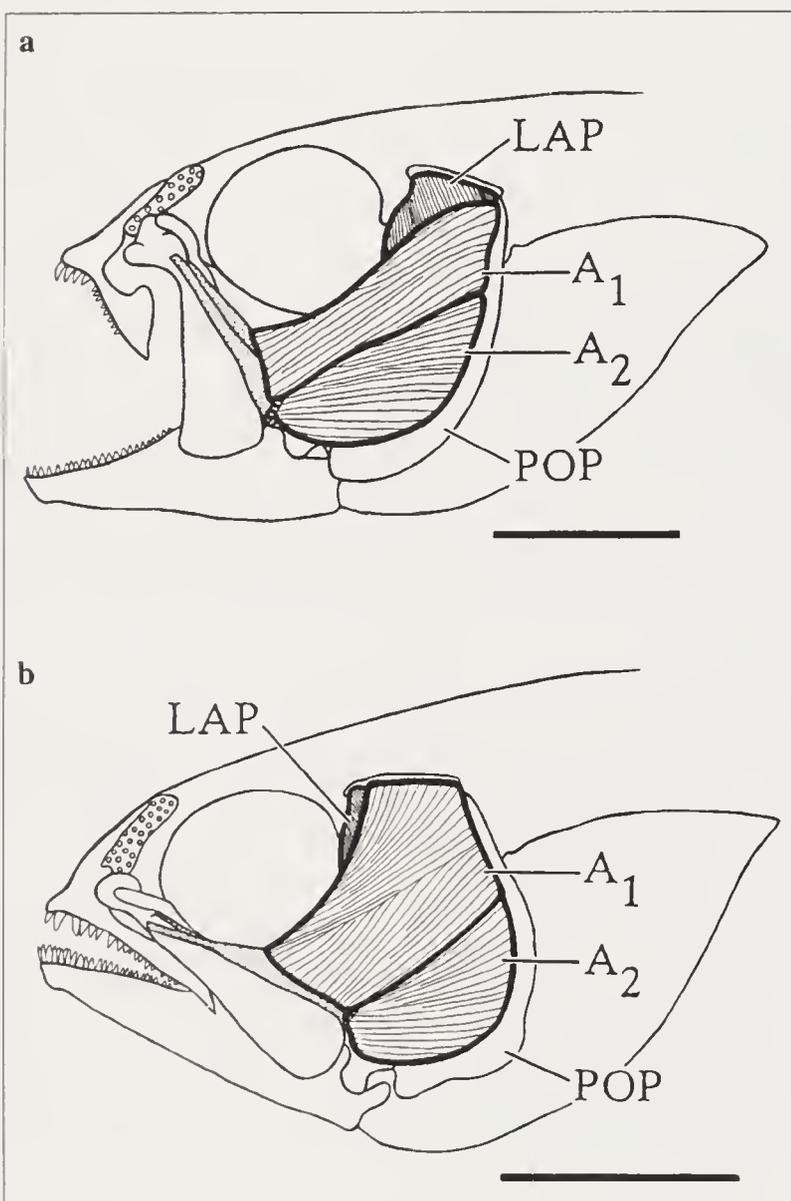


FIG. 39a-b. Cheek musculature of 2 species of *Plesiops*. Muscles outlined in bold. Ligamentum primordium stippled. Rostral cartilage open circles. A_1 , A_2 = sections of adductor mandibulae, LAP = levator arcus palatini, POP = preopercle. Scale bar for (a) 5 mm, for (b) 10 mm.

a. *P. multisquamata*, RUSI 76-16, 49.5 mm. Note that the A_1 section of adductor mandibulae does not originate from the cranium.

b. *P. corallicola*, AMS I.15360-042, 74.0 mm. Note that the A_1 section of adductor mandibulae originates from the cranium.

been modified. *Gramma* of the Grammatidae has independently derived such a state which might be an autapomorphy for the genus, as *Lipogramma* Böhlke, 1960, its sister genus (Gill and Mooi, 1993), does not exhibit this condition. If *Lipogramma* is progenetic, as suggested by Mooi (1993), the lack of a cranial muscle attachment might be a consequence of the pedomorphic developmental pathway. The Opisthognathidae also has a block of fibres of the A_1 originating from the cranium, but this condition is again likely to be of independent origin from both the derived plesiopine state and that of *Gramma* because of other details of the adductor morphology (Gill and Mooi, 1993). *Notograptus* Günther, 1867, a possible member of the acanthoclininae, has a massive A_1 that does in part originate from the skull (Gill and Mooi, 1993:fig. 8a). But as with the opisthognathid condition, the muscle is highly modified with a number of unique characteristics that are not present in *Plesiops*.

Node D: Character 9

9. Body scales with central blue or pale spots.

Plesiomorphy. Acanthoclinines, *Fraudella*, and most species of *Plesiops* have body scales without pale or blue central spots.

Apomorphy. *Plesiops multisquamata* and the three taxa of Node D, *P. corallicola*, *P. nigricans*, and *P. nakaharai*, all have pale or blue central spots on the body scales (Figs. 13c-d, 15, 25, 27, 28; pp. 20, 26, 43, 47, 49).

Homoplasies. Initially I had considered the possession of blue spots on the body scales as a plesiomorphic condition for the genus, and the basal position of *P. multisquamata* appeared to justify this polarity. Loss of blue spots would have occurred independently in *P. malalaxus* and those species above Node F. Members of *Paraplesiops* and *Calloplesiops* have body scales with pale central spots. However, primary and secondary outgroup comparison indicates that the most parsimonious interpretation is that blue spots are derived in *P. multisquamata* and again independently in the other blue-spotted taxa at Node C. The demonstration of homoplasy in this character makes me reluctant to use it to hypothesize monophyly for *P. corallicola*, *P. nigricans*, and *P. nakaharai*.

Node E: Character 10

10. Elongate dorsal-fin stay.

Plesiomorphy. Most basal percoids possess a dorsal- and anal-fin stay, a small bone which is the most posterior element of these two median fins, usually articulating with the middle radial of the last pterygiophore (Johnson, 1984). In most of the plesiopines and their immediate outgroups, the stay is shaped vaguely like a horizontally oriented V or Y (Fig. 40a,b). In more distant outgroups the

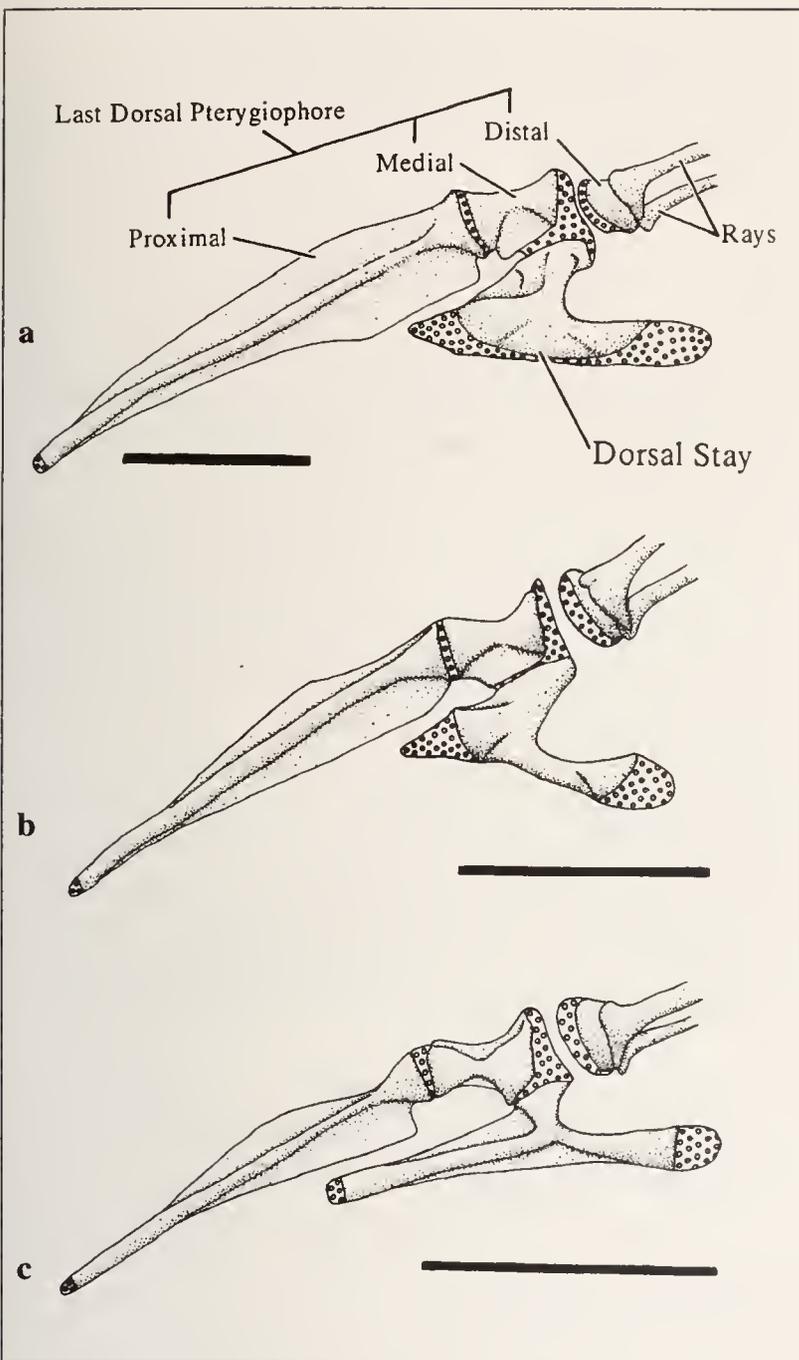


FIG. 40a-c. Posterior elements of the dorsal fin of 3 plesiopids. Anterior to left. Bone stippled. Cartilage closed circles. Scale bars = 1 mm.

a. *Paraplesiops poweri*, USNM 274578, 47.8 mm.

b. *Plesiops gracilis*, CAS 67423, 41.8 mm.

c. *P. corallicola*, ROM 893CS, 34.5 mm. Note the anterior extension of the dorsal stay.

stay varies in shape, but is usually somewhat V- or anvil-shaped.

Apomorphy. Both *P. nigricans* and *P. corallicola* are unique in having dorsal-fin stays with elongate anterior spurs that are longer than the posterior spur and extend farther anteriorly than those of other species (Fig. 40c). The anal-fin stay also has a somewhat longer anterior spur than other species, but this is usually less pronounced than that of the dorsal stay.

Homoplasies. Although no members of *Plesiops* other than *P. nigricans* and *P. corallicola* possess the elongate anterior spur, in the outgroups, the basal genus of acanthoclinines (*Acanthoclinus* Jenyns, 1842) has a

similarly shaped dorsal-fin stay. Although not as extreme, two paraplesiopine genera, *Calloplesiops* and *Steeneichthys*, have relatively long anterior spurs. Other basal percoids such as *Girella* Gray, 1835 also exhibit this feature (G. D. Johnson, pers. comm.). Some pseudochromine species have dorsal-fin stays that can be quite variable in shape, (e.g., *Pseudochromis marshallensis* Schultz, 1943). However, such dramatic variability does not appear in *Plesiops*, and FIG/FOG analysis as well as global parsimony indicate that the dorsal stay feature unites two species at Node E.

Node F: Character 11

11. Some yellow on cheek and/or opercle at some stage of the life cycle.

Plesiomorphy. None of the species of *Plesiops* below Node F nor any immediate outgroups are known to have yellow on the cheek or opercle. *P. corallicola* does have a narrow yellow outline around its opercular ocellus, but not a broad area of yellow. None of the immediate outgroups are described as having yellow on the cheek or opercle.

Apomorphy. Species above Node F have a broad area of yellow over the cheek, the opercle, and sometimes the branchiostegal membranes. This colour is more frequent in some species than others, and appears to be related to the breeding condition of the individual. In some cases (*P. gracilis*), the amount of yellow is apparently sexually dimorphic, with the male displaying more yellow. Whether *P. facicavus* has yellow cheeks is difficult to determine, as only two specimens are available and both have been in preservative for a long period. This species also has a unique head colour of small dark spots, which might obscure or have replaced the yellow colouration. The yellow cheek colour is also not apparent on any of the *P. polydactylus* specimens, but there are very few available; this species has been coded as unknown (?) for analysis (Table 15).

Homoplasies. None.

Node G: Character 12

12. Dark spot on scales of the pectoral-fin base.

Plesiomorphy. Almost all members of immediate outgroups and plesiopines, including basal members of the Acanthoclininae, do not have a dark spot on the scales of the pectoral-fin base.

Apomorphy. A dark spot is present on scales of the pectoral-fin base of *P. genaricus* (Fig. 19, p. 32) and *P. insularis*, although occasionally this spot is obscure.

Homoplasies. A very few specimens of *P. verecundus* have a darker region on the pectoral-fin base, although its occurrence is inconsistent. Its presence could be attrib-

uted to differential retention of colour on surrounding scales. The rare occurrence of such a dark area is not considered homologous. A pectoral-fin spot is characteristic of the genus *Acanthoplesiops* Regan, 1912 of the acanthoclinines (Smith-Vaniz and Johnson, 1990), but this is not a basal group for that subfamily, indicating that this colouration is an independent derivation.

Node H: Characters 13–14

13. Reduction in number of pectoral-fin ray branches.

Plesiomorphy. All plesiopines below Node H have more than 20 branches in total on the ventral six pectoral-fin rays as adults (Table 2). Small individuals (< 30 mm) can have fewer than 20 branches in some species, whereas adults often greatly exceed this number. Only *P. genaricus* and *P. insularis* (Fig. 2, p. 3) ordinarily do not exceed 30 branches as adults.

Apomorphy. All plesiopine species above Node H ordinarily have fewer than 20 branches in total on the ventral six pectoral-fin rays. Rare individuals exceed 20 branches, but never exceed 30. The common number of branches for the majority of species is 12 or fewer (Table 2).

Homoplasies. Overlapping character states are problematic and generally should be avoided, or if used, should not be considered greatly reliable indicators of phylogeny. In this instance, the overlap is small and, in more mature specimens (> 30 mm), occurs only rarely.

14. Dorsal-fin spines with pale or coloured tips.

Plesiomorphy. All plesiopines below Node H have dark dorsal-fin spines, or have tips that are only slightly paler than the more proximal portion of the spine (e.g., Figs. 24, 25, 27, 28).

Apomorphy. All plesiopines above Node H have obviously pale dorsal-fin spine tips, usually red or yellow in life (e.g., Figs. 11, 12, 22, 26, 29, 33). All acanthoclinines also have pale tips to the dorsal-fin spines.

Homoplasies. This character exhibits the largest degree of homoplasy. Using the acanthocline condition as the primitive state, dark spine tips are a synapomorphy for members of the genus *Plesiops*, but this character reverses to the primitive state in those species above Node H. *P. thysanopterus*, which is apparently the sister species of *P. auritus* (see Node I below), must regain dark dorsal-fin spine tips. Hence, the character requires three steps, rather than one, to account for its distribution within *Plesiops*. However, if further plesiopine outgroups are considered, pale spine tips, not dark, is the derived condition. This then requires an independent gain of pale tips in the acanthoclinines, and the feature requires only two steps within the genus *Plesiops*, a gain at Node H, and a subsequent reversal to the primitive state in *P. thysanopterus*. *Steeneichthys*, another plesiopid, also has

pale spine tips which must have been acquired independently. FIG/FOG methodology indicates that the occurrence of pale or coloured spine tips is the derived state among plesiopids.

Node I: Characters 15–16

15. Increased number of pectoral-fin rays.

Plesiomorphy. All plesiopines other than *P. auritus*, *P. polydactylus*, and *P. thysanopterus* have fewer than 25 pectoral-fin rays (Table 1). All immediate outgroups have fewer than 21 pectoral-fin rays.

Apomorphy. *Plesiops auritus* and *P. thysanopterus* have 25–27 and 28–30 pectoral-fin rays respectively, and *P. polydactylus* has 26–28 pectoral-fin rays (Table 1). No other species nor any outgroups attain these counts, and pectoral-fin ray numbers are quite conservative within each subfamily.

Homoplasies. Ordinarily, this would appear to provide ample evidence to place these three species in a monophyletic group. However, other characters suggest a sister-group relationship between *P. polydactylus* and *P. coeruleolineatus*. Such a relationship would indicate a convergence in pectoral-fin ray number with the *auritus-thysanopterus* clade.

16. Reduced number of predorsal scale rows.

Plesiomorphy. Members of *Plesiops* generally have more than six predorsal scale rows (Table 4).

Apomorphy. *Plesiops auritus*, *P. polydactylus*, and *P. thysanopterus* have from 4–6 predorsal scale rows, usually only five (Table 4).

Homoplasies. *Plesiops coeruleolineatus* very rarely has five predorsal scale rows, but frequently has only six (Table 4); *P. polydactylus* exhibits six scale rows in three of the nine known specimens. This overlap in meristics make this character a less reliable indicator of relationship than might be desired. If these two last-mentioned species are related, then a decrease in number of predorsal scale rows would have occurred twice within the genus. Acanthoclinines have naked heads; *Steeneichthys* have seven predorsal scale rows; *Paraplesiops* have 7–29; *Callopleiops* 9–11; *Assessor* 19–20; *Fraudella* 9–10; *Trachinops* > 12.

Node J: Character 17

17. All body scales with closed centres.

Plesiomorphy. Body scales of all members of *Plesiops* other than *P. auritus* and *P. thysanopterus* are variably open- or closed-centred (Mooi and Randall, 1991:fig. 1; Fig. 1b,c), becoming predominantly open-centred posteriorly. Basal species such as *P. multisquamata* and *P. malalaxus* display this primitive condition.

Comparable scales do not exist in immediate outgroups.

Apomorphy. The two species above Node J invariably have closed-centred body scales as far posteriorly as the caudal base.

Homoplasies. None.

Node K: Character 18

18. Colour pattern of spinous portion of dorsal fin.

Plesiomorphy. Half of the plesiopine species do not have coloured distal portions of the dorsal-fin spines (see character 14, Node H). Of the other species, most have a simple colour pattern of a dark or pale proximal portion and a coloured distal portion; the distal portion is red or yellow in life (Figs. 11, 22, 29, 33).

Apomorphy. *Plesiops coeruleolineatus* and *P. mystaxus* share a derived condition where the distal coloured tips are bordered proximally by a black or dusky stripe, which is followed by the pale uncoloured region of the fin (Figs. 12, 13a–b, 26). This feature is not evident in the few specimens of *P. polydactylus* available, and is not always a prominent feature of the former two species. This feature is coded as unknown for *P. polydactylus* until further specimens are available for examination.

Homoplasies. None.

Node L: Characters 3.2, 19–20

3.2. Further modification of the pelvic iliac process.

Plesiomorphy. All species of *Plesiops* below Node L have a well-developed iliac process that is an elongate spur directed anteriorly (Fig. 36c, p. 63). It becomes slightly narrower distally and ends in a rounded tip.

Apomorphy. The species above Node L have a prominent, wide iliac process with a flat ventral surface that sweeps anteriorly into a sharp point (Fig. 36d, p. 63).

Homoplasies. None.

19. Medial (dorsal) epaxial musculature extends beyond lateral epaxial musculature onto frontal bones.

Plesiomorphy. All plesiopines below Node L have epaxial musculature where the lateral fibres extend further anteriorly onto the cranium than the medial (dorsal) fibres (Fig. 41a,b). Acanthoclinines and *Fraudella* also have this arrangement of epaxial musculature, although neither lateral nor medial fibres extend as far onto the cranium as they do in plesiopines.

Apomorphy. The four species of *Plesiops* above Node L, the *oxycephalus* clade, have medial (dorsal) epaxial muscles which extend onto the frontals beyond the lateral epaxial muscles (Fig. 41c).

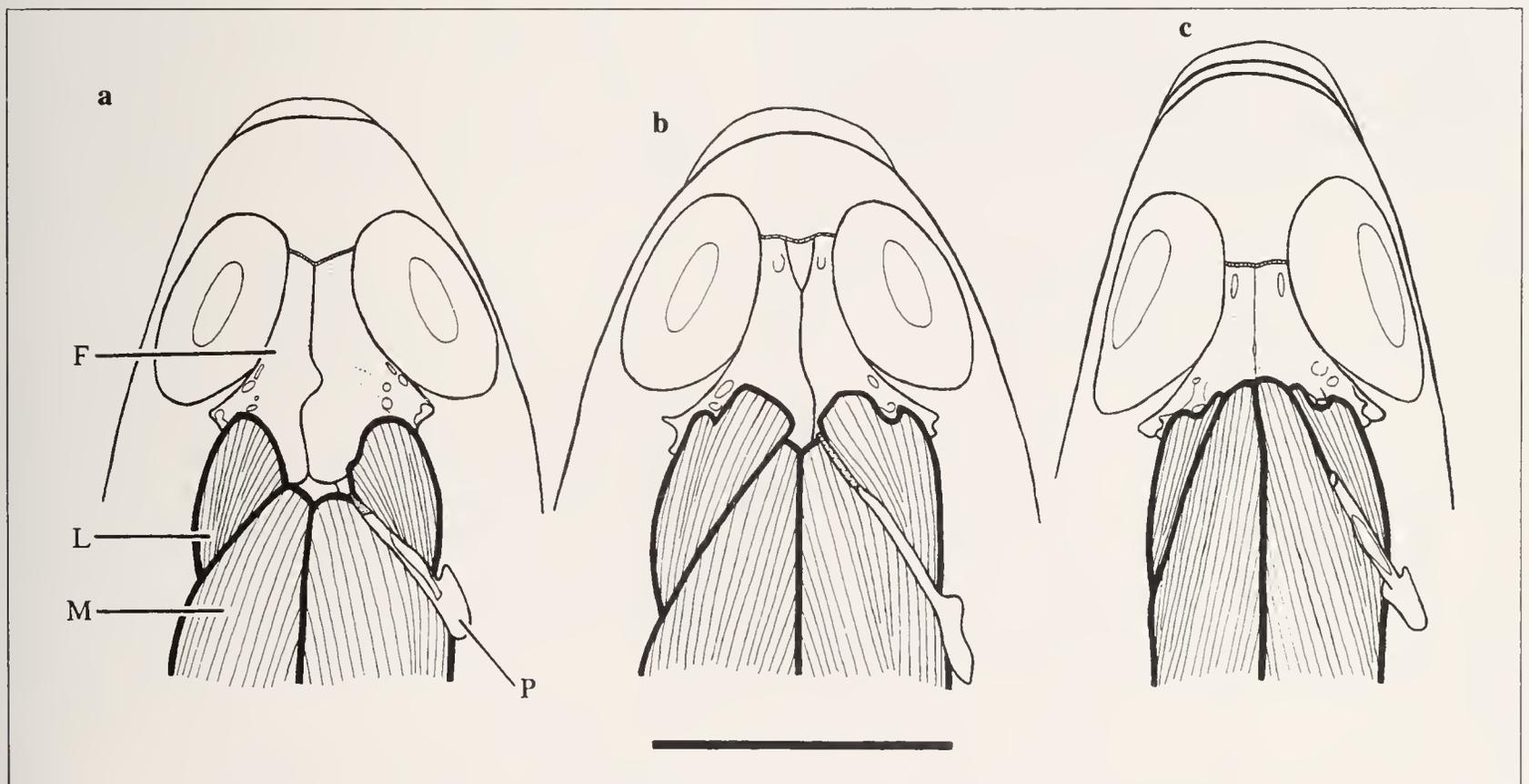


FIG. 41a–c. Dorsal view of the epaxial musculature in 3 species of *Plesiops*. F = frontal bone, L = lateral epaxial muscle, M = medial epaxial muscle, P = posttemporal bone. Ligament stippled. Scale bar = 10 mm.

a. *P. insularis*, AMS I.17363-004, 59.0 mm.

b. *P. corallicola*, AMS I.15360-042, 74.5 mm.

c. *P. oxycephalus*, USNM 274575, 63.0 mm.

Homoplasies. All immediate outgroups except *Calloplesiops* have the plesiomorphic condition of epaxial musculature. *Calloplesiops* has a very similar condition to that of the species of *Plesiops* above Node L, although its epaxial muscles extend further anteriorly and have a wider origin (the frontals of *Calloplesiops* are also wider). Despite its similarity, I do not consider this morphology homologous with that of the Node L species because *Calloplesiops* is too distantly related to the *oxycephalus* clade (Node L) for this muscle pattern to share a common ancestry (Mooi, 1993). Within *Plesiops* this character exhibits no homoplasy.

20. First dorsal pterygiophore narrow.

Plesiomorphy. All members of *Plesiops* except *P. coeruleolineatus*, *P. polydactylus*, and those species above Node L have a wide first dorsal pterygiophore that supports two supernumerary spines (Fig. 42a). A wide first dorsal pterygiophore is also present in outgroups bearing two supernumerary spines.

Apomorphy. Species above Node L have a narrow first dorsal pterygiophore which bears two supernumerary spines (Fig. 42c). Figure 42b superimposes the plesiomorphic and apomorphic condition and shows the larger area exhibited by the plesiomorphic state.

Homoplasies. *Plesiops coeruleolineatus*, *P. polydactylus*, and outgroups such as the *acanthoclinines* and *Steeneichthys* each have a narrow first dorsal pterygiophore, but this element supports only one supernumerary spine. I believe this unique dorsal-fin element arrangement has independently resulted in the development of a narrow first dorsal pterygiophore in each of these taxa. This inter-

pretation suggests that the putatively derived condition of the character at Node L is free of homoplasy despite this apparent similarity of the pterygiophore noted here.

Node M: Characters 21–24

21. Posterior upper lateral-line scales with anterior pore of sensory canal not covered by preceding scale.

Plesiomorphy. All immediate outgroups and plesiopines below Node M have upper lateral-line scales that overlap such that the anterior pore of the sensory canal is covered by the preceding scale. Occasionally the last one or two scales have exposed anterior pores.

Apomorphy. The three species above Node M exhibit the derived state of the lateral line; the posterior 4–16 scales (usually at least 8) have exposed anterior sensory canal pores (Fig. 5, p. 9).

Homoplasies. None.

22. Body with a series of pale, narrow stripes.

Plesiomorphy. The plesiomorphic condition is one of no stripes on the body. This is the state found in all immediate outgroups (but one, see below) and all species of *Plesiops* below Node M.

Apomorphy. All three species above Node M have pale, narrow stripes on the body and caudal peduncle (Figs. 11, 17, 22; pp. 16, 30, 36).

Homoplasies. Among the species of immediate outgroups, only *Acanthoclinus matti* (Hardy, 1985) has pale, narrow body stripes. However, the stripes are formed by pale dorsal and ventral margins of the scales rather than a pale central region on the scales as they are in the striped

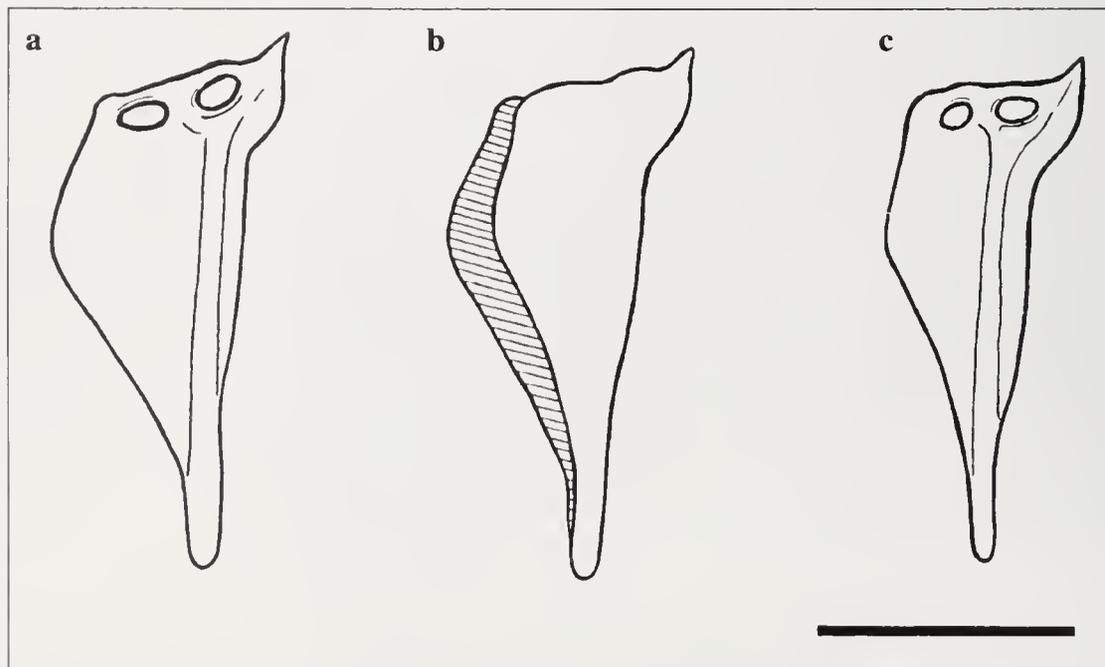


FIG. 42a–c. Anterior dorsal-fin pterygiophore of 2 species of *Plesiops*. Anterior to left. Scale bar = 2 mm.

a. *P. corallicola*, ANSP 122597, 55.0 mm. Example of the wide form.

b. Outline of narrow form of (c) superimposed onto wide form of (a), crosshatching indicates additional area of wide form.

c. *P. cephalotaenia*, ROM 1325CS, 53.0 mm. Example of the narrow form.

Plesiops species. The stripes in these groups are not considered homologous.

23. Reduced number of pectoral-fin rays.

Plesiomorphy. The plesiomorphic condition for pectoral-fin ray number is 20 or more. All species of *Plesiops* below Node M usually have this state (Table 1). In the rare instances where there are 19, the opposite pectoral fin usually has a higher count.

Apomorphy. The three species above Node M have 19 or fewer pectoral-fin rays (Table 1).

Homoplasies. *Plesiops cephalotaenia* uncommonly has 20 pectoral-fin rays, and the sister group to the Node M species, *P. oxycephalus*, has 19 pectoral-fin rays in about 30% of the specimens. This overlap in fin-ray number implies that this character is of dubious value, but the conservative nature of fin-ray number in the genus suggests that the decrease in the *oxycephalus* clade is real and is likely to be indicative of phylogeny. It is possible that this character might be better considered a tentative synapomorphy for the *oxycephalus* clade at Node L.

Remarks. An increase in number of pectoral-fin rays to 25 or more has previously been argued as derived among plesiopines (character 15). Indeed, a low pectoral-fin ray count, ranging from 16–21, is a consistent feature of all immediate outgroups, suggesting that a low count is plesiomorphic. However, this apparent plesiomorphic number of rays in the *oxycephalus* clade can be interpreted *a posteriori* as derived if the low number of rays can be attributed to a truncated development (see discussion) and if FIG/FOG analysis is employed. This would suggest that the low pectoral-fin ray counts of the non-plesiopine plesiopids and the *oxycephalus* clade are non-homologous despite their similarity.

24. Reduced number of dentary pores.

Plesiomorphy. Basal plesiopines (those below node H) all have very numerous small sensory pores on the dentary (Fig. 7, p. 10). *P. auritus*, *P. thysanopterus*, and some populations of *P. verecundus* also share this condition. When compared to individuals of similar size, *Fraudella* has equivalent numbers of dentary pores as *Plesiops* below node M.

Apomorphy. The species above Node M have reduced or greatly reduced numbers of sensory pores on the dentary (Figs. 6, 18; pp. 10, 30).

Homoplasies. No other species of the genus as adults has the low dentary pore numbers that *P. gracilis* and *P. facicavus* have as adults. However, *P. cephalotaenia* has a variable number of dentary pores and just overlaps both the low counts of its most closely related species and the higher counts of its more distant congeners. On average, its dentary pore number is lower than species below Node M. The acanthoclinines also exhibit low dentary pore

counts of from 3–7 (Smith-Vaniz and Johnson, 1990). However, the canal pores in the dentary bone are much larger than those in *Plesiops* or those in *Fraudella*. I interpret this as being a derived condition in acanthoclinines, which suggests that the decreased number of pores in this subfamily is likely to be a nonhomologous decrease. Among paraplesiopines, *Paraplesiops* has large numbers of dentary pores, whereas both *Calloplelesiops* and *Steeneichthys* have reduced numbers.

Node N: Character 25

25. Lateral shelf from the pterotic sensory canal.

Plesiomorphy. No pterotic shelf is found in immediate outgroups or plesiopine taxa below Node N.

Apomorphy. A shelf extending laterally from the pterotic sensory canal is present in *P. cephalotaenia* and *P. gracilis* (Fig. 43). The condition of this feature in *P. facicavus* is unknown, hence this character might be a more inclusive synapomorphy providing support for Node M.

Homoplasies. None.

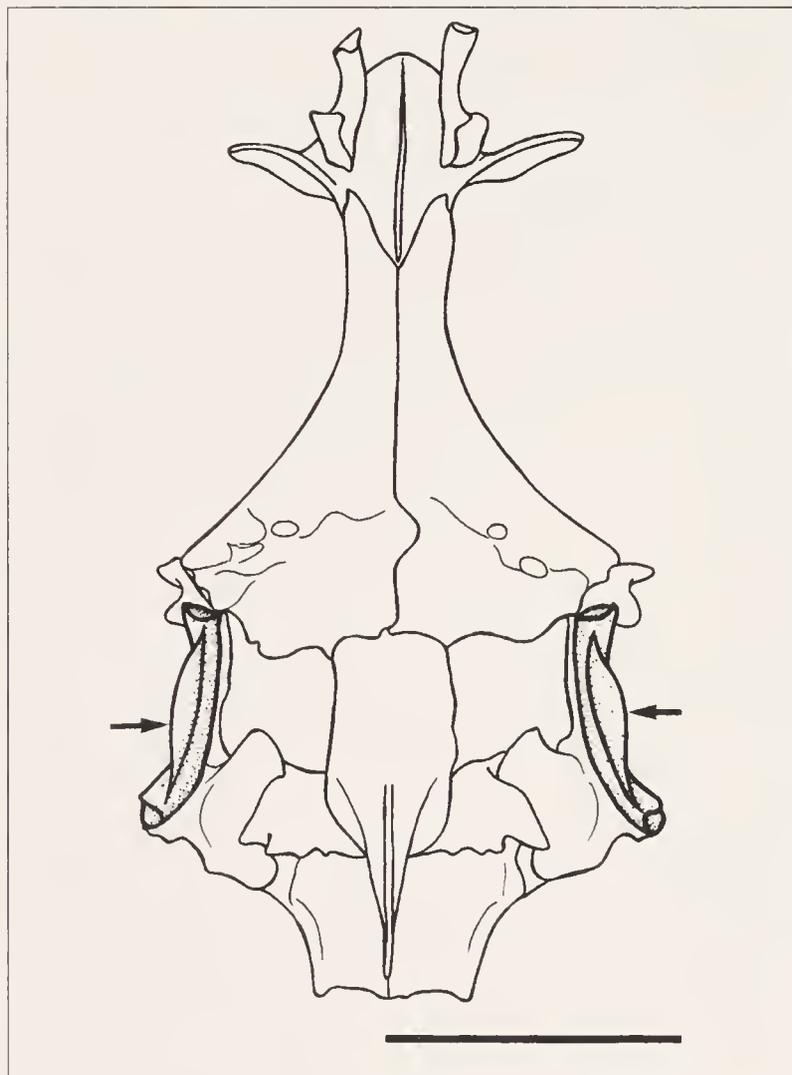


FIG. 43. *Plesiops cephalotaenia*, ROM 1325CS, 53.0 mm. Dorsal view of cranium. Bold lines outline sensory tube of pterotic, stippled. Arrow points to the lateral shelf. Scale bar = 5 mm.

Unresolved Characters

26. A single supernumerary spine on the first dorsal-fin pterygiophore.

Plesiomorphy. All species of *Plesiops* other than *P. coeruleolineatus* and *P. polydactylus* have two supernumerary spines on the first pterygiophore as do all plesiopid outgroup taxa. This is also the usual condition in most percoid groups, including most plesiopid outgroups: *Trachinops*, *Assessor*, most species of *Paraplesiops*, *Calloplelesiops*, and *Fraudella*.

Apomorphy. A single supernumerary spine on the first pterygiophore is found among plesiopines only in *P. coeruleolineatus* and *P. polydactylus*.

Homoplasies. Although most plesiopids have two supernumerary spines, there are exceptions. More distant outgroups to the plesiopines, such as one species of *Paraplesiops*, *P. alisonae* Hoese and Kuitert, 1984, and the genus *Steeneichthys* have only one supernumerary spine on the first pterygiophore. All members of the hypothesized sister taxon, Acanthoclininae, have only one supernumerary spine on the first dorsal-fin pterygiophore. Despite this variability, the apparent positions of *Plesiops coeruleolineatus* and *P. polydactylus* within *Plesiops*, and the application of the FIG/FOG algorithm of Watrous and Wheeler (1981), indicates that the presence of a single supernumerary spine has been independently derived in each of these two taxa (but see Discussion).

Discussion

This species-level cladogram (Figure 34, p. 61) is incompletely resolved. The arrangement of its central portion, *P. nigricans* to *P. mystaxus*, remains tentative despite the fact that PAUP generated only one tree with the branch-and-bound algorithm. The consistency index (CI) of the shortest tree is 0.78 (27 steps with a minimum of 21), which includes neither basal synapomorphies (characters 1–6) nor autapomorphies in its calculation. This value is above what would be found in random data sets of this size (Klassen, Mooi, and Locke, 1991), and the high retention index (RI = 0.84) also attests to this claim. However, there are 26 trees that are only one step longer. These trees are longer as a result of one character being forced to have an additional character state change, and such a manipulation, of course, has most effect on nodes that are supported by single apomorphies. It should be kept in mind that the new topologies are a result of homoplasy introduced into the data without biological evidence in most instances.

An exception might be the placement of *P. polydactylus* as the sister species to *P. coeruleolineatus* on the basis of a shared derived condition of a single supernumerary spine (character 26). This would entail hypothesizing independent origins of high pectoral-fin ray count (character 15) and low number of predorsal scale rows (character 16), resulting in 28 steps on the resulting new topology. Because I have coded dorsal-fin colour (character 18) as unknown for *P. polydactylus* (Table 15), this character can remain consistent as a synapomorphy for a *mystaxus-coeruleolineatus-polydactylus* clade, whereas it is considered a synapomorphy for only the first two of these species in the 27-step tree (Node K, Fig. 34). As noted previously, the modified dorsal-fin colour is very occasionally absent in collections of *P. coeruleolineatus* and *P. mystaxus*, and the few specimens of *P. polydactylus* do not provide enough evidence for coding this feature. Which arrangement among these taxa is preferred, whether the most parsimonious (Fig. 34) or the 28-step version with *P. polydactylus* the sister species to *P. coeruleolineatus*, becomes an argument of which characters are more, or less, likely to change among species and result in an interpretation of homoplasy (predorsal scale row and pectoral-fin ray number vs. supernumerary spine number). With no information regarding the relative simplicity of developmental processes regarding these characters, I tentatively accept the most parsimonious hypothesis (Fig. 34, p. 61).

Despite these problems with the data set, the characters that support monophyly of the genus are convincing (characters 1–6). Similarly, the placement of *P. multisquamata* and *P. malalaxus* as the consecutive sister

groups to the remaining species, based on the cheek musculature, seems reasonable, and the *oxycephalus* clade (Node L, Fig. 34, p. 61) is well-supported. Despite some reluctance to make any broad pronouncements about evolution within the genus using this hypothesis, I believe that it provides a framework to explore some areas that are of general interest.

Changes in developmental rates or timing and their epigenetic consequences, termed heterochronies, are believed to play a major role in the evolution of new morphologies. There are two main categories: 1) pedomorphosis (including neoteny, postdisplacement, and progenesis [see McNamara, 1986]), defined as those processes that produce adults with the juvenile morphology of an ancestor; and 2) peramorphosis (including hypermorphosis, predisplacement, and acceleration [see McNamara, 1986]), those processes that result in adults with morphology transcending that of an ancestor (Gould, 1977; Alberch et al., 1979). Present techniques do not permit identification of ancestors or their ontogenies, but a phylogeny does allow comparison of related ontogenies and polarization of developmental states and pathways. As inferred by Fink (1982) and formalized by Mooi (1987), pedomorphosis can only be identified when at least some of the characters producing a phylogeny are not pedomorphic, a condition called mosaic heterochrony. If this is not the case, pedomorphic states will appear to be primitive, an incorrect assessment of polarity will be used in reconstruction of the phylogeny, and the heterochrony will be misinterpreted (see character 23, Remarks).

In *Plesiops*, the heterochrony exhibits a mosaic pattern among the characters surveyed within the *oxycephalus* clade. Derived characters uniting these four taxa (*P. oxycephalus*, *P. facicavus*, *P. cephalotaenia*, and *P. gracilis*) include a modified iliac process, epaxial muscle morphology, and a narrow first dorsal-fin pterygiophore (characters 3.2, 19, and 20). Other derived characters place them deep within the Plesiopinae, all of which are unlikely to be related to truncation of development. However, the *oxycephalus* clade appears to have homoplastically returned to the primitive number of pectoral-fin rays (character 23). This anomaly can instead be explained as a novel character—truncation of ontogeny of the pectoral girdle resulting in the development of a low number of pectoral-fin rays. As just noted, other characters which are not truncated place the *oxycephalus* clade well within the Plesiopinae, and permit this reinterpretation of the pectoral-fin ray character as a truncation, as opposed to having to retain it as an unexplained homoplasy. More complete knowledge of the pattern of ontogeny of two additional features, the number of dentary pores and the

lateral-line scale morphology, lends credence to this reinterpretation.

Truncated development appears to have been responsible for the retention of a juvenile pattern of dentary sensory pores (character 24). The pattern of adult *P. gracilis* is identical to that of juvenile specimens of other *Plesiops* species (Fig. 44). *P. facicavus* has taken this arrested development to an extreme and retained an almost larval dentary pore pattern, even retaining the relative size of these pores as found in juveniles (Fig. 18, p. 30). Truncated development might not be the only factor involved in the dentary pore pattern found in these two species, as development of dermal sensory morphology is quite complex (Webb, 1990).

Potentially correlated or linked to the paedomorphism exhibited by the dentary pores is the retention of the exposed anterior sensory pore on scales of the upper lateral line (character 21) (Fig. 5; p. 9), which might be attributable to truncated development, or perhaps postdisplacement. Juvenile *P. coeruleolineatus* show this feature of the exposed anterior pore quite clearly (Fig. 45), whereas adults do not. Although the scales of adults of *P. cephalotaenia*, *P. facicavus*, and *P. gracilis* are somewhat modified from a truly juvenile condition (cf. Fig. 5 and 45), I believe this is a paedomorphic character. Perhaps

more detailed analysis of the development of the sensory system, particularly of innervation patterns, will be useful in determining the exact nature of the paedomorphism. With only body size available as a relative measure of time, it is difficult to identify the type of paedomorphism involved in these cases.

Large size appears to be primitive within the genus. *P. multisquamata* is the largest representative (200 mm SL) and is also the sister group to all other species. Relatively large sizes (> 80 mm SL) are reached by all species in the bottom half of the cladogram below Node H. Only *P. verecundus* is known to exceed 80 mm SL among species above Node H. This might suggest that *P. verecundus* can be removed from the polytomy at Node H and all remaining species above this node could be united by the derived condition of smaller maximum body size. However, only 3 of 494 specimens of *P. verecundus* reached more than 80 mm, which might beg the question as to what a maximum size really means biologically or statistically. The basal members of *Plesiops* are much larger than any members of the sister group (although *Acanthoclinus* reaches 210 mm SL) or secondary outgroup, and it is possible that this size increase is an example of peramorphism. Some of the meristic characters that generally increase with body size, such as total number of

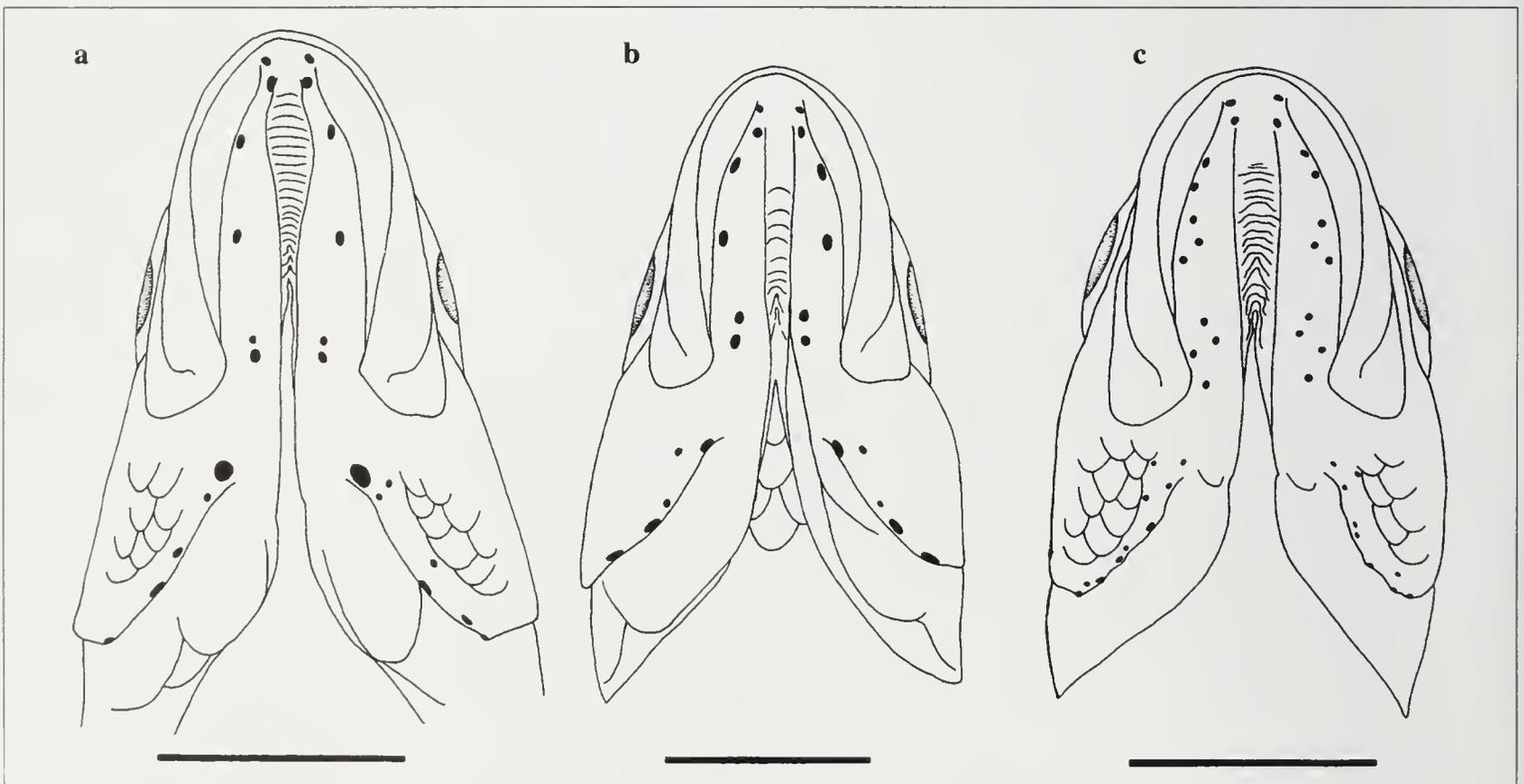


FIG. 44a-c. Ventral view of the heads of 2 species of *Plesiops*. Sensory pores in black. Note that the dentary pore pattern of the adult *P. gracilis* (a) is similar to that of the juvenile *P. coeruleolineatus* (b), but is different from the pattern in an adult *P. coeruleolineatus* (c). The adult fish are the same size. Scale bars in (a) and (c) 5 mm, in (b) 2 mm.

- a. *P. gracilis*, CAS 67419, 40.0 mm. Adult.
- b. *P. coeruleolineatus*, TAU P.9094, 15.8 mm. Juvenile.
- c. *P. coeruleolineatus*, FMNH 44335, 40.0 mm. Adult.

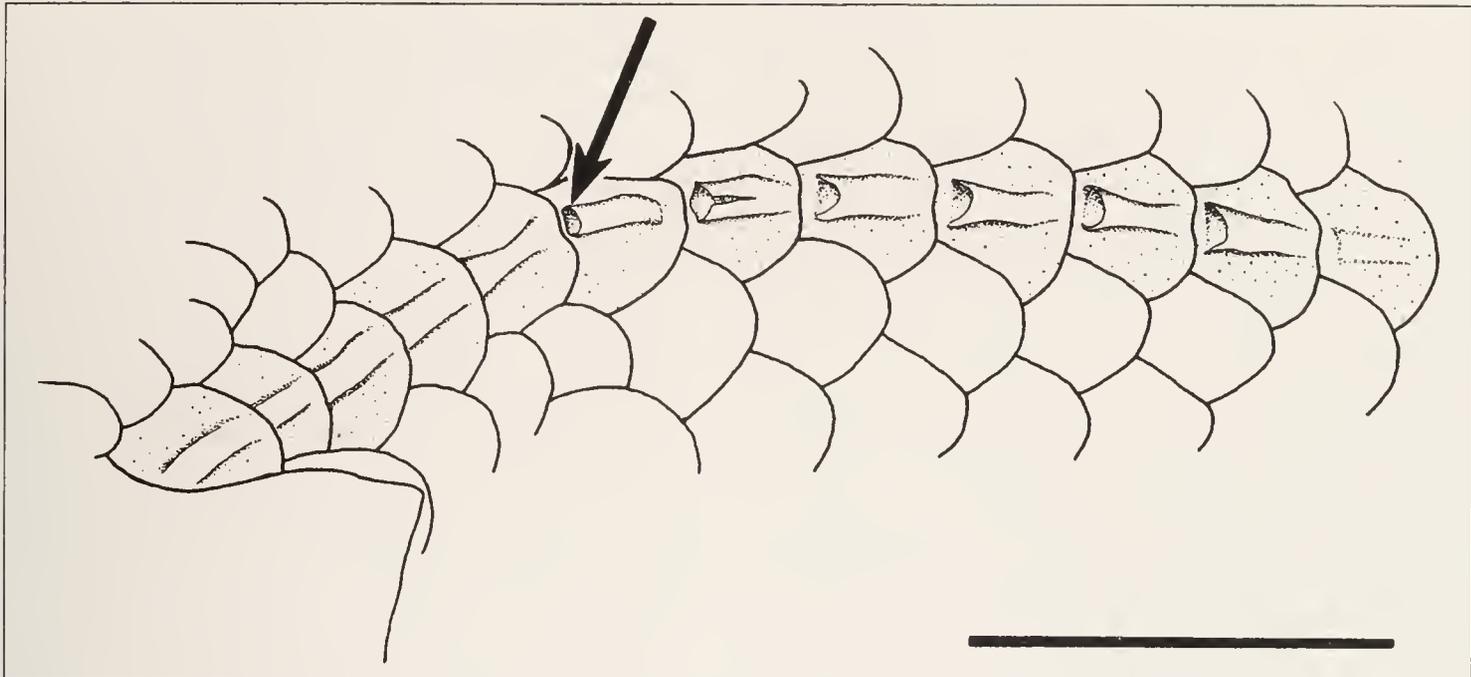


FIG. 45. Anterior 12 upper lateral-line scales of a juvenile *Plesiops coeruleolineatus*, ANSP 108721, 10.6 mm. Lateral-line scales stippled. Arrow indicates the anteriormost canal pore not covered by preceding scale. Scale bar = 1 mm.

branches on the pectoral-fin rays and numbers of dentary sensory pores, are highest in the largest species (Tables 2, 5). These increases might be a natural consequence of becoming large, with numerous features continuing to follow a primitive growth trajectory, and (in this instance) increasing in number as body size increases.

Reaka (1980) has demonstrated that large-sized stomatopods have wider distributions than smaller stomatopods. A similar positive correlation of body size with range has been documented for freshwater fishes (McAllister et al., 1986). *Plesiops* appears to exhibit the reverse relationship of body size to area of distribution, at least in some species. *P. multisquamata*, *P. nigricans*, and *P. malalaxus*, three of the largest species (all > 100 mm SL), have relatively restricted ranges of the south-east African coast, Madagascar, and Red Sea respectively (Fig. 16, p. 26). In contrast, one of the smallest species (< 70 mm SL), *P. coeruleolineatus*, has an enormous range stretching from the east coast of Africa to the Tonga Islands in the Pacific (Fig. 14, p. 23). These inverse relationships of body size with range size do not seem attributable to differing reproductive modes. Both *Plesiops* and stomatopods have generally similar life histories, where parent-guarded, demersal eggs produce pelagic larvae. In a recent review of patterns of geographical ranges, Gaston (1990:116) concluded that "there are theoretical reasons why range size might be either positively or negatively correlated with species body size. Most empirical studies have found a positive relationship, but it seems unlikely that this will be either consistent across taxa or driven by the same processes." The negative trend found in *Plesiops* awaits further analysis pending more detailed life history studies.

Life history information might be unnecessary if the

apparent trend could be argued to be merely an historical artifact. As numerous authors have pointed out, the observation that some species can and do disperse does not necessarily imply that all species disperse. This leads to the possibility that the distributions of the taxa of a monophyletic lineage are portions of an ancestral distribution that has been divided by speciation events. The vicariant biogeography of the genus *Plesiops* will be investigated below, but possible modes of speciation will be examined here. Lynch (1989) outlined a methodology by which different modes of speciation might be identified using range maps for taxa of a monophyletic group for which a phylogeny has been hypothesized.

The method can infer three types of speciation by the following criteria: 1) allo/parapatric or vicariant speciation, where the sister taxa exhibit only trivial sympatry, defined as 10 per cent or less of the distributional area of the least widely distributed species; 2) peripheral isolate speciation, where an isolate is defined as a sister taxon with five per cent or less of the distributional area of the more widely distributed species; and 3) sympatric speciation, which theoretically requires 100 per cent overlap, but substantial overlap (> 10 per cent) is reviewed case by case. Of course, these criteria are arbitrary and problems are immediately apparent, not least of which is how one calculates the areas of the ranges, in many cases imperfectly known, for comparison. For coral reef dwellers, only habitable coral areas should be used for the calculation, but I am unaware of such figures being available. I have estimated ranges by roughly calculating coastal margin occupied by a species. The peripheral isolates criteria of "2" above requires that the species retain their original relative range sizes, and does not take into account the possibility of range retraction of the "ancestral" species or

non-sympatric expansion of the range of the daughter species. Hence, differentiating between vicariant and peripheral isolates speciation seems unrealistic. And a final problem is, of course: what is sympatry? Although some mixed collections of *Plesiops* are known, most species are taken independently of others, and it is possible that similar mapped ranges are misleading and the species are separated by microhabitat preferences. The current study cannot assess the validity of this possibility. Recognizing that any such investigation is only a crude estimate of true speciation modes operating on *Plesiops*, results should be treated with caution.

I have summarized my findings in Table 16. All resolved portions of the cladogram have been incorporated, including the more doubtful resolutions (e.g., Node D, Node G; Fig. 34, p. 61). *P. coeruleolineatus* has an enormous range which overlaps the distributions of most of the other species, but its presence does not greatly affect the general picture seen in Table 16; although the size of the distributional areas would change, as would the percentage of overlap, a high percentage of overlap would remain even with *P. coeruleolineatus* removed from consideration. The degree of range overlap among the sister taxa is high, much higher than that found in the data sets analyzed by Lynch (1989). Eight of the 13 taxon pairs exhibit substantial distributional overlap, five of these reaching 100 per cent (Table 16). Of the widely overlapping taxon pairs, three occur at the level of sister species, theoretically rather recent events that might preclude postspeciation dispersal as a reasonable explanation for the overlap. This leaves sympatric speciation as an alternative, despite the fact that there is no resolution as to what mechanism might permit this mode of speciation (except for polyploidy which is an unlikely possibility here). Four of the widely overlapping taxon pairs occur at more inclusive nodes of the cladogram, implying older speciation events that might better allow for an ad hoc

hypothesis of dispersal to explain the common distributions. The 60 percent overlap of *genaricus* + *insularis* with Node H is left uninterpreted because of the confusion resulting from the wide distribution of *P. coeruleolineatus*. Of the five taxon pairs that exhibit no distributional overlap, three fit the peripheral isolates model, and two appear to be instances of vicariant speciation.

Whereas Lynch (1989) attributed about 70 per cent of speciation to vicariance, 15 per cent to sympatry, and 5 per cent to peripheral isolates for the data sets he examined, I could attribute 60 per cent of speciation in *Plesiops* to the sympatric model, 15 per cent to the vicariance model, and 25 per cent to peripheral isolation using his estimation technique. This apparently anomalous situation can have one of three, or a combination of three, explanations: 1) sympatric speciation is real in *Plesiops*, and perhaps the genus should be investigated for polyploidy or some other possible evidence of this mode; 2) the sympatry is due to postspeciation dispersal; or 3) the assumptions of Lynch's technique are too stringent. A major assumption of the technique is that the organisms have maintained their original distributions from the time of speciation. This is similar to the assumption of most vicariance models, but this assumption is also a requirement of sympatric speciation models (or any others) that use evidence from current distributions.

One pattern that does appear is that current distributions of taxon pairs are congruent with vicariant or peripheral isolates explanations when these occur outside of the Indonesian region. This might suggest that distributions outside of this region remain more stable over time, whereas those distributions within the Indonesian archipelago are unstable. This is consistent with distributions that have been continually altered by cycles of extinction and reinvasion following the Pleistocene (or earlier) changes in sea level.

Biogeography

APPROACH

Historical biogeography is the study of the spatial and temporal distributions of organisms. It provides explanations for these distributions based on past events (Platnick and Nelson, 1978; Wiley, 1981). Numerous authors have contrasted the traditionally dichotomized dispersal and vicariance paradigms (Platnick and Nelson, 1978; Wiley, 1981; Hocutt, 1987). Dispersal models of historical biogeography have been criticized because any and all distributional patterns can be "explained" by dispersal. Every organism has some capability to disperse, and every disjunction could be explained in terms of an independent dispersal event. Under this model, even common patterns of distribution among taxa involve a series of independent, *ad hoc* dispersals. As such, they are unfalsifiable and, furthermore, do not permit alternative explanations, such as vicariance, to be discovered (Wiley, 1981). However, the vicariance model is falsifiable, or can at least be questioned, on the basis of conflicting area cladograms derived from different groups of organisms. If conflicting cladograms are found, dispersal (*sensu* Wiley, 1981) and other biological factors can be used to explain these distributions (Platnick and Nelson, 1978; Wiley, 1981). Page (1989) has pointed out that the dichotomy of dispersal and vicariance is false, and that cladistic techniques and congruent cladograms can similarly be used to explore dispersal and vicariance. He suggested a shift from *a priori* questions of process to methodological questions of area relationships.

Because a cladistic approach is methodologically superior to *ad hoc* dispersal models, it is employed here to explore the historical biogeography of the genus *Plesiops*. Analytical biogeography of Humphries and Parenti (1986) or vicariant biogeography in the "strong" sense of Wiley (1988a) is the ultimate goal of biogeographic study, where several groups are analysed by a rigorous method of cladogram comparison and distributional data reduction. This is difficult to accomplish for the Indo-Pacific region. Few cladistic studies have been performed on groups whose distributions span this region, and among those that do exist, the cladograms are often not fully resolved. The present work on *Plesiops* is an example of this problem, but this is also true of studies on pseudochromids (Gill, 1990; Winterbottom, 1986), blenniids (Springer, 1988; Williams, 1988), priacanthids (Starnes, 1988), chaetodontids (Blum, 1989) and gobiids (Murdy, 1989). As well, distributional data for many groups are incomplete, and changes in these data can dramatically alter interpretations of area cladograms. Because of these limitations, I have taken a narrative approach to the subject, vicariant biogeography in the

"weak" sense of Wiley (1988a). The philosophy remains the same as that for an analytical approach; dispersal is rejected as a first-order explanation of distribution in favour of a vicariance explanation, but dispersal and/or modes of speciation other than vicariance may be invoked as second-order explanations. I compare the area relationships and vicariance scenarios for species of *Plesiops* with those presented in the literature for other fishes, but not in a methodologically rigorous fashion (i.e., neither Component Analysis [Nelson and Platnick, 1981; Humphries and Parenti, 1986] nor Brooks Parsimony Analysis [Brooks, 1981, 1990; Wiley 1988b] is employed). Rather, the discussion is one of viability of possible vicariant scenarios, and is a heuristic approach which I hope will provide a framework from which further research can be initiated.

PATTERNS AND SCENARIOS

Figure 46 summarizes the relationships of the genera of the subfamily Acanthoclininae as presented by Smith-Vaniz and Johnson (1990), and lists their distributions. This subfamily is the sister group of the Plesiopinae (with one genus, *Plesiops*) (Fig. 4, p. 6; Mooi, 1993). Both subfamilies occur throughout the Indo-West Pacific, but their distributions differ in two major ways. Acanthoclinines are absent from the Red Sea and coast of Oman where *Plesiops* is known to occur, and one genus, *Acanthoclinus*, is confined to the coasts of New Zealand, where no other plesiopid has been found. *Acanthoclinus* is the sister group to all other acanthoclinines (Fig. 46), and the distributions are congruent with a hypothesis of Gondwana breakup, where the separation of New Zealand from the rest of Gondwana could have resulted in the disjunction of an ancestral acanthoclinine population, eventually resulting in its speciation. However, such a hypothesis suggests that the event involving differentiation of the plesiopines and acanthoclinines is even older than the late Cretaceous (about 80 m.y.a.). Speciation events involving the other plesiopid taxa must be older, and phylogenetic relationships at higher taxonomic levels would imply even greater relative ages. The substantial overlap of the distributions of Acanthoclininae and its sister taxon Plesiopinae suggests that secondary sympatry by dispersal occurred after the initial speciation event between them. A possible alternative explanation would be sympatric speciation of their ancestor. Implications for historical biogeography of the inclusion of the Notograptidae, a chiefly Australian family, with acanthoclinines as suggested by Gill and Mooi (1993) has not been explored here.

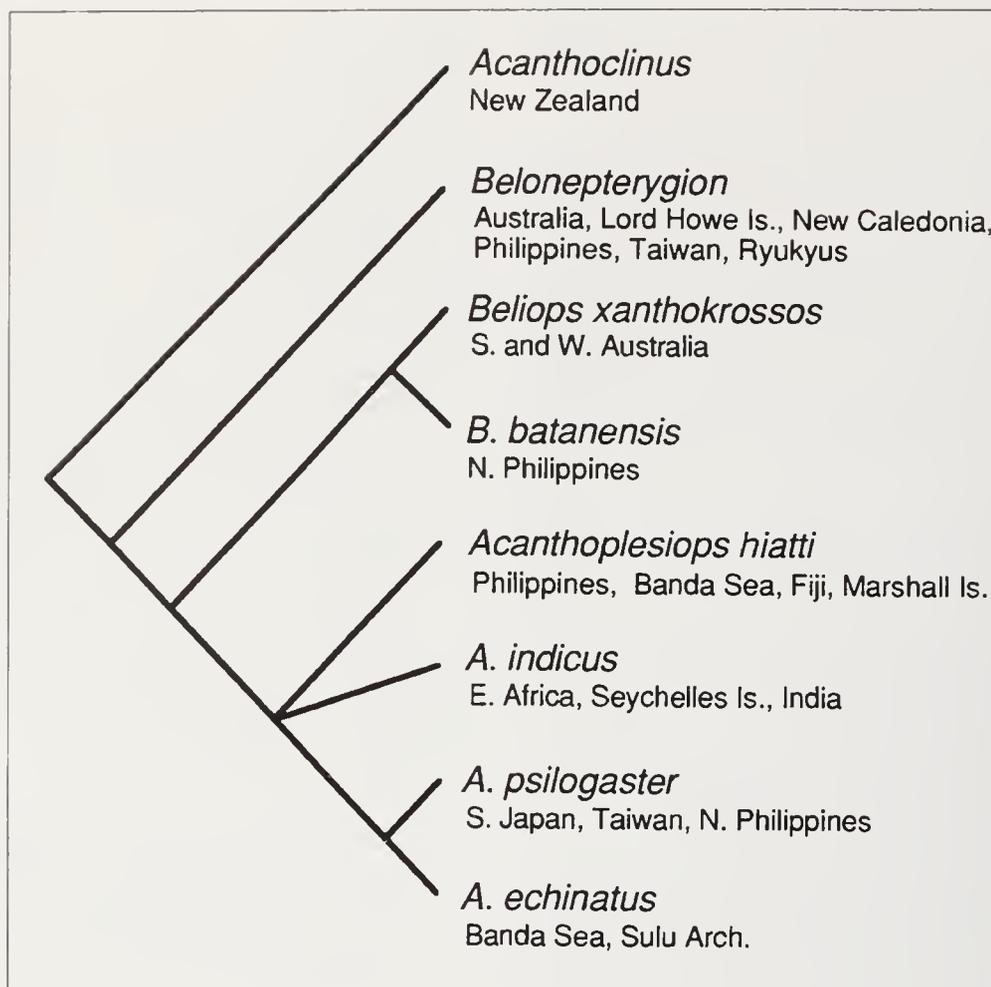


FIG. 46. Cladogram of the Acanthoclininae with distributions of the taxa. After Smith-Vaniz and Johnson (1990).

Within *Plesiops* itself, *P. multisquamata* is interesting because it is restricted to the east coast of South Africa, apparently to the exclusion of its congeners, but other species of *Plesiops* occur in the nearby waters off Madagascar and the Seychelles (Figs. 9, 14, 16; pp. 13, 23, 26). This suggests an initial speciation event in the region of South Africa. Winterbottom (1986) proposed a similar hypothesis to explain the distribution of the Congrogadinae, a derived subfamily of the Pseudochromidae, postulating two speciation events in a proto-western Indian Ocean prior to the breakup of Gondwanaland about 100–120 m.y.a. He further suggested dispersal of some taxa to the Indo-Australian plate before it separated from Africa, an event that led to the allopatry and speciation of some of the congrogadine genera. A. C. Gill (pers. comm.) has questioned this scenario based on the distribution patterns of older members of the Pseudochromidae. More basal area relationships of the Pseudochromidae appear to involve the Indo-Australian Archipelago only, suggesting that faunal exchange has been from the Indo-Australian plate westwards to the African region rather than vice versa. This might also be true of the Plesiopidae, as the basal taxa (Fig. 4, p. 6), *Trachinops* and *Assessor*, are restricted to Australia and Australia to Japan, respectively. *Paraplesiops*, *Steeneichthys*, and *Fraudella* also occur on or near Australian coasts, imply-

ing that the western Indian Ocean distributions of *Callopleiops*, *Plesiops*, and acanthoclinines are a result of an east-to-west dispersal. However, these dispersal hypotheses are not mutually exclusive. The initial diversification of taxa in the Malaysian area could have been followed by an east-to-west dispersal to the African coast and proto-western Indian Ocean where the initial speciation of congrogadines and *Plesiops* might have resulted following Winterbottom's (1986) scenario. Subsequent eastward dispersal of these new western taxa could then have occurred. Such a scenario is highly speculative, and results in the intuitively disturbing conclusion that the pseudochromids and plesiopids, because they must predate the hypothesized 120 m.y. age of congrogadines and *Plesiops*, might well date back to the Jurassic. There are few records of perciform families from even the Paleocene (65–55 m.y.a.), and only two from the Cretaceous (Nolf, 1985; Sepkoski, 1992). Another possibility, of course, is that the estimated times for the tectonic events are in error.

Hocutt (1987) postulated an initial dispersal of Tethyan biota onto the African coast when India and Madagascar separated from this area, followed by dispersal from Africa to Australia along the Antarctic coast. This scenario is similar to Winterbottom's (1986) in that speciation events due to the drift of Madagascar and India from

Africa are followed by dispersal to Australia. In a study of the blennioid genus *Ecsenius* McCulloch, 1923, Springer (1988) suggested that the drift of India resulted in the vicariance and eventual divergence of the *yaeyamaensis* and *oculus* sister-species groups. He also relied on a post-vicariance west-to-east dispersal of both groups to occupy the Malay Archipelago, Australia, and Melanesian arcs, and the western Australia and Melanesian arcs, respectively. Other studies (e.g., Carpenter, 1987, 1990 on caesionids; Russell, 1988, on labrids; Smith-Vaniz, 1976, on the nemophine blenniids; Williams, 1988, on the blennioid genus *Cirripectes* Swainson, 1839) do not provide convincing support for either an east-west or west-east hypothesis, as the taxa are often widespread or present conflicting area relationships at different levels within their respective cladograms. These dispersal scenarios greatly increase the number of *ad hoc* assumptions to explain present-day distributions, and none is particularly satisfying from a cladistic biogeography perspective.

The hypothesized sister taxa *P. corallicola* and *P. nigricans* suggest an area relationship between the Red Sea and Gulf of Aden with the Eastern Indian Ocean, Indonesia and Micronesia. Other percoid taxa show a similar relationship. Smith-Vaniz (1989) reports similar distributions for two species pairs of *Stalix* Jordan and Snyder, 1902 (Opistognathidae): a Red Sea endemic has a sister species on the coasts of Japan and Australia; a Gulf of Oman endemic has its sister species on the western Australian coast. The blennioid *Petroscirtes ancylodon* Rüppell, 1935, of the Red Sea and Persian Gulf, has for its apparent sister taxa *P. variabilis* Cantor, 1850 and/or *P. thepassi* Bleeker, 1853b of the eastern Indian Ocean and west Pacific (Smith-Vaniz, 1976). The congrogadine genus *Haliophis* consists of two species, *H. guttatus* (Forsskål, 1775) ranging from the northern Red Sea to Madagascar, and its sister species, *H. aethiopus* Winterbottom, 1985, apparently found only in the Indonesian archipelago (Winterbottom, 1986). Recent work by A. C. Gill on another pseudochromid subfamily, the Pseudoplesiopinae, shows that the genus *Chlidichthys* Smith, 1953 (about 11 species) is restricted to the west-central Indian Ocean and Red Sea, whereas its sister taxon *Pseudoplesiops* Bleeker, 1858 (about 11 species) ranges from the central and eastern Indian Ocean to the Pitcairn Islands of the Pacific. All of these distributions are congruent with the hypothesis of Hocutt (1987), Springer (1988), and Murdy (1989) that the drift of India northward acted as a vicariant event. This drifting could have resulted in the disjunction of a previously continuous ancestral Tethyan distribution.

As pointed out by Winterbottom (pers. comm.), such a scenario requires the extinction (or primitive absence) of these taxa from India as it drifted north, and there is no evidence that suitable habitat was absent during this drift.

Although much of the Indian coastline is barren of coral reefs today, some exist on its southernmost portion and on Sri Lanka. In discussing biogeography of the *Priacanthus hamrur* (Forsskål, 1775) group, Starnes (1988) suggested a mechanism which avoids this criticism. Noting that India probably projected much further southward through equatorial waters in the middle Tertiary, he postulated that this geology, in conjunction with global cooling and compression of the tropics during the Oligocene, might have resulted in isolated faunas in the west and east Indian Oceans. This would permit the separated taxa to remain as members of the Indian fauna. However, the absence of *P. nigricans* and *P. corallicola* from either Indian coast still requires explanation even with this scenario if these sister taxa are to fit the general pattern; subsequent extinction from India remains as an *ad hoc* hypothesis.

Generally, the relationship of the Red Sea to other areas appears complex. The Red Sea has been considered allied with the northwest Indian Ocean (Klausewitz, 1978). Examples of sister species where one member occurs in the Red Sea and the other in the northwest Indian Ocean are provided by Blum (1989) for members of the Chaetodontidae, and Winterbottom (1985) lists additional taxa. A. C. Gill (pers. comm.) has found evidence for yet another different sister-area relationship between the Red Sea and east Africa for pseudochromid taxa, a pattern previously recognized for only a limited number of taxa (see Winterbottom, 1985; e.g., *Chromis pelloura* Randall and Allen, 1982, Gulf of Aqaba with *C. axillaris* [Bennett, 1831], Somalia, Mozambique, and Mauritius). The examples above provide repeating area relationships of the Red Sea with three areas: 1) the Indonesian/Australian area; 2) the northwest Indian Ocean; and 3) east Africa. At present, general explanations are elusive, but the complex history of the Red Sea region (Cochran, 1983; Braithwaite, 1987) makes it possible that numerous overlapping patterns of different ages will be found. More area cladograms and an analytical approach (*sensu* Humphries and Parenti, 1986) might help to resolve the faunal history of this region.

The hypothesized relationship of *P. nakaharai* with *P. nigricans* and *P. corallicola* forms a three-taxon statement involving allopatric taxa. The area relationships implied (Japan + (Red Sea + Eastern Indian Ocean, Indonesia, Micronesia)) are not repeated by any known fish groups. A perhaps comparable pattern is found among three species of *Cirripectes* (Williams, 1988). *C. imitator* Williams, 1985 ranges from Japan to the Babuyan Islands (northern Philippines) and is sister to *C. fuscoguttatus* Strasburg and Schultz, 1953 of the Pacific tectonic plate and *C. gilberti* Williams, 1988 of the Indian Ocean. Differences between these two patterns are immediately evident. *P. corallicola* occurs non-marginally on the Pacific plate, as does its "equivalent" taxon *C.*

fuscoguttatus, but the former is also found in the Malay archipelago and onto the eastern margin of the Indo-Australian plate, thus overlapping the distribution of *C. gilberti*. *P. nigricans* occurs only in the Red Sea, whereas *C. gilberti* is found across the Indian Ocean exclusive of the Red Sea. Species of the genus *Acanthoplesiops* (Acanthoclininae) have very similar distributions to those of the *Cirripectes* species complex described here (Fig. 46), and further resolution of the relationships among *Acanthoplesiops* might help shed light on these patterns.

One other possible species pair that warrants some attention is that of *P. genaricus* and *P. insularis*. Unfortunately, the evidence for their monophyly is questionable (only character 12) and I have no certain out-group. They do, however, have allopatric distributions and there is some evidence that at least one other non-pleysiopid group exhibits the same distribution pattern. The present-day distribution of *P. insularis* and *P. genaricus* includes three major geological regions: the eastern margin of Australia (the Great Barrier Reef), the Lord Howe Rise (Lord Howe Island, Elizabeth and Middleton

Reefs, Chesterfield Islands), and the Norfolk Ridge (Norfolk Island, New Caledonia) (Fig. 47). Until the late Cretaceous, these three regions were closely adjoined (Parker and Gealey, 1985; Kroenke, 1984). About 89–72 m.y.a., the Norfolk Ridge and New Caledonia rifted from the Lord Howe Rise and eastern Australia. Subsequent seafloor spreading opened the New Caledonia Basin which resulted in the migration of the Norfolk Ridge to the northeast (Parker and Gealey, 1985; Kroenke, 1984). It is believed that the Lord Howe Rise rifted from Australia somewhat later than did the Norfolk Ridge (Kroenke, 1984), although the exact chronology remains uncertain, and the riftings may have been almost concurrent. The opening of the Middleton and Lord Howe Basins displaced the Lord Howe Rise to the east, away from Australia. Current distributions suggest that the *genaricus-insularis* ancestor may have occurred on the pre-rifted coast of eastern Australia in the late Cretaceous. If true, the rifting of the Lord Howe Rise-Norfolk Ridge and subsequent seafloor spreading provides a vicariant event congruent with the differentiation of the present-day species.

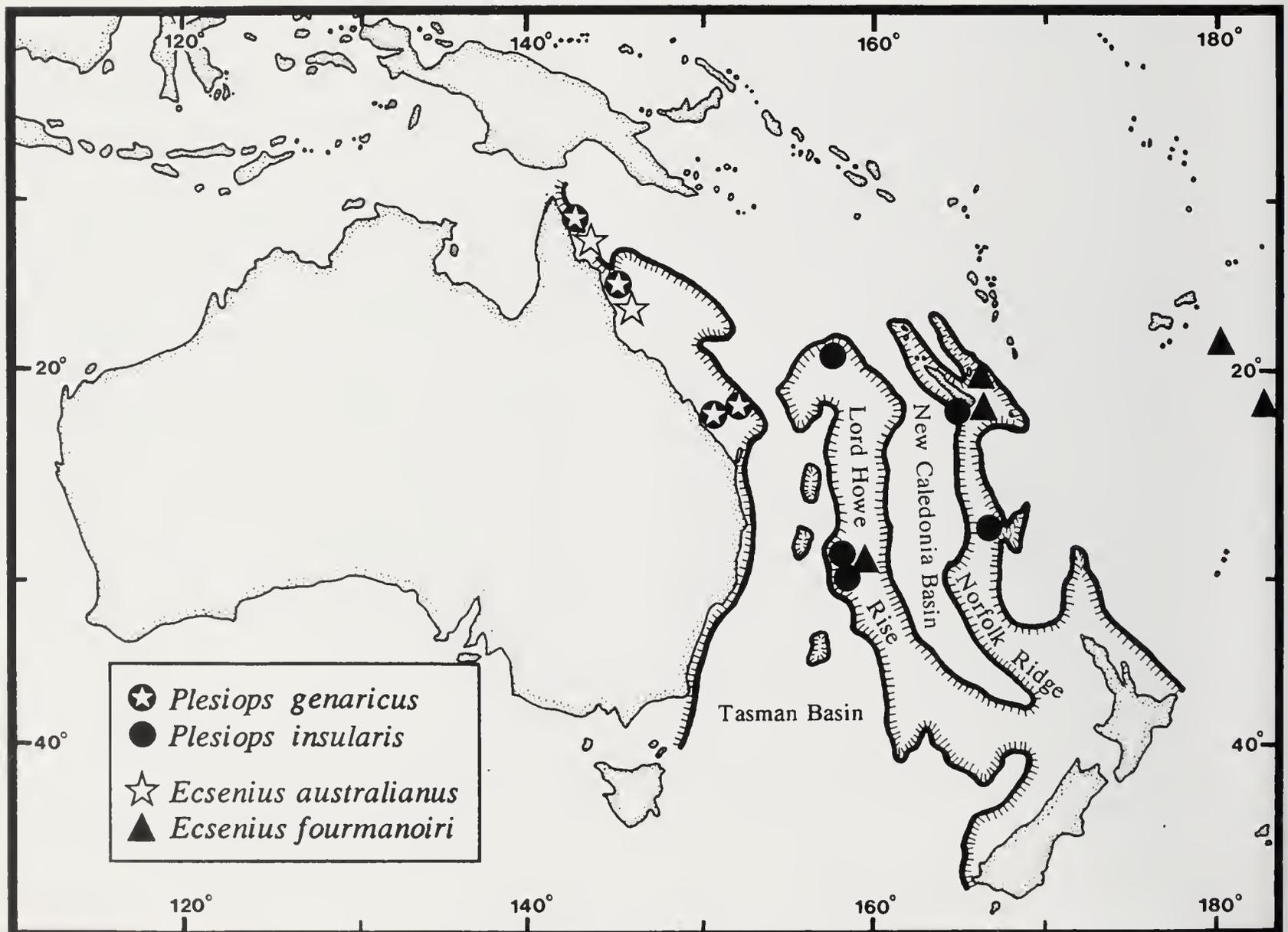


FIG. 47. Distributions of 2 sets of hypothesized sister taxa, *Plesiops genaricus* + *P. insularis* and *Ecsenius australianus* + *E. fourmanoiri*. Bold line with hatching denotes margins of shelves or rises relevant to the vicariant scenario discussed in text.

Springer (1988) outlined a similar scenario for two sister species of the blennioid genus *Ecsenius*. *E. australianus* Springer, 1988 is restricted to the Great Barrier Reef and, at the time Springer wrote (1988), *E. fourmanoiri* Springer, 1972 was known from New Caledonia, the Loyalty Islands, and the Lau and Tonga ridges (Fig. 47). Because the Lau and Tonga ridges are so much younger than Australia-New Caledonia, Springer (1988) argued that the presence of *E. fourmanoiri* on these ridges is more recent than its occurrence in New Caledonia. Following this reasoning, he suggested that the *australianus-fourmanoiri* common ancestor ranged from eastern Australia to New Caledonia. From this distribution, he hypothesized that rifting of the New Caledonia-Norfolk Ridge from the coast of Australia about 75 m.y.a. might be the event resulting in speciation of this ancestor.

However, with the recent addition of the Elizabeth and Middleton Reefs on the Lord Howe Rise as localities for *E. fourmanoiri* (Gill and Reader, 1992; Springer, 1989, 1991) (Fig. 47), the hypothesized distribution of the *australianus-fourmanoiri* ancestor must be modified accordingly. This modified distribution closely matches that of the ancestor of the two *Plesiops* species mentioned above (Fig. 47). As a result, Springer's (1988) vicariant scenario can be altered to employ the rifting of the Lord Howe Rise from Australia rather than the rifting of the Norfolk Ridge as the vicariant event (as suggested by Springer, 1989). The formation of the New Caledonia Basin after the rifting of the Norfolk Ridge has not initiated a further speciation event for either the *Plesiops* or *Ecsenius* species pairs. Springer's modified hypothesis is congruent with my own, though far from corroborated. Few workers would be willing to acknowledge the possibility of 70-million-year-old species, although, as noted above, Winterbottom (1986) has suggested similar time frames for speciation within the Congrogadinae, as Murdy (1989) has done for some gobiids. It should be noted that the actual speciation event (i.e., interruption of genetic exchange) might have occurred some time later than the vicariance of the areas in question, meaning that the age of the species might not correspond with the maximum age implied by the vicariant event. In this instance, it seems unlikely that species cohesion was immediately lost once the Lord Howe Rise began rifting from the Australian coast. Some critical distance was probably required before gene exchange halted or reached low enough levels to permit differentiation of the disjunct populations. The Lord Howe Rise reached its present position no later than about 47 m.y.a., suggesting that the "critical distance" might have been attained as late as 50 m.y.a. Hence the speciation event could have post-dated the initial vicariance by 20-25 m.y.! Additional corroboration for this vicariance scenario might be found in the pseudochromid genus *Ogilbyina* Fowler, 1931, where *O.*

salvati (Plessis and Fourmanoir, 1966) of New Caledonia is sister to *O. queenslandiae* (Saville-Kent, 1893) + *O. novaehollandiae* (Steindachner, 1880) of the Great Barrier Reef, a pattern reminiscent of that found in the *Plesiops* and *Ecsenius* species pairs. In passing, I note that other workers have also found close faunal associations between Australia, Lord Howe Island, Norfolk Island and New Caledonia (e.g., Croizat, 1964). Most recently, such an association was confirmed for mosses (Tangney, 1989). Unfortunately, these studies lack a rigorous cladistic methodology and area cladograms are not available.

One dubious taxon pair, *P. polydactylus* and *P. auritus* + *P. thysanopterus*, suggests an area relationship between the eastern Indian Ocean and the western Malay Archipelago with Fiji. The former species is apparently restricted to Fiji (although only one collection is known), a distribution found among other perciform taxa including *Ecsenius pardus* Springer, 1988 and *E. fijiensis* Springer, 1988, *Meiacanthus ovalauensis* (Günther, 1880) (Smith-Vaniz, 1987), *Siganus uspi* Gawal and Woodland, 1974 and others. Most of the remaining relationships among taxa of *Plesiops* are either insufficiently resolved, or involve species with greatly overlapping distributions (Table 16). Both of these situations make interpretation of their biogeographic history difficult. It appears that either substantial dispersal (*sensu* Wiley, 1981) has occurred in these taxa, obscuring ancestral distributions, or that sympatric speciation is common (see above).

However, looking at individual taxa one can discover areas of endemism, or at least restricted ranges, that are congruent with areas found by other workers. *P. multi-squamata* is restricted to the east coast of South Africa, an area recognized by Hocutt (1987) as an area of endemism. He reports that of the 2100 species recorded in Smith and Heemstra (1986), 301 are endemic to southern African waters, yielding a percentage of endemism comparable to that of other classically recognized regions (see Briggs, 1974). *P. nigricans* is found only in the Red Sea and western Gulf of Aden, one of many species restricted to this region (about 10% endemism in fishes [Randall, 1983]). *P. mystaxus* ranges from western Madagascar and the Comores Islands to the Red Sea and Oman. This distribution is similar to that of the congrogadine *Haliophis guttatus* (Winterbottom, 1985) and the pseudochromine *Pseudochromis persicus* Murray, 1887 complex (Gill, 1990).

Plesiops corallicola is found marginally on the Eurasian tectonic plate in the Malay Archipelago region, on the Philippines plate, and on the Pacific plate (Fig. 16, p. 26; see Fig. 48 for outlines of plate boundaries). It is found on the Indo-Australian plate only on Christmas Island and Cocos-Keeling Islands. Except for the wide-ranging *P. coeruleolineatus*, this is the only species of the

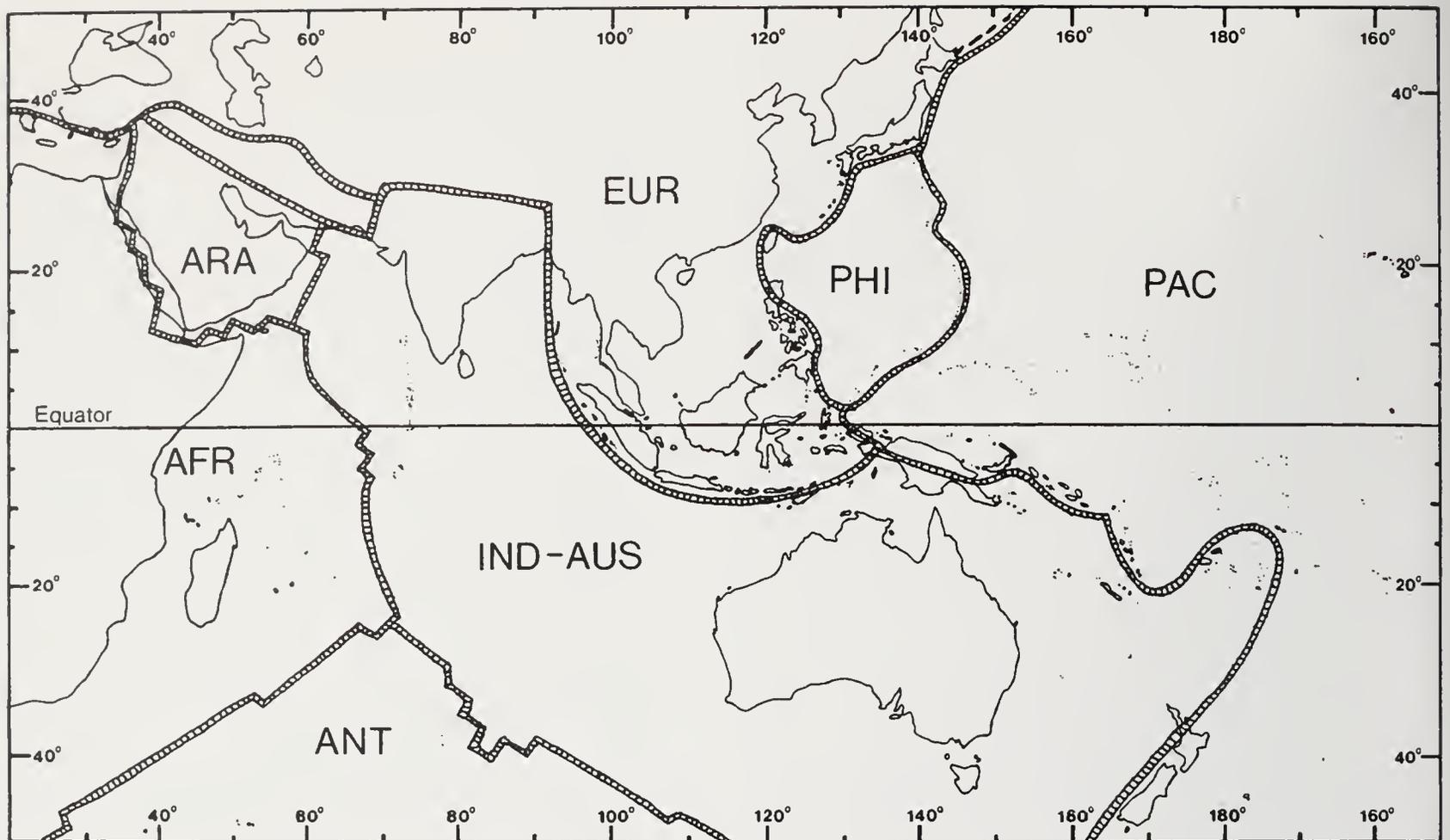


FIG. 48. Approximate margins of the major tectonic plates of the Indo-Pacific region (after Toksöz, 1975). AFR = African, ANT = Antarctic, ARA = Arabian, EUR = Eurasian, IND-AUS = Indo-Australian, PAC = Pacific, PHI = Philippines.

genus that occurs non-marginally on the Pacific plate. It appears to be an example of dispersal along the Caroline Islands conduit, a mechanism suggested by Springer (1982) to account for the occurrence of groups on the Pacific plate not ordinarily associated with it.

Three species exhibit only a marginal Pacific plate distribution: *P. cephalotaenia*, *P. gracilis*, and *P. oxycephalus* (cf. Figs. 10, 48). These species are not known to occur along the Caroline Islands conduit. *P. gracilis* is known to occur as far east towards the Caroline Ridge as Yap Island, but this island is more nearly a component of the Palau-Kyushu and West Mariana Ridge systems than the Carolina Ridge, being separated by the Yap trench. The Palau-Kyushu and West Mariana Ridges are island arcs that formed on the floor of the proto-West Philippine Basin and moved eastward by seafloor spreading in the late Eocene or early Oligocene (ca. 40 m.y.a.) (Shih, 1980). This could explain how this species extended its range eastward without invoking dispersal. Many groups, including some molluscs, appear to have a similar distribution which lends support to this hypothesis (Springer, 1982). All three of these *Plesiops* species occur in the Melanesian borderlands, with *P. oxycephalus* reaching Vanuatu (New Hebrides). This is also a common pattern among other shorefishes (Springer, 1982). *P. gracilis* is unusual among these three species in having one known

locality on the Indo-Australian plate on the west coast of Australia (cf. Figs. 10, 48). Although hypothesized relationships among this *oxycephalus* clade are resolved, their sympatric distributions make this group of little value for biogeographic discussion.

Springer (1988:128) noted that the Great Barrier Reef has numerous endemic species among many different families. To his list can be added three species of *Ogilbyina* and *Pseudochromis flammicauda* Lubbock and Goldman, 1976 of the Pseudochromidae (Gill, 1990), and *Plesiops genaricus* of the Plesiopidae. I have found no fish species that exhibits an identical distribution to *Plesiops insularis*, but, as mentioned, a modified distribution of *Ecsenius fourmanoiri* (Blenniidae) is similar (Fig. 47). There are a number of species that share distributional elements with *P. insularis* (all from Gill and Reader, 1992): *Gymnothorax annasona* Whitley, 1937 and *Eviota* sp. nov. C from Lord Howe Island, Middleton and Elizabeth Reefs, and Norfolk Island; *Apogon norfolcensis* Ogilby, 1888 and *Chrysiptera notialis* (Allen and Randall, 1974) occurring on New Caledonia, Lord Howe Island, Middleton and Elizabeth Reefs, and Norfolk Island; *Genicanthus semicinctus* Waite, 1900 found on Lord Howe Island, Elizabeth and Middleton Reefs, and the Kermadec Islands; *Amphiprion mccullochi* Whitley, 1929 from Lord Howe Island and Elizabeth and Middleton

Reefs; and *Vauclusella rufopilea* (Waite, 1904) from Lord Howe Island, Elizabeth and Middleton Reefs, Norfolk Island, and Kermadec Island. *Ogilbyina salvati* (Pseudochromidae) is known from southern New Caledonia (Gill, 1990), and shares this one element with *Plesiops insularis*.

Plesiops verecundus has a broader distribution, including portions of the Indo-Australian plate, marginal Pacific plate, and the Malay Archipelago of the Eurasian plate (cf. Figs. 9, 48). *P. coeruleolineatus* has an enormous range, found in all localities of its congeners except those of *P. multisquamata* in South Africa, and those of *P. insularis* at Lord Howe, Norfolk, and Chesterfield Islands. The ranges of *P. malalaxus*, *P. facicavus*, and *P. polydactylus* are too poorly known to indicate patterns. The species mentioned in this paragraph (except *P. multisquamata* and *P. insularis*) have little to offer for biogeographic analysis for one of three reasons: wide sympatric distributions, uncertain distributions, and/or unknown sister-group relationships.

Despite the ability to identify areas of similar distribution of species from distantly related taxa, these areas are of little or no value for biogeographic research unless relationships among them can be hypothesized. Until more fully resolved and robust cladograms of fishes and other organisms of the Indo-Pacific are postulated, it remains impossible to approach biogeography of this region with any scientific rigour. Testing of vicariant and dispersal scenarios cannot be performed without the necessary historical information provided by phylogenies. Current work on pseudochromids, gobiids, pempheridids, and blenniids by various researchers will begin to furnish some of these data, and the next ten years should be exciting ones for Indo-Pacific cladistic biogeographers.

The foregoing discussion focuses on Gondwanian or plate tectonic explanations for Indo-Pacific fish distribution. A possible alternative explanation for speciation and current distribution patterns involves, instead, the Quaternary glacial periods. Sea-level changes and possible temperature fluctuations might have created allopatric populations that would give rise to new species, and these species would then have become sympatric when ecological conditions changed. Such a scenario might explain the sympatric species of *Plesiops* in the Malay Archipelago and Australian region. There is ample evidence that much of the Sunda and Sahul shelves were exposed during the glacial maxima. Submarine channels on both shelves indicate the probable courses of rivers across them

(Verstappen, 1975), and submarine peat deposits have been found on the Sunda shelf (Biswas, 1973). In the Gulf of Carpentaria there is evidence of subaerial erosion and a former freshwater or brackish lake at ca. 60 m below sea level (Torgersen et al., 1985).

Myers (1989) attributed the high diversity and endemism within the Malay Archipelago to speciation during the Pleistocene glacial period. Fleminger (1986) suggested that the coldwater upwellings found off western New Guinea today were more extensive during the Pleistocene glacial stages. He postulated a wide band of such upwellings stretching from the Sahul to Sunda shelves through the Moluccan region which would have acted as a barrier and vicariant event. He provided cladograms and distributions for pontellid copepods that present a pattern that could be a result of such a vicariant event. Springer and Williams (1990) favoured this hypothesis, and invoked the extensive emergence of land and increased freshwater runoff during the Pleistocene to enhance this coldwater barrier effect. These changes in environmental conditions are expected to have resulted in extinction in the Indo-Malayan area and allopatry between the remaining populations of the Indian and Pacific oceans. Currently disjunct populations of one species and allopatric distributions of sister species across the Indo-Malayan region were explained as a result of these Pleistocene barrier effects (Springer and Williams, 1990).

Distributions of species or clades of *Plesiops* do not provide evidence for these Pleistocene scenarios. Three species (*P. coeruleolineatus*, *P. corallicola*, and *P. verecundus*) span the entire Indo-Malayan region and show no sign of disjunction (Figs. 9, 14, 16). Only the possible sister relationship of *P. polydactylus* with *P. auritus* + *P. thysanopterus* vaguely resembles a disjunct distribution attributable to sea level changes through Indo-Malaysia, although the range of the former is so severely restricted that other explanations are equally plausible (Fig. 9, p. 13).

The suggestion by Myers (1989) and others that Pleistocene sea level fluctuations contributed to higher speciation rates is not testable by *Plesiops* distributions. The *oxycephalus* clade has all species occurring in the Indo-Malaysian region, but these are all sympatric. Only allopatric species of known relationship can contribute to this debate. Hypotheses regarding glacially-affected speciation will have to be tested with other taxonomic groups. Resolved cladograms of the blenniid genus *Ecsenius* and of pseudochromids that exhibit appropriate allopatric distributions will likely be more informative.

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Literature Cited

- AHLSTROM, E. H., J. L. BUTLER, and B. Y. SUMIDA
 1976 Pelagic stromateoid fishes (Pisces, Perciformes) of the eastern Pacific: kinds, distributions and early life histories and observations on five of these from the northwest Atlantic. *Bulletin of Marine Science* 26:285-402.
- ALBERCH, P., S. J. GOULD, G. F. OSTER, and D. B. WAKE
 1979 Size and shape in ontogeny and phylogeny. *Paleobiology* 5:296-317.
- ALLEN, G. R. and J. E. RANDALL
 1974 Five new species and a new genus of damselfishes (family Pomacentridae) from the South Pacific Ocean. *Tropical Fish Hobbyist* 22:36-49.
 1985 A new genus and species of plesiopid fish from Western Australia and the central-south Pacific Ocean. *Records of the Western Australian Museum* 12:185-191.
- ALLEN, G. R., D. F. HOESE, J. R. PAXTON, J. E. RANDALL, B. C. RUSSELL, W. A. STARCK II, F. H. TALBOT, and G. P. WHITLEY
 1976 Annotated checklist of fishes of Lord Howe Island. *Records of the Australian Museum* 30:365-454.
- AOYAGI, H.
 1941 Long-fin, "Tanabata-uo," found in the waters of the Riu-Kiu Islands, with the description of one new subspecies. *Zoological Magazine (Tokyo)* 53:428-430.
 1943 Coral fishes. Part I. Tokyo, Maruzen. 224 pp.
- BARNARD, K. H.
 1927 A monograph of the marine fishes of South Africa. Part II. *Annals of the South African Museum* 21:419-1065.
 1947 A pictorial guide to South African fishes, marine and freshwater. Cape Town, Maskew Miller. 226 pp.
- BENNETT, E. T.
 1831 Observations of a collection of fishes from Mauritius, presented by Mr. Telfair with characters of new genera and species. *Proceedings of the Zoological Society of London Part 1*:59-61, 165-176.
- BISWAS, B.
 1973 Quaternary changes in sea-level in the South China Sea. *Proceedings, Regional Conference on the Geology of Southeast Asia. Geological Society of Malaysia, Bulletin* 6:229-255.
- BLEEKER, P.
 1849 Bijdrage tot de kennis der ichthyologische fauna van het eiland Bali, met beschrijving van eenige nieuwe species. *Verhandelingen van het Bataviaasch Genootschap van Kunsten en Wetenschappen* 22:1-11.
 1853a Derde bijdrage tot de kennis der ichthyologische fauna van Amboina. *Natuurkundig Tijdschrift voor Nederlandsch Indie* 4:91-130.
 1853b Bijdrage tot de kennis der ichthyologische fauna van Ternate. *Natuurkundig Tijdschrift voor Nederlandsch Indie* 4:131-140.
 1853c Diagnostische beschrijvingen van nieuwe of weinig bekende vischsoorten van Sumatra: Tiental V-X. *Natuurkundig Tijdschrift voor Nederlandsch Indie* 4:243-302.
 1855 Bijdrage tot de kennis der ichthyologische fauna van de Batoe Eilanden. *Natuurkundig Tijdschrift voor Nederlandsch Indie* 8:305-328.
 1857 Over eenige Vischverzamelingen van verschillende gedeelten van Java. *Natuurkundig Tijdschrift voor Nederlandsch Indie* 8:475-480.
 1858 Bijdrage tot de kennis der vischfauna van den Goram-Archipel. *Natuurkundig Tijdschrift voor Nederlandsch Indie* 15:197-218.
 1865 Énumération des espèces de poissons actuellement connues de l'île d'Amboine. *Nederlandsch Tijdschrift voor de Dierkunde* 2:270-293 (pagination 273-276 used twice).
 1875 Sur la famille des Pseudochromidoïdes et révision de ses espèces insulindiennes. *Natuurkundig verhandelingen der Koninklijke Akademie van Wetenschappen* 15:1-32.
 1876 Systema percarum revisum. Pars II. *Archives Néerlandaises des Sciences exactes et naturelles* 11:289-340.
 1875-1878 Atlas ichthyologique des Indes Orientales Néerlandaises, publié sous les auspices du Gouvernement colonial néerlandais. Tome IX. Toxotoidei, Pempheridoidei, Chaetodontoidei, Nandoidei, etc. Amsterdam, Frederic Müller. 80 pp.
- BLOCH, M. E. and J. G. SCHNEIDER
 1801 M. E. Bolchii, Systema Ichthyologiae iconibus ex illustratum. Post obitum auctoris opus inchoatum absolvit, correxit, interpolavit Jo. Gottlob Schneider, Saxo. Berolini. Sumtibus Auctoris Impressum et Bibliopolio Commissum. 584 pp.
- BLUM, S. D.
 1989 Biogeography of the Chaetodontidae: an analysis of allopatry among sibling species and species groups. *Environmental Biology of Fishes* 17:220-237.
- BOCK, W. J. and C. R. SHEAR
 1972 A method of gross dissection of vertebrate muscles. *Anatomischer Anzeiger* 130,S:222-227.
- BÖHLKE, J. E.
 1960 Comments on serranoid fishes with disjunct lateral lines, with the description of a new one from the Bahamas. *Notulae Naturae, Philadelphia* 330:1-11.
- BOSC, L. A. G.
 1818 Nouveau dictionnaire d'histoire naturelle. Vol. 27. Poissons. Appliquée aux arts, à l'agriculture, à l'économie rurale et domestique, à la médecine, etc. Paris, Deterville. 586 pp.
- BOULENGER, G. A.
 1895 Catalogue of the fishes of the British Museum. Vol. I. Catalogue of the perciform fishes of the British Museum. London, British Museum of Natural History. 394 pp.

- BRAITHWAITE, C. J. R.
1987 Geology and palaeogeography of the Red Sea region. *In* Edwards, A. J. and S. M. Head, eds., *The Red Sea*. Oxford, Pergamon Press, pp. 22–44.
- BRIGGS, J. C.
1974 *Marine zoogeography*. New York, McGraw-Hill. 475 pp.
- BROOKS, D. R.
1981 Hennig's parasitological method: a proposed solution. *Systematic Zoology* 30:229–249.
1990 Parsimony analysis in historical biogeography and coevolution: methodological and theoretical update. *Systematic Zoology* 39:14–30.
- BURGESS, W. E. and H. R. AXELROD
1975 *Pacific marine fishes. Book 6: Fishes of Melanesia*. Neptune City, T.F.H. Publications, pp. 1383–1654.
- CANTOR, T. E.
1850 Catalogue of Malayan fishes. *Journal of the Royal Asiatic Society of Bengal* 18:981–1143 [for 1849].
- CARPENTER, K. E.
1987 Revision of the Indo-Pacific fish family Caesionidae (Lutjanoidea), with descriptions of five new species. *Indo-Pacific Fishes* 15:1–56.
1990 A phylogenetic analysis of the Caesionidae (Perciformes: Lutjanoidea). *Copeia* 1990:692–717.
- COCHRAN, J. R.
1983 A model for development of Red Sea. *American Association of Petroleum Geologists, Bulletin* 67:41–69.
- CROIZAT, L.
1964 *Space, time, form: the biological synthesis*. Caracas, published by the author. 881 pp.
- CUVIER, G. L. C. F. D.
1816 *La règne animal distribué d'après son organisation, pour servir de base à l'histoire naturelle des animaux et d'introduction à l'anatomie comparée. Tome II. Les reptiles, les poissons, les mollusques et les annélides*. Paris, Deterville. 532 pp.
- DAY, F.
1871 On the fishes of the Andaman Islands. *Proceedings of the Zoological Society of London* 1870:677–705.
1875 *The fishes of India; being a natural history of the fishes known to inhabit the seas and fresh waters of India, Burma, and Ceylon*. London. Part 1:1–168.
1889 *Fishes*. *In* Blanford, W. T., ed., *The fauna of British India, including Ceylon and Burma. Fishes. Vol. II*. London, Taylor and Francis, pp. 1–509.
- DE LA PAZ, R. M., N. ARAGONES, and D. AGULTO
1988 Coral reef fishes off western Calatagan, Batangas (Luzon Island, Philippines) with notes on new and rare captures and controversial taxa. *Philippine Journal of Science* 117:237–318.
- DINGERKUS, G. and L. D. UHLER
1977 Enzyme clearing of alcian blue stained whole small vertebrates for demonstration of cartilage. *Stain Technology* 52:229–232.
- DIXON, J. M. and L. M. HUXLEY
1982 A catalogue of the Bleeker collection of fishes in the National Museum of Victoria. *Reports of the National Museum of Victoria* 1:111–123.
- DOR, M.
1984 *Checklist of the fishes of the Red Sea*. Jerusalem, Israel Academy of Sciences and Humanities. 437 pp.
- FARRIS, J. S.
1989 The retention index and homoplasy excess. *Systematic Zoology* 38:406–407.
- FINK, W. L.
1982 The conceptual relationship between ontogeny and phylogeny. *Paleobiology* 8:254–264.
- FLEMINGER, A.
1986 The Pleistocene equatorial barrier between the Indian and Pacific Oceans and a likely cause for Wallace's Line. *Unesco Technical Papers in Marine Science, No. 49, Pelagic Biogeography, Proceedings of an International Conference, The Netherlands, 29 May–5 June, 1985*:84–97.
- FORSSKÅL, P.
1775 *Descriptiones Animalium. Hauniae, Heinech and Faber*. 164 pp.
- FOURMANOIR, P.
1957 Poissons téléostéens des eaux malgaches du canal de Mozambique. *Mémoires de L'Institut Scientifique de Madagascar, Tome I, Série F*:1–316.
- FOWLER, H. W.
1928 *The fishes of Oceania. Memoirs of the Bernice P. Bishop Museum* 10:1–540.
1931 Contributions to the biology of the Philippine Archipelago and adjacent regions. The fishes of the families Pseudochromidae, Lobotidae, Pempheridae, Priacanthidae, Lutjanidae, Ponadasyidae, and Teraponidae, collected by the United States Bureau of Fisheries steamer "Albatross," chiefly in Philippine seas and adjacent waters. *Bulletin of the United States National Museum* 100(11):1–388.
1932 Fishes obtained at Samoa in 1929. *Occasional Papers of the Bernice P. Bishop Museum* 9:3–16.
1935 South African fishes received from Mr. H. W. Bell-Marley in 1935. *Proceedings of the Academy of Natural Sciences of Philadelphia* 87:361–408.
- FOWLER, H. W. and B. A. BEAN
1930 The fishes of the families Amiidae, Chandidae, Duleidae, and Serranidae, obtained by the United States Bureau of Fisheries steamer "Albatross" in 1907 to 1910, chiefly in the Philippine Islands and adjacent seas. *United States National Museum, Bulletin* 100, 10:1–334.
- FRICKE, R.
1991 Types and historical materials in the fish collection of the Staatliches Museum für Naturkunde in Stuttgart. Part 1. The Bleeker collection. *Stuttgarter Beiträge zur Naturkunde, Serie A (Biologie)* 471:1–85.
- GASTON, K. J.
1990 Patterns in the geographical ranges of species.

- Biological Reviews of the Cambridge Philosophical Society (London) 65:105–129.
- GAWEL, M. and D. J. WOODLAND
1974 *Siganus (Lo) uspi*, a new species from Fiji; and a comparison with the nominal species *S. vulpinus* and *S. unimaculatus*. *Copeia* 1974:855–861.
- GILCHRIST, J. D. F. and W. W. THOMPSON
1911 Descriptions of fishes from the coast of Natal (Part III). *Annals of the South African Museum* 11:29–58.
- GILL, A. C.
1990 A taxonomic revision of the fish subfamily Pseudochrominae (Perciformes: Pseudochromidae). Ph.D. Thesis, University of New England, Armidale, Australia. 497 pp.
1995 Identification of the primary types of pseudochromine species described by Pieter Bleeker, with lectotype designations for *Pseudochromis tapeinosoma* and *P. xanthochir* (Perciformes: Pseudochromidae). *Copeia* 1995(1):243–246.
- GILL, A. C. and R. D. MOOI
1993 Monophyly of the Grammatidae and of the Notograptidae, with evidence for their phylogenetic positions among perciforms. *Bulletin of Marine Science* 52:327–350.
- GILL, A. C. and S. READER
1992 Fishes. In *Australian Museum, Sydney, Reef biology: a survey of Elizabeth and Middleton Reefs, South Pacific*. *Kowari* 3:90–93, 193–228.
- GOEDEN, G. B.
1974 Revised list of fishes of Heron Wistari Marine National Park. Department of Forestry, Queensland, Technical Paper Number 2:1–19.
- GOULD, S. J.
1977 *Ontogeny and phylogeny*. Cambridge, Cambridge University. 501 pp.
- GRANT, E. M.
1982 *Guide to fishes*. Brisbane, Department of Harbours and Marine. 896 pp.
- GRAY, J. E.
1835 *Illustrations of Indian zoology; chiefly selected from the collection of Major-General Hardwicke*. 202 pls.
- GÜNTHER, A.
1861 *Catalogue of the acanthopterygian fishes in the collection of the British Museum*. Vol. 3. London, British Museum (Natural History). 586 pp.
1867 *Additions to the knowledge of Australian reptiles and fishes*. *Annals and Magazine of Natural History, Series 3*, 20(115):45–68.
1873–1910 *Andrew Garrett's Fische der Südsee, beschrieben und redigirt von A. C. L. G. Günther*. Band I. *Journal des Museum Godeffroy* 1–515.
1880 *Report on the shore fishes procured during the voyage of H. M. S. Challenger in the years 1873–1876*. *Zoology* 1(6):1–82.
- HARDY, G. S.
1985 Revision of the Acanthoclinidae (Pisces: Perciformes), with descriptions of a new genus and five new species. *New Zealand Journal of Zoology* 11[1984]:357–393.
- HAYASHI, M.
1984 Family Plesiopidae. In Masuda, H., K. Amoaka, C. Araga, T. Uyeno, and T. Yoshino, eds., *The fishes of the Japanese Archipelago*. Tokyo, Tokai University Press, pp. 140–141.
- HOCUTT, C. H.
1987 Evolution of the Indian Ocean and the drift of India: a vicariant event. *Hydrobiologia* 150:203–223.
- HOESE, D. F. and R. H. KUITER
1984 A revision of the Australian plesiopid fish genus *Paraplesiops*, with notes on other Australian genera. *Records of the Australian Museum* 36:7–18.
- HUBBS, C. L. and K. F. LAGLER
1949 *Fishes of the Great Lakes region*. Cranbrook Institute of Science, *Bulletin* 26:1–186.
- HUBRECHT, A. A. W.
1879 *Catalogue des collections formées et laissées par M. P. Bleeker*. De Breuk and Smits, Leiden.
- HUMPHRIES, C. L. and L. R. PARENTI
1986 *Cladistic biogeography*. Oxford Monographs on Biogeography. Oxford, Clarendon. 98 pp.
- INGER, R. F.
1955 A revision of the fishes of the genus *Plesiops* Cuvier. *Pacific Science* 9:259–276.
- JENYNS, L.
1842 *Fishes*. In Darwin, C. W., ed., *The zoology of the voyage of the HMS Beagle, under the command of Captain Fitzroy, RN, during the years 1832 to 1836*. Part 4. London, Smith, Elder, and Co. 172 pp.
- JOHNSON, G. D.
1984 Percoidei: development and relationships. In: Moser, H. G., W. J. Richards, D. M. Cohen, M. O. Fahay, A. W. Kendall, Jr., and S. L. Richardson, eds., *Ontogeny and systematics of fishes—an international symposium dedicated to the memory of Elbert Halvor Ahlstrom, 15–18 August 1983, La Jolla, California*. Gainesville, American Society of Ichthyologists and Herpetologists, pp. 464–498.
- JONES, S. and M. KUMARAN
1980 *Fishes of the Laccadive Archipelago*. Kerala, The Natural Conservation and Aquatic Sciences Services. 761 pp.
- JORDAN, D. S. and A. SEALE
1906 *The fishes of Samoa; description of the species found in the archipelago, with a provisional checklist of the fishes of Oceania*. *Bulletin of the Bureau of United States Fisheries* 25:173–455.
- JORDAN, D. S. and J. O. SNYDER
1902 A review of the trachinoid fishes and their supposed allies found in the waters of Japan. *Proceedings of the United States National Museum* 24:461–497.
- KLASSEN, G., R. D. MOOI, and A. LOCKE
1991 Consistency indices and random data. *Systematic Zoology* 40[1992]:446–457.

- KLAUSEWITZ, W.
1978 Zoogeography of the littoral fishes of the Indian Ocean, based on the distribution of the Chaetodontidae and Pomacanthidae. *Senckenbergiana Biologica* 59:25-39.
- KLUNZINGER, C. B.
1871 Synopsis der Fische des Rothen Meeres. II. Theil. Verhandlungen der Kaiserlich-Koniglichen Zoologisch-Botanischen Gesellschaft in Wien 21:441-688.
- KNER, R.
1868 Folge neuer Fische aus dem Museum der Herren Joh. Cäs. Godeffroy un Sohn in Hamburg. (IV), I Abtheilung: Acanthopteri. Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften, Mathematisch-Naturwissenschaftlichen Classe 58:293-356.
- KROENKE, L. W.
1984 Cenozoic tectonic development of the Southwest Pacific. United Nations Economic and Social Commission for Asia and the Pacific, Committee for Co-ordination of Joint South Pacific Offshore Areas, Technical Bulletin 6:1-126.
- KULBICKI, M., J. E. RANDALL, and J. RIVATON
1994 Checklist of the fishes of the Chesterfield Islands (Coral Sea). *Micronesica* 27(1/2): 1-43.
- LEIS, J. M. and T. TRNSKI
1989 The larvae of Indo-Pacific shore fishes. Kensington, New South Wales University. 371 pp.
- LEVITON, A. E., R. H. GIBBS, Jr., E. HEAL, and C. E. DAWSON
1985 Standards in herpetology and ichthyology. Part I. Standard symbolic codes for institutional resource collections in herpetology and ichthyology. *Copeia* 1985:802-832.
- LUBBOCK, R. and B. GOLDMAN
1976 Two distinctive new Australasian *Pseudochromis* (Teleostei: Perciformes). *Journal of Natural History* 10:57-64.
- LYNCH, J. D.
1989 The gauge of speciation: on the frequencies of modes of speciation. In Otte, D. and J. A. Endler, eds., *Speciation and its consequences*. Sunderland, Sinauer, pp. 527-553.
- MADDISON, W. P., M. J. DONOGHUE, and D. R. MADDISON
1984 Outgroup analysis and parsimony. *Systematic Zoology* 33:83-103.
- MARSHALL, N. B.
1950 Fishes from the Cocos-Keeling Islands. *Bulletin of the Raffles Museum, Singapore* 22:166-206.
- MASUDA, H. and G. R. ALLEN
1987 Sea fishes of the world. Tokyo, Yama-kei Publishers. 528 pp.
- MASUDA, H., C. ARAGA, and T. YOSHINO
1975 Coastal fishes of southern Japan. Tokyo, Tokai University. 379 pp.
- MASUDA, H., K. AMAOKA, C. ARAGA, T. UYENO, and T. YOSHINO
1984 The fishes of the Japanese Archipelago. Tokyo, Tokai University. 437 pp.
- MAUGÉ, L. A.
1967 Contribution préliminaire à l'inventaire ichthyologique de la région de Tuléar. *Recueil des Travaux de la Station marine d'Endoume, Marseille* 7:101-132.
- McALLISTER, D. E., S. P. PLATANIA, F. W. SCHUELLER, M. E. BALDWIN, and D. S. LEE
1986 Ichthyofaunal patterns on a geographical grid. In Hocutt, C. H. and E. O. Wiley, eds., *Zoogeography of freshwater fishes of North America*. New York, Wiley and Sons, pp. 17-51.
- McCULLOCH, A. R.
1923 Fishes from Australia and Lord Howe Island, No. 2. *Records of the Australian Museum* 14:113-125.
- McNAMARA, K. J.
1986 A guide to the nomenclature of heterochrony. *Journal of Paleontology* 60:4-13.
- MEES, G. F.
1962 A preliminary revision of the Belonidae. *Zoologische Verhandelingen* 54:1-96.
- MITO, S.
1955 Breeding habits of a percoid fish, *Plesiops semeion*. *Science Bulletin, Faculty of Agriculture, Kyushu University* 15:95-99.
- MOOI, R. D.
1990 Egg surface morphology of pseudochromoids (Perciformes: Percoidae), with comments on its phylogenetic implications. *Copeia* 1990:455-475.
1993 Phylogeny of the Plesiopidae (Pisces: Perciformes) with evidence for the inclusion of the Acanthoclinidae. *Bulletin of Marine Science* 52:284-326.
- MOOI, R. D. and J. E. RANDALL
1991 Three new species of the genus *Plesiops* (Teleostei: Plesiopidae) from tropical Australian and adjacent seas. *Copeia* 1991(2):373-387.
- MOOI, R. J.
1987 A cladistic analysis of the sand dollars (Clypeasteroidea: Scutellina) and the interpretation of heterochronic phenomena. Ph.D. Thesis, University of Toronto, Toronto, Canada. 204 pp.
- MUNRO, I. S. R.
1955 The marine and fresh water fishes of Ceylon. Canberra, Department of External Affairs. 351 pp.
1967 The fishes of New Guinea. Port Moresby, Department of Agriculture, Stock and Fisheries. 650 pp.
- MURDY, E. O.
1989 A taxonomic revision and cladistic analysis of the oxudercine gobies (Gobiidae: Oxudercinae). *Records of the Australian Museum, Supplement* 11:1-93.
- MURRAY, J. A.
1887 New species from Kurrachee and the Persian Gulf. *Journal of the Bombay Natural History Society* 2:47-49.
- MYERS, R. F.
1989 Micronesian reef fishes, a practical guide to the identification of the coral reef fishes of the tropical central and western Pacific. Barrigada, Coral Graphics. 298 pp.

- NELSON, G. and N. I. PLATNICK
1981 Systematics and biogeography; cladistics and vicariance. New York, Columbia University. 567 pp.
- NOLF, D.
1985 Otolithi piscium. Handbook of paleoichthyology, Vol. 10. Stuttgart, Gustav Fischer Verlag. 145 pp.
- OGILBY, J. D.
1888 Report on a small zoological collection from Norfolk Island. ii—Reptiles and fishes. Proceedings of the Linnaean Society of New South Wales 2:990–993.
- OKEN, L.
1817 V. Kl. Fische. *In* Isis oder Encyclopädische Zeitung. Vol. 8 (No. 148):1779–1782 [for 1179–1182 + 1182a].
- PAGE, R. D. M.
1989 New Zealand and the new biogeography. New Zealand Journal of Zoology 16:471–483.
- PALMER, G.
1970 New records, and one new species, of teleost fishes from the Gilbert Islands. Bulletin of the British Museum of Natural History (Zoology) 19:213–234.
- PARKER, E. S. and W. K. GEALEY
1985 Plate tectonic evolution of the western Pacific-Indian Ocean region. Energy 10:249–261.
- PAXTON, J. R., D. F. HOESE, G. R. ALLEN, and J. E. HANLEY
1989 Zoological catalogue of Australia. Vol. 7: Pisces. Petromyzontidae to Carangidae. Canberra, Australian Government Publishing Service. 665 pp.
- PLATNICK, N. I. and G. J. NELSON
1978 A method of analysis of historical biogeography. Systematic Zoology 27:1–16.
- PLESSIS, Y. and P. FOURMANOIR
1966 Une nouvelle espèce de poisson des récifs coralliens de Nouvelle Calédonie: *Pseudochromis salvati* n. sp. Bulletin de Muséum National d'Histoire Naturelle de Paris, Séries 2, 38:227–229.
- POEY, F.
1868 Synopsis piscium cubensium. Catalogo Razonado de los peces del la isla de Cuba. Repertor. Fisico-natural de la Isla de Cuba 2:279–484.
- RANDALL, J. E.
1973 Tahitian fish names and a preliminary checklist of the fishes of the Society Islands. Occasional Papers of the Bishop Museum 24:167–214.
1983 Red Sea fishes. London, Immel Publishing. 192 pp.
- RANDALL, J. E. and G. R. ALLEN
1982 *Chromis pelloura*: a new species of damselfish from the northern Red Sea. Freshwater and Marine Aquarium 5(11):15–19.
- RANDALL, J. E., G. R. ALLEN, and R. C. STEENE
1990 Fishes of the Great Barrier Reef and Coral Sea. Honolulu, University of Hawaii. 507 pp.
- REAKA, M. L.
1980 Geographic range, life history patterns, and body size in a guild of coral-dwelling mantis shrimps. Evolution 34:1019–1030.
- REGAN, C. T.
1912 The classification of the percoid fishes. Annals and Magazine of Natural History, Series 8, 7:111–145.
- RIVATON, J., P. FOURMANOIR, P. BOURRET, and M. KULBICKI
1989 Catalogue des poissons de Nouvelle-Calédonie. Catalogues Sciences de la Mer, Biologie Marine. Nouméa, ORSTOM. 170 pp.
- ROFEN, R. R.
1958 The marine fishes of Rennell Island. *In* The natural history of Rennell Island, British Solomon Islands, Vol. I. Copenhagen, Danish Science, pp. 149–218.
- RÜPPELL, E.
1828 Atlas zu der Reise im nördlichen Afrika. Fische des rothen Meers. Frankfurt am Main, Gedruckt und in Commission bei Heinr. Ludw. Bronner, Part 1:1–26.
1830 Atlas zu der Reise im nördlichen Afrika. Fische des rothen Meers. Frankfurt am Main, Gedruckt und in Commission bei Heinr. Ludw. Bronner, Part 3:95–141.
1835 Neue Wirbelthiere zu der Fauna von Abyssinien gehörig. Fische des rothen Meeres. Frankfurt am Main, in Commission bei Siegmund Schmerber, pp. 1–28.
- RUSSELL, B. C.
1983 Annotated checklist of the coral reef fishes in the Capricorn-Bunker Group, Great Barrier Reef, Australia. Mackay, Hatfields Printers. 184 pp.
1988 Revision of the labrid fish genus *Pseudolabrus* and allied genera. Records of the Australian Museum, Supplement 9:1–72.
- SANO, M., M. HAYASHI, H. KISHIMOTO, H. MANABE, and K. KOBAYASHI
1984 Validity of the plesiopid fish *Plesiops nakaharae* Tanaka, 1917, with a record of *Plesiops cephalotania* from Japan. Science Report of the Yokosuka City Museum 32:11–22.
- SAVILLE-KENT, W.
1893 The Great Barrier Reef of Australia: its products and potentialities. London, W. H. Allen. 388 pp.
- SCHMIDT, P. J.
1931 An additional list of the fishes of the Riu-Kiu Islands with description of *Pseudochromichtys* [*sic*] *riukianus* n. g. n. sp. Transactions of the Pacific Committee of the Academy of Sciences of the United Soviet Socialist Republics 2:177–185.
- SCHROEDER, R. E.
1980 Philippine shore fishes of the western Sulu Sea. Manila, National Media Production Center. 266 pp.
- SCHULTZ, L. P.
1943 Fishes of the Phoenix and Samoan Islands collected in 1939 during the expedition of the U.S.S. "Bushnell". Bulletin of the United States National Museum 180:1–316.
- SCHULTZ, L. P., E. S. HERALD, E. A. LACHNER, A. D. WELANDER, and L. P. WOODS
1953 Fishes of the Marshall and Marianas Islands, Vol. I: Families from Asymmetrontidae through Siganidae. Bulletin of the United States National Museum 202(1):1–685.

- SCHULTZ, L. P., L. P. WOODS, and E. A. LACHNER
 1966 Fishes of the Marshall and Marianas Islands, Vol. III: Families Kraemeriidae through Antennariidae + Addenda. *Bulletin of the United States National Museum* 202(3):1-176.
- SEPKOSKI, J. J., Jr.
 1992 A compendium of fossil marine animal families 2nd edition. Milwaukee Public Museum Contributions in Biology and Geology 83:1-156.
- SHEN, S.-C.
 1984 Coastal fishes of Taiwan. Taipei, National Taiwan University. 189 pp.
- SHIH, T.-C.
 1980 Marine magnetic anomalies from the western Philippine Sea: implications for the evolution of marginal basins. In Hayes, E. D., ed., *The tectonic and geologic evolution of the southeast Asian seas and islands*. American Geophysical Union, Monograph 23:49-75.
- SMITH, J. L. B.
 1946 New species and new records of fishes from South Africa. *Annals and Magazine of Natural History, Series 11*, 8:793-821.
 1949 The sea fishes of southern Africa. Cape Town, Central News Agency. 550 pp.
 1952 Plesiopid fishes from South and East Africa. *Annals and Magazine of Natural History, Ser. 12*, 5:139-151.
 1953 The sea fishes of southern Africa. Third edition. Cape Town, Central News Agency. 564 pp.
 1961 The sea fishes of southern Africa. Fourth edition. Johannesburg, Central News Agency. 580 pp.
- SMITH, M. M. and P. C. HEEMSTRA
 1986 Smith's sea fishes. Johannesburg, Macmillan South Africa. 1047 pp.
- SMITH-VANIZ, W. F.
 1976 The saber-toothed blennies, tribe Nemophini (Pisces: Blenniidae). *Academy of Natural Sciences of Philadelphia* 19:1-196.
 1987 The saber-toothed blennies, tribe Nemophini (Pisces: Blenniidae): an update. *Proceedings of the Academy of Natural Sciences of Philadelphia* 139:1-52.
 1989 Revision of the jawfish genus *Stalix* (Pisces: Opistognathidae), with descriptions of four new species. *Proceedings of the Academy of Natural Sciences of Philadelphia* 141:375-407.
- SMITH-VANIZ, W. F. and G. D. JOHNSON
 1990 Two new species of Acanthoclininae (Pisces: Plesiopidae) with a synopsis and phylogeny of the subfamily. *Proceedings of the Academy of Natural Sciences of Philadelphia* 142:211-260.
- SNYDER, J. O.
 1912 The fishes of Okinawa, one of the Riu Kiu Islands. *Proceedings of the United States National Museum* 42:487-519.
- SOKAL, R. R. and F. J. ROHLF
 1981 *Biometry*, 2nd ed. New York, W. H. Freeman. 859 pp.
- SPRINGER, V. G.
 1972 Additions to revisions of the blennioid fish genera *Ecsenius* and *Entomacrodus*, with descriptions of three new species of *Ecsenius*. *Smithsonian Contributions to Zoology* 134:1-13.
 1982 Pacific plate biogeography, with special reference to shorefishes. *Smithsonian Contributions to Zoology* 367:1-182.
 1988 The Indo-Pacific blennioid fish genus *Ecsenius*. *Smithsonian Contributions to Zoology* 465:1-134.
 1989 *Ecsenius*: the world's most interesting genus of marine fishes. Part II. *Tropical Fish Hobbyist* 37(9):50-51, 53, 56, 58-61.
 1991 *Ecsenius randalli*, a new species of blennioid fish from Indonesia, with notes on other species of *Ecsenius*. *Tropical Fish Hobbyist* 39(12):100-113.
- SPRINGER, V. G. and J. T. WILLIAMS
 1990 Widely distributed Pacific plate endemics and low-ered sea-level. *Bulletin of Marine Science* 47(3):631-640.
- STARNES, W. C.
 1988 Revision, phylogeny and biogeographic comments on the circumtropical marine percoid fish family Priacanthidae. *Bulletin of Marine Science* 43:117-203.
- STEINDACHNER, F.
 1880 *Ichthyologische Beiträge. Sitzungberichte Akademie der Wissenschaften in Wien* 80:119-191.
- STIASSNY, M. L. J. and J. G. MEZEY
 1993 Egg attachment systems in the family Cichlidae (Perciformes: Labroidei), with some comments on their significance for phylogenetic studies. *American Museum Novitates* 3058:1-11.
- STRASBURG, D. W. and L. P. SCHULTZ
 1953 The blennioid fish genera *Cirripectes* and *Exallias* with descriptions of two new species from the tropical Pacific. *Journal of the Washington Academy of Sciences* 43:128-135.
- SWAINSON, W.
 1839 *The natural history and classification of fishes, amphibians, and reptiles, or monocardian animals*. Vol. 2. London, Longman, Orme, Brown, and Longmans. 452 pp.
- TANAKA, S.
 1917 Six new Japanese fishes. *Zoological Magazine (Tokyo)* 29:198-201.
 1918 Figures and descriptions of the fishes of Japan including the Riukiu Islands, Bonin Islands, Formosa, Kurile Islands, Korea, and southern Sakhalin. Vol. 28:495-514.
 1935. Figures and descriptions of fishes of Japan, 1-30. Tokyo, Kazama Shobô. 557 pp.
- TANGNEY, R. S.
 1989 Moss biogeography in the Tasman Sea region. *New Zealand Journal of Zoology* 16:665-678.
- TAYLOR, W. R. and G. C. VAN DYKE
 1985 Revised procedures for staining and clearing small fishes and other vertebrates for bone and cartilage study. *Cybium* 9:107-119.

- TOKSÖZ, M. N.
1975 The subduction of the lithosphere. *Scientific American* 233(5):88-98.
- TORGERSEN, T., M. R. JONES, A. W. STEPHENS, D. E. SEARLE, and W. J. ULLMAN
1985 Late Quaternary hydrological changes in the Gulf of Carpentaria. *Nature* 313:785-787.
- VAILLANT, L.
1889 Sur les espèces qui composent le genre *Plesiops*, Cuvier. *Bulletin de la Société Philomathématique de Paris*, Ser. 8, 1:57-60.
- VERSTAPPEN, H. Th.
1975 On paleo climates and landform development in Malesia. *Modern Quaternary Research in Southeast Asia* 1:3-35.
- VIVIEN, M. L.
1973 Contribution à la connaissance de l'éthologie alimentaire de l'ichtyofaune du platier interne des récifs coralliens de Tuléar (Madagascar). *Tethys*, Supplement 5:221-308.
- WAITE, E. R.
1900 Additions to the fish-fauna of Lord Howe Island. *Records of the Australian Museum* 3:193-209.
1904 Additions to the fish-fauna of Lord Howe Island, No. 4. *Records of the Australian Museum* 5:135-186.
- WATROUS, L. E. and Q. D. WHEELER
1981 The out-group comparison method of character analysis. *Systematic Zoology* 30:1-11.
- WEBB, J. F.
1990 Comparative morphology and evolution of the lateral line system in the Labridae (Perciformes: Labroidei). *Copeia* 1990:137-146.
- WEBER, M. and L. F. de BEAUFORT
1929 The fishes of the Indo-Australian Archipelago. Vol. 5. Leiden, E. J. Brill. 458 pp.
- WHITEHEAD, P. J. P., M. BOESEMAN, and A. C. WHEELER
1966. The types of Bleeker's Indo-Pacific elopoid and clupeoid fishes. *Zoologische Verhandelingen* 84:1-159.
- WHITLEY, G. P.
1929 Some fishes of the order Amphiprioniformes. *Memoirs of the Queensland Museum* 9:207-246.
1935 Studies in ichthyology, No. 9. *Records of the Australian Museum* 19:215-250.
1937 The Middleton and Elizabeth Reefs, South Pacific Ocean. *Australian Zoologist* 8:199-273.
- WILEY, E. O.
1981 Phylogenetics, the theory and practice of phylogenetic systematics. New York, John Wiley and Sons. 439 pp.
1988a Vicariance biogeography. *Annual Review of Ecology and Systematics* 19:513-542.
1988b Parsimony analysis and vicariance biogeography. *Systematic Zoology* 37:271-290.
- WILLIAMS, J. T.
1985 *Cirripectes imitator*, a new species of western Pacific blennioid fish. *Proceedings of the Biological Society of Washington* 98:533-538.
1988 Revision and phylogenetic relationships of the blennioid fish genus *Cirripectes*. *Indo-Pacific Fishes* 17:1-78.
- WINTERBOTTOM, R.
1974 A descriptive synonymy of the striated muscles of the Teleostei. *Proceedings of the Academy of Natural Sciences of Philadelphia* 125:225-317.
1985 A revision of the congrogadid *Haliophis* (Pisces: Perciformes), with the description of a new species from Indonesia, and comments on the endemic fish fauna of the northern Red Sea. *Canadian Journal of Zoology* 63:209-217.
1986 Revision and vicariance biogeography of the subfamily Congrogadinae (Pisces: Perciformes: Pseudochromidae). *Indo-Pacific Fishes* 9:1-34 [for 1985].
- WOODLAND, D. J.
1990 Revision of the fish family Siganidae with descriptions of two new species and comments on distribution and biology. *Indo-Pacific Fishes* 19:1-136.

TABLE 1. Number of pectoral-fin rays of *Plesiops* species. A number in parentheses denotes an abnormal count on one side only.

	No. of Pectoral-fin Rays													
	17	18	19	20	21	22	23	24	25	26	27	28	29	30
<i>auritus</i>					(2)				21	23	14			
<i>cephalotaenia</i>		13	36	11										
<i>coeruleolineatus</i>			1	8	85	133	42	4						
<i>corallicola</i>		(1)	(1)	17	112	20								
<i>facicavus</i>	1	1												
<i>genaricus</i>					2	17	25	2	1					
<i>gracilis</i>	4	25	16											
<i>insularis</i>					1	18	37	3						
<i>malalaxus</i>		(1)				1	2	1						
<i>multisquamata</i>					1	10	3							
<i>mystaxus</i>			1	10	17	9	1							
<i>nakaharai</i>					3	8								
<i>nigricans</i>			1	3	12	10								
<i>oxycephalus</i>			12	31	3									
<i>polydactylus</i>										5	2	2		
<i>thysanopterus</i>												1	1	1
<i>verecundus</i>			1	20	66	79	48	6						

TABLE 2. Number of branches on pectoral-fin rays of species of *Plesiops*.

	No. of Branches on Ventralmost Pectoral-fin Ray						Total No. of Branches on 6 Ventralmost Pectoral-fin Rays								
	1	2	3	4	5	≥ 6	< 10	10-14	15-19	20-24	25-29	30-34	35-39	40-44	≥ 45
	<i>auritus</i>	10	47	1					56	2					
<i>cephalotaenia</i>	47	11					3	50	4						
<i>coeruleolineatus</i>	2	267	4				2	253	14	4					
<i>corallicola</i>	2	22	20	78	10	17	1	4	7	16	16	48	34	16	6
<i>facicavus</i>	2						1	1							
<i>genaricus</i>		9	22	16					2	29	14	2			
<i>gracilis</i>	45							42	2						
<i>insularis</i>		8	18	30	3				3	38	13	5			
<i>malalaxus</i>				1	1	2						1		2	1
<i>multisquamata</i>			3	1		10					1		1		12
<i>mystaxus</i>	10	24	3	1			2	12	16	6	2				
<i>nakaharai</i>				2	2	6								2	8
<i>nigricans</i>		7	7	11		1		1		6	3	9	5	2	
<i>oxycephalus</i>	4	34						5	24	5					
<i>polydactylus</i>	1	8						9							
<i>thysanopterus</i>		2	1					1	2						
<i>verecundus</i>	19	206	3					167	55	6					

TABLE 3. Number of gill rakers on the first arch in species of *Plesiops*.

	Upper Limb						Lower Limb						Total																	
	3	4	5	6	7		6	7	8	9	10	11	12	13	14	15	9	10	11	12	13	14	15	16	17	18	19	20	21	
<i>auritus</i>	20	34	4						11	38	7	1	1				7	16	24	9				2						
<i>cephalotaenia</i>	3	37	20						5	11	20	18	6				1	3	7	19	18	9	3							
<i>coeruleolineatus</i>	150	115	7	1			1	18	147	74	28	5					1	16	95	80	54	18	9							
<i>corallicola</i>	3	42	87	18	2		1	1	3	46	65	33	3				1	1	3	13	49	47	30	7	1					
<i>facicavus</i>	2								1										1					1						
<i>genaricus</i>	5	33	9								7	10	16	10	4									13	17	9	6	2		
<i>gractilis</i>	7	26	12						1	1	4	13	17	8	1				1					2	5	8	17	8	3	1
<i>insularis</i>	14	36	9								3	15	16	17	5	3								6	10	15	20	4	2	2
<i>malalaxus</i>	2	2										1	1	1	1										1		2		1	
<i>multisquamata</i>	6	7	1								1	1	4	3	4	1								1	1	2	3	2	4	1
<i>mystaxus</i>	3	23	8						2	4	10	9	7	2			2	1	2	11	7	6	5							
<i>nakaharai</i>	1	4	5	1					1	7	2						2	2	2	6			1							
<i>nigricans</i>	4	19	2	1								5	6	11	4									7	5	10	3	1		
<i>oxycephalus</i>	4	33	9						1	4	19	17	2	1	1		1		1					6	15	15	6	2	1	
<i>polydactylus</i>	4	5								2	3	2	1	1					2				5	1	1					
<i>thysanopterus</i>	1	2							1	1	1						1		1	1	1									
<i>verecundus</i>	4	103	109	2			1	2	29	101	54	26	4	1			2	3	17	62	69	43	19	3						

TABLE 4. Selected meristics of scale characters of *Plesiops* species.

	Predorsal Scale Rows											Cheek Scale Rows							No. of Upper LL Scales With Anterior Sensory Canal Pore Exposed							
	4	5	6	7	8	9	10	11	2	3	4	5	6	7	0	1	2	3	4	5	6	7	8			
<i>auritus</i>	6	47	5						1	57					52	5	1									
<i>cephalotaenia</i>			13	40	3	1				22	36						1	4	5	11	8	27				
<i>coeruleolineatus</i>	1	68	181	10						96	166	2			201	58	13	1								
<i>corallicola</i>	1	16	110	24						113	37	1			104	29	9	1								
<i>facicavus</i>							2				2												2			
<i>genaricus</i>			6	29	12					13	26	8			44	3										
<i>gracilis</i>						9	14	20			13	31														
<i>insularis</i>			2	40	17					22	33	4			56	3										
<i>malalaxus</i>			2	2							4															
<i>multisquamata</i>					2	5	7					1	10	3	14											
<i>mystaxus</i>	4	18	12							13	25				38											
<i>nakaharai</i>			3	6	2						8	3			8	1	2									
<i>nigricans</i>					4	9	13					1	16	9	19	5	2									
<i>oxycephalus</i>					4	12	12	3			9	29			9	11	11	3								
<i>polydactylus</i>	5	3								6	1				2	4	1									
<i>thysanopterus</i>	2	1									3				3											
<i>verecundus</i>			12	149	44	1				8	172	23	3		173	28	5									

TABLE 5. Dentary sensory pore:SL ratios and dentary pore number for species of *Plesiops*. Pore:SL ratios are not provided for those species in which pore number remains essentially constant during ontogeny.

	N	Size Range (mm)	Mean Pore:SL	Minimum Pore:SL	Maximum Pore:SL	Minimum Pore No.	Maximum Pore No.
<i>auritus</i>	62	29.9–75.9	0.76	0.44	1.1	12	83
<i>cephalotaenia</i>	60	13.7–62.1	0.26	0.12	0.46	5	23
<i>coeruleolineatus</i>	273	20.2–66.0	0.33	0.20	0.61	6	33
<i>corallicola</i>	155	11.5–142.6	0.34	0.22	0.56	4	58
<i>facicavus</i>	2	45.8–46.3	–	–	–	5	5
<i>genaricus</i>	125	21.9–82.3	1.8	1.1	2.8	10	171
<i>gracilis</i>	45	30.8–70.0	–	–	–	5	9
<i>insularis</i>	128	23.0–98.2	0.76	0.44	1.4	8	127
<i>malalaxus</i>	4	96.2–110.3	1.7	1.4	2.1	145	210
<i>multisquamata</i>	14	44.2–198.0	1.86	0.63	3.0	28	435
<i>mystaxus</i>	42	12.9–65.5	0.39	0.26	0.66	5	38
<i>nakaharai</i>	11	73.2–107.4	0.93	0.61	1.36	48	145
<i>nigricans</i>	26	29.5–117.5	0.59	0.33	0.94	10	110
<i>oxycephalus</i>	46	33.8–74.2	0.38	0.21	0.60	11	40
<i>polydactylus</i>	9	23.2–45.8	0.44	0.39	0.49	9	21
<i>thysanopterus</i>	3	37.8–63.4	1.1	1.06	1.13	40	69
<i>verecundus</i>	274	19.2–94.5	0.57	0.25	1.76	7	115

TABLE 6. A comparison of selected meristics of *Plesiops verecundus* (USNM 295533) and *P. coeruleolineatus* (USNM 313023) from the same collection site off Cuyo Is., Philippines. N = 40 for both samples; 20 males and 20 females in *P. verecundus*, 18 males, 18 females and 4 unknowns in *P. coeruleolineatus*.

		<i>verecundus coeruleolineatus</i>	
Mean SL (mm)		33.3	32.3
Range of SL (mm)		26.0–47.8	19.0–42.5
Scales in Midlateral Series	23	–	36*
	24	39	–
	25	1	–
No. of Gill Rakers on Upper Limb of First Arch	3	1	36
	4	14	4
	5	24	–
	6	1	–
No. of Gill Rakers on Lower Limb of First Arch	7	1	5
	8	3	32
	9	21	3
	10	13	–
	11	2	–
Total No. of Gill Rakers on First Arch	10	–	5
	11	1	29
	12	2	5
	13	8	1
	14	20	–
	15	6	–
Mean Dentary Pore:SL Ratio		0.51	0.34
Range of Pore:SL		0.46–0.75	0.27–0.45
Range of No. of Dentary Pores		12–36	7–16

* 4 specimens were missing midlateral scale rows.

TABLE 7. Pectoral-fin ray meristics of populations of *Plesiops coeruleolineatus* from selected localities.

	No. of Pectoral-fin Rays						Total No. of Branches on 6 Ventralmost Pectoral-fin Rays							
	19	20	21	22	23	24	10	11	12	13	14	15-19	20-24	
Aldabra		1	7	4	1					10	1	1	1	
Carolines	1		6	3				1	9					
Cocos-Keeling			2	6	4	2		2	9	2	1			
Comores			3	6	2		1		9	1				
Borneo			1	6	3				9		1			
East Africa			2	6				1	6		1			
Fiji			2	7	1				8			2		
Great Barrier Reef			1	12	2			3	11	1				
Laccadives and Maldives			4	4	3			2	9					
Madagascar -Tuléar		1	2	10				1	16		2	4	5	
-Nose Bé			1	4				1	2	1				
Marianas			4	2	1			1	6					
Marshalls			10	3					13					
Mauritius					1	1			2					
Moluccas			6	1				1	6					
New Caledonia and Loyalties			1	1	4		2		4					
New Guinea		1	3	3	1			1	6		1			
New Hebrides (Vanuatu)			5	4	1				9		1			
Philippines		3	2	4	3			1	8	1	1		1	
Red Sea		1	2	10	4			3	11	1	1		1	
Ryukyus			4	6	5			3	6	4	1	1		
Samoa			1	8	1			1	9					
Seychelles			7	7	1			3	6	4	1	1		
Sumatra			1						1					
Taiwan			3	6	1				8	2				
Thailand			2	3	4	1		1	8			1		
Timor Sea			3	7				2	7	1				
Vietnam				5	1			1	3	2				
Western Australia (Scott Reef)		1	1	1				1	2					

TABLE 8. Gill raker counts on the first arch of populations of *Plesiops coeruleolineatus* from selected localities.

	Upper Limb				Lower Limb						Total					
	3	4	5	6	6	7	8	9	10	11	10	11	12	13	14	15
Aldabra	8	5					5	6	1	1		4	5	2	1	1
Carolines	2	7					2	1	4	2			3	1	3	2
Cocos-Keeling	9	4		1		1	9	4			1	7	3	2		1
Comores	7	4					7	3	1			5	4	1	1	
Borneo	9	1				1	8	1			1	7	2			
East Africa	5	3					6	2				4	3	1		
Fiji	7	3					4	6				4	3	3		
Great Barrier Reef	7	8					3	4	6	2		1	3	7	3	1
Laccadives and Maldives	10	1				3	7	1			3	7		1		
Madagascar-Tuléar	3	10				1	10	2				4	7	2		
-Nose Bé	1	3	1				3	2				1	1	3		
Marianas	3	4					4	3				3	1	3		
Marshalls	2	12					4	6	3				5	6	3	
Mauritius		2					2						2			
Moluccas	7	1				1	4	3			1	4	2	1		
New Caledonia and Loyalties	1	4	1				2	2	1	1		1	1	1	2	1
New Guinea	5	3					4	4				3	3	2		
New Hebrides (Vanuatu)	7	2	1				8	1	1			6	3			1
Philippines	7	4	1				7	4	1			6	2	3		1
Red Sea	5	11	1			1	9	6	1		1	2	8	5	1	
Ryukyus	10	5					10	3	2			7	5	2	1	
Samoa	4	5	1				4	3	3			3	1	3	3	
Seychelles	11	4				3	10	2			3	7	4	1		
Sumatra		1					1						1			
Taiwan	9		1			4	3	1	2		4	3	1	1		1
Thailand	8	2					8	1	1			6	3	1		
Timor Sea	8	2				1	8	1			1	7	1	1		
Vietnam	6					2	3	1			2	3	1			
Western Australia (Scott Reef)		3					2	1					2	1		

TABLE 9. Dentary sensory pore:SL ratios and pore number of populations of *Plesiops coeruleolineatus* from various localities.

	N	Mean Pore:SL	Minimum Pore:SL	Maximum Pore:SL	Minimum Pore No.	Maximum Pore No.
Aldabra	11	0.28	0.20	0.35	7	18
Carolines	10	0.32	0.26	0.42	10	13
Cocos-Keeling	14	0.30	0.23	0.38	9	20
Comores	11	0.37	0.30	0.57	11	26
Borneo	10	0.35	0.28	0.42	10	19
East Africa	8	0.33	0.26	0.40	9	17
Fiji	10	0.31	0.27	0.38	11	18
Great Barrier Reef	15	0.28	0.23	0.40	11	20
Laccadives and Maldives	11	0.39	0.33	0.44	10	23
Madagascar –Tuléar	13	0.43	0.26	0.60	9	27
–Nose Bé	5	0.35	0.27	0.38	10	16
Marianas	7	0.30	0.25	0.36	9	14
Marshalls	13	0.29	0.22	0.34	10	16
Mauritius	2	0.37	0.34	0.40	14	17
Moluccas	7	0.33	0.23	0.46	11	18
New Caledonia and Loyalties	6	0.32	0.26	0.36	6	19
New Guinea	8	0.32	0.26	0.37	9	16
New Hebrides (Vanuatu)	10	0.29	0.25	0.34	9	19
Philippines	52	0.33	0.22	0.48	7	19
Red Sea	17	0.34	0.27	0.44	7	21
Ryukyus	15	0.31	0.22	0.39	9	19
Samoa	10	0.30	0.23	0.37	11	15
Seychelles	15	0.33	0.22	0.47	7	20
Sumatra	1	0.33	–	–	–	12
Taiwan	10	0.29	0.21	0.36	8	23
Thailand	10	0.33	0.22	0.46	9	15
Timor Sea	10	0.30	0.25	0.38	11	16
Vietnam	6	0.35	0.28	0.40	12	17
Western Australia (Scott Reef)	3	0.33	0.31	0.35	8	12

TABLE 10. Selected meristic characters of populations of *Plesiops corallicola* from various localities.

	No. of Gill Rakers on the First Arch																						
	Upper Limb										Lower Limb										Total		
	20	21	22	3	4	5	6	7	6	7	8	9	10	11	12	10	11	12	13	14	15	16	17
Andamans	3			1	1	1						3									1	1	1
Carolines	2			1	1							2									1	1	1
Cocos-Keeling	1	4		2	2	1					2	3								3	2		
Fiji	1	9	1	3	6	2					2	7	2						1	3	3	4	
Gilberts	1	3		1	2	1					3		1						1	1	1	1	1
Howland/Baker	2	2		4						1	3								1	3			
Japan	1					1				1										1			
Marianas	1	19	11	2	5	19	4	1			12	11	7	1			2	3	7	10	5	4	
Marshalls	2	17		1	6	11	1		1	1	1	3	9	4		1	1	1	5	7	2	1	
Moluccas	1	4	1	1	3		1				1	2	2						2	1	1	1	
New Hebrides (Vanuatu)	14	2		5	10	1					5	6	5					1	6	5	4		
Philippines	6	1		4	3						3	4						2	3	2			
Phoenix/Tokelau	5	3		3	3	2					2	6						1	2	4	1		
Samoa	2	15	5	5	15	3					6	11	6	1				1	8	6	6	1	
Solomons	1	8		4	4	1					3	5		1					5	3	1		
Sumatra	2			1	1						1		1						1		1		

TABLE 11. Dentary sensory pore:SL ratios and dentary pore number in populations of *Plesiops corallicola* from various localities.

	N	Mean Pore:SL	Minimum Pore:SL	Maximum Pore:SL	Minimum Pore No.	Maximum Pore No.
Andamans	3	0.38	0.32	0.45	23	38
Carolines	2	0.35	0.32	0.37	20	28
Cocos-Keeling	6	0.38	0.26	0.55	7	54
Fiji	12	0.37	0.27	0.56	8	50
Gilberts	4	0.26	0.22	0.29	20	29
Howland/Baker	2	0.32	0.32	0.33	29	34
Japan	1	0.35	—	—	—	50
Marianas	32	0.32	0.23	0.46	4	45
Marshalls	18	0.36	0.29	0.47	5	48
Moluccas	2	0.29	0.28	0.30	26	30
New Hebrides (Vanuatu)	15	0.34	0.26	0.47	14	35
Philippines	6	0.32	0.25	0.44	10	50
Phoenix/Tokelau	8	0.28	0.25	0.36	16	30
Samoa	24	0.36	0.23	0.49	10	41
Solomons	8	0.30	0.27	0.34	7	28
Sumatra	1	0.30	—	—	—	26

TABLE 12. Head scale and pectoral-fin meristics of *Plesiops verecundus* from various localities.

	Predorsal Scale Rows			Cheek Scale Rows						No. of Pectoral Rays						Total No. of Branches on 6 Ventralmost Rays			
	6	7	8	9	3	4	5	6	19	20	21	22	23	24	10-14	15-19	20-24		
Fiji	1	33	17	1	2	42	8		15	40	1				37	17	2		
Great Barrier Reef	1	30	20		1	34	13	3	2	8	33	11	3		52	3	1		
Indonesia		2			2	6			1	1					2				
Japan	1	5			6					1	2	3			5	1			
New Caledonia		6	3			8	1				5	6			11				
New Guinea	1	18	2	1	1	19		1		3	14	2			16	4			
New Hebrides (Vanuatu)		6			6						2	4			6				
Sumatra	2	6				8			2	5	1				4	4			
Taiwan	6	19			3	22				2	5	17	3		13	10	2		
Vietnam	1	10	1			12				2	8	2			5	6	1		
Western Australia		14	1		1	13	1			5	8	3			16				

TABLE 13. Gill raker counts on the first arch in populations of *Plesiops verecundus* from various localities.

	Lower Limb						Upper Limb						Total							
	3	4	5	6	7	8	9	10	11	12	13	14	11	12	13	14	15	16	17	18
Fiji	1	18	37				8	31	16	1					1	6	9	27	12	1
Great Barrier Reef	1	28	25	1		1	8	18	15	10	2	1			1	6	13	12	14	7
Indonesia		1	1				1	1												
Japan		1	5					5	1	1						1	4	1		
New Caledonia		5	6				2	9								7	4			
New Guinea		13	7				1	11	4	3	1					10	3	5	2	
New Hebrides (Vanuatu)		2	4					1	1	4						1		2	3	
Philippines	1	14	24	1	1	3	21	13	2					1	2	8	20	6	3	
Sumatra			6	2			1	5	2						1	3	4			
Taiwan		12	12	1			1	10	8	5	1				1	7	6	5	5	1
Vietnam		8	4				1	3	5	3					1	1	6	3	1	
Western Australia	2	9	6		1	1	6	7	2					2	1	2	8	3	1	

TABLE 14. Dentary sensory pore:SL ratios and dentary pore number in populations of *Plesiops verecundus* from various localities.

	N	Mean Pore:SL	Minimum Pore:SL	Maximum Pore:SL	Range of Pore No.
Fiji	58	0.39	0.28	0.61	7-52
Great Barrier Reef	72	0.70	0.40	1.17	14-75
Indonesia	2	0.44	0.43	0.44	15-24
Japan	6	0.70	0.49	0.89	22-52
New Caledonia	11	0.32	0.25	0.42	10-30
New Guinea	20	0.62	0.42	0.94	13-62
New Hebrides (Vanuatu)	6	0.39	0.27	0.60	12-18
Philippines	40	0.51	0.46	0.75	12-36
Sumatra	8	0.61	0.44	1.11	17-62
Taiwan	25	0.86	0.57	1.76	28-115
Vietnam	12	0.61	0.40	0.92	13-56
Western Australia	16	0.42	0.32	0.63	8-35

TABLE 16. Summary data for determining speciation modes for sister elements of *Plesiops* (Fig. 34, p. 61) employing the criteria of Lynch (1989). Speciation mode symbol: I - vicariant speciation; II - peripheral isolates; S - sympatric speciation; ? - equivocal.

Compared Sister Elements	Distributional Areas (km ²)	% Overlap	Separation (km)	Speciation Mode
<i>multisquamata</i> (Node B)	600:54000	0	<100	II
<i>malalaxus</i> (Node C)	1500?:54000	100	-	S
<i>nakaharai</i> (Node E)	1500:32500	0	1500	II
<i>nigricans</i> (<i>corallicola</i>)	4500:28000	0	5500	I
Node D (Node F)	34000:54000	100	-	S
<i>genaricus</i> (<i>insularis</i>)	3000:3000	0	400	I
<i>genaricus</i> + <i>insularis</i> (Node H)	6000:54000	60	-	?
<i>polydactylus</i> (Node J)	100?:5700	0	7600	II
<i>auritus</i> (<i>thysanopterus</i>)	5700:500?	100	-	S
<i>mystaxus</i> (<i>coeruleolineatus</i>)	9000:54000	100	-	S
<i>oxycephalus</i> (Node M)	5000:12000	75	-	S
<i>facicavus</i> (Node N)	500?:12000	100	-	S
<i>cephalotaenia</i> (<i>gracilis</i>)	10000:7500	70	-	S

APPENDIX

Material Examined for Osteological and Myological Characters

Material is listed alphabetically by family, then alphabetically by species. Each species is followed by a catalogue number, number of specimens, and size range in mm SL. Following the size is a notation in square brackets indicating whether the material was examined for osteological features (CS = cleared and stained, X = X-ray) and/or myological features (M). For the genus *Plesiops*, X-rays were available for much of the "Additional Material Examined" in the species descriptions and are not listed here. Institutional abbreviations follow Leviton et al. (1985), and are defined in "Materials and Methods." Additional material examined is listed in Mooi (1993) and Gill and Mooi (1993).

Family APOGONIDAE

Pseudamiops gracilicauda, ROM 908CS (28.0) [CS].
Sphaeramia nemaptera, ROM 780CS (5:40.0–68.0) [CS].

Family CALLANTHIDAE

Callanthias allporti, ROM 1336CS (57.1) [M,CS]; WAM P.25200 (127.0) [CS]. *C. legras*, SAM 25022 (133.0) [CS]. *C. parini*, ANSP 152995 (153.0) [CS]. *C. platei*, SIO 65-629 (114.0) [CS]. *C. ruber*, ISH 220/77 (93.0) [CS]. *Grammatonotus laysanus*, BPBM 22757 (93.0) [CS]. *G. crosnieri*, OR 360239 (95.0) [CS].

Family CLINIDAE

Gibbonsia metzi, ROM 859CS (77.0) [CS].

Family GRAMMATIDAE

Gamma loreto, ROM 749CS (6:31.0–52.0) [CS], 997CS (4:39.6–43.5) [CS], ROM Uncat. (62.5) [M], 31324 (44.8) [M]. *G. melacara*, ANSP 117359 (55.7) [M]; ROM 1006CS (50.0) [CS]. *Lipogramma anabantoides*, USNM 216405 (17.0) [CS]. *L. klayi*, ANSP 127671 (2:23.8[M,CS]–27.3[M]).

Family MORONIDAE

Morone americanus, ROM 349CS (4:40.0–52.3) [CS], 29525 (120.1) [M], 43403 (115.8) [M], 1064CS (2:70.0–89.0) [CS]. *M. chrysops*, ROM 27793 (118.9) [M].

Family NOTOGRAPTIDAE

Notograptus guttatus, ROM 717CS (82.2) [CS].

Family OPISTOGNATHIDAE

Opistognathus darwinensis, ROM 1329CS (51.0) [M,CS]. *O. maxillosus*, ROM 1330CS (58.0) [M,CS], 40692 (67.1) [M]. *Opistognathus* sp., ROM 778CS (54.0) [CS].

Family PLESIOPIDAE

Acanthoclinus fuscus, NMNZ P.14719 (3:19.0–60.0) [M,CS], P.14719 (74.2) [M]; USNM 200547 (2:68.7–84.2) [M]. *A. littoreus*, ROM 1335CS

(2:58.0–72.0) [M,CS]. *Assessor macneilli*, ROM 890CS (31.5) [CS]; USNM 269466 (3:43.0–48.9) [M,CS]. *Belonepterygion fasciolatus*, ROM 1212CS (30.7) [M,CS], 1328CS (39.7) [M,CS]. *Calloplesiops altivelis*, AMS I.15684-032 (77.4) [M]; ROM 894CS (50.0) [CS], 1334CS (69.5) [M,CS]; USNM 217964 (65.2) [M]. *Fraudella carassiops*, QM IA.4788 (5:16.0–25.0) [X], IA.6302 (7:28.5–45.0) [X], I.10783 (36.5) [X], I.19760 (6:26.9–45.0 [X], 45.0 [M,CS]), I.21376 (2:32.3–46.0) [X]. *Paraplesiops alisonae*, NMV A2259 (64.5) [M,CS], A2259 (63.8) [M]; WAM P.27578-001 (59.5) [M,CS]. *P. bleekeri*, AMS I. 20815-001 (29.0) [M,CS]. *P. meleagris*, WAM 26812-007 (70.0) [M,CS]. *P. poweri*, AMS I.17445-006 (66.3) [M]; USNM 274578 (2:47.8–50.5) [M,CS], 274579 (95.0) [M]. *Plesiops auritus*, ROM 60180 (62.0) [M]. *P. cephalotaenia*, ROM 1325CS (53.0) [M,CS]. *P. coeruleolineatus*, ANSP 108721 (2:9.3–11.0) [CS], 108721 (53.7) [M]; ROM 776CS (4:21.3–46.0) [CS], 1324CS (10.0) [CS], 1326CS (10.8) [CS], 1337CS (4:12.6–20.0) [CS]; USNM 264168 (4:15.0–53.0) [CS], 288548 (10.0) [CS]. *P. corallicola*, AMS I.15360-042 (70.0) [CS], I.15360-042 (4:74.5–94.3) [M]; ANSP 51528 (36.2) [M], 108275 (55.5) [M], 122597 (55.0) [CS], 122597 (89.4) [M]; LACM 6674-44 (107.0) [M]; ROM 893CS (34.5) [CS]; USNM 154392 (110.5) [M], 274574 (2:27.5–65.0) [CS]. *P. facicavus*, USNM 146471 (46.3) [M]. *P. genaricus*, AMS I.19483-026 (2:50.0–59.0) [M,CS]. *P. gracilis*, CAS 67423 (2:41.8–63.5) [M,CS]. *P. insularis*, AMS I.17363-004 (40.0) [M,CS], I.17363-004 (2:60.0–94.0) [M]. *P. malalaxus*, MMNH 71-PE3 (98.2) [M]; USNM 320020 (110.3) [M]. *P. multisquamata*, RUSI 76-16 (49.5) [M,CS]; USNM 246690 (123.6) [M]. *P. mystaxus*, USNM 313012 (47.5) [M]. *P. nakaharai*, IORD 80-167 (107.4) [M]. *P. nigricans*, USNM 274569 (63.2) [M,CS], 274569 (68.8) [M]. *P. oxycephalus*, USNM 274575 (63.0) [M,CS]. *P. polydactylus*, USNM 324960 (34.7) [M,CS]. *P. thysanopterus*, USNM 315537 (37.8) [M]. *P. verecundus*, AMS I.15681-043 (2:47.3–57.7) [M]; CAS 67574 (60.0) [M]; ROM 903CS (3:21.0–82.0) [CS]. *Steeneichthys plesiopsus*, BPBP 20012 (30.2) [M,CS], 20012 (2:24.1–29.2) [X], 24110 (2:21.3–25.6) [X]; ROM 1331CS (25.8) [M,CS]; USNM

242118 (25.4) [X], 288926 (3:10.5–18.4) [X], 288927 (20.1) [X]; WAM P.28031-018 (26.3) [X]. *Trachinops brauni*, AMS I.20845-018 (47.3) [M]; ROM 1327CS (2:40.0–46.0) [M,CS]. *T. caudimaculatus*, ROM 49183 (2:50.7–60.5) [M]. *T. noarlungae*, ROM 1332CS (2:41.0–48.0) [M,CS], 49180 (51.0) [M].

Family POMACENTRIDAE

Eupomacentrus bifasciatus, ROM 37300 (87.0) [M].

Family PSEUDOCROMIDAE

Anisochromis straussi, ROM 557CS (24.2) [CS]. *Chlidichthys inornatus*, ROM 857CS (3:30.0–37.0) [CS], 46327 (36.8) [M]. *Congrogadus spinifer*, ROM 855CS (2:58.0–67.0) [CS]. *Cypho purpurascens*, ROM 1338CS (2:37.4–50.0) [M,CS], 46753 (53.5) [M]. *Haliophis guttatus*, ROM 853CS (4:48.0–85.0) [CS]. *Labricinus lineatus*, ROM 684CS (95.0) [CS]. *Ogilbyina queenslandiae*, ROM 685CS (84.0) [CS]. New genus *A porphyreus*, ROM 1333CS (38.0) [CS], 55450 (44.4) [M,CS]. *Pseudochromis marshallensis*, ROM 1339 (5:14.1–35.0) [CS], 53982 (46.9) [M]. *P. paradutoiti*, ROM 177CS (62.0) [CS], 40009 (70.0) [M]. *P. tapeinosoma*, ROM 46831 (39.5) [M]. *Pseudoplesiops rosae* ROM 46723 (8:15.7–20.6) [M]. *P. typus*, ROM 858CS (49.0) [CS].

Family SERRANIDAE

Anthias squammipinnis, ROM 1344CS (2:33.2–45.0) [CS]. *Belonoperca chabanaudi*, ROM 1346CS (33.8) [CS]. *Cephalopholis leopardus*, ROM 44656 (80.0) [M]. *C. nigripinnis*, ROM 884CS (2:55.0–90.0) [CS]. *Diploprion bifasciatus*, ROM 39058 (64.0) [X]. *Epinephelus merra*, ROM 845CS (3:71.4–95.0) [CS], 44635 (2:112.6–117.2) [M], 44586 (77.0) [M]. *Grammistes ocellatus*, ROM 53527 (93.0) [X]. *G. sexlineatus*, ROM 1347CS (32.9) [CS]. *Hemanthias vivanus*, ROM 1350CS (44.0) [CS]. *Holanthias martinicensis*, ROM 1351CS (29.5) [CS]. *Liopropoma susumi*, ROM 1348CS (52.6) [CS]. *Nemanthias carberryi*, ROM 1349 (4:39.4–44.3) [CS]; ROM 43468 (2:56.5–64.0) [M]. *Plectranthias longimanus*, ROM 1352CS (27.0) [CS]. *Pseudanthias* sp., ROM 775CS (4:52.0–58.0) [CS]. *Pseudogramma polyacantha*, AMS I.24548-004 (2:11.9–13.8) [CS], I. 23764-004 (2:8.4–11.6) [CS], I. 20948-011 (3.4) [CS], I. 23764-004 (2.7) [CS]; ROM 867CS (5:15.6–33.1) [CS], 1340CS (6:11.5–18.0) [CS], 1341CS (2:12.0–12.8) [CS], 1342CS (11.7) [CS], 1343CS (2:15.3–18.8) [CS]. *Rainfordia opercularis*, ROM 39059 (64.3) [X]. *Rypticus saponaceus*, ROM 39095 (72.0) [M]. *Serranus tigrinus*, ROM 1345CS (33.0) [CS]. *Suttonia lineata*, ROM 53532 (51.1) [X].

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