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Two New Species of Anchovies of the Genus *Stolephorus* (Engraulidae), with a Key to Species of *Engraulis*, *Encrasicholina*, and *Stolephorus*

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ABSTRACT

Two species of anchovies of the genus *Stolephorus*, *S. multibranchus* and *S. nelsoni*, are described from Ponape, Caroline Islands and Wallal, Western Australia, respectively. They possess a rounded posterior edge of the preoperculum, a long maxilla which reaches posteriorly beyond the anterior margin of the preoperculum, 12–13 branchiostegal rays, 20–23 anal-fin rays, 13–15 pectoral-fin rays; they lack a predorsal spine and an interpelvic scute. *S. multibranchus* is similar to *S. pacificus* in having a high gill-raker count (25–27 + 32–35 and 21–27 + 33–38, respectively), but that species has a much shorter maxilla. Compared to all other congeneric species which have comparatively fewer gill rakers (13–24 + 18–31), *S.*

multibranchus is closest to *S. commersonii* in having a similar pair of dusky bands on the midline of the back from occiput to origin of dorsal fin. *S. nelsoni* resembles *S. apiensis* and *S. commersonii*, but differs from them in having toothed knobs at the bases of the anterior gill rakers on epibranchial one, greater body depth (22.9–23.3 vs. 17.0–22.6% SL), longer head (26.7–27.3 vs. 19.8–26.4% SL), fewer predorsal scales (15 vs. 17–19), and series of dark dots at the bases of the dorsal and anal fins usually absent. Included are figures of the new species, and a key to 18 species of *Stolephorus* together with an Indo-Pacific species of *Engraulis* and five species of *Encrasicholina*.

INTRODUCTION

Indo-Pacific clupeoid fishes exist in such bewildering diversity, numbering some 185 species within 39 genera and 4 families plus

two more species of different genera introduced from the New World, that ichthyologists who are not familiar with them fre-

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quently came to grief in their identification. Even at present, fish collections made in almost any part of the Indo-Pacific or careful study of specimens in museums continuously reveal more new species. Among the smaller forms of *Encrasicholina* and *Stolephorus*, the resemblance between species is often so great that errors are commonly made even by experienced ichthyologists. It is futile to work on the taxonomy of these two genera without complete comparative data, frequency tables, reliable distributional ranges, good drawings, or the advice of someone familiar with the group, especially without large collections of comparative material.

The species of *Encrasicholina* and *Stolephorus* which are widely distributed in the Indo-Pacific have been studied regionally by various authors, who have defined many of the valid species and have clarified the status of many nominal species. Wongratana (1980) has made the most extensive revision. He later described four new species (Wongratana, 1983); and presented a key to the known species (Wongratana, 1985). Two additional species have been described recently from Guam (Baldwin, 1984) and Northern Territory of Australia (Wongratana, 1987).

All species of these two genera have been assigned by most authors to *Stolephorus* until recently Nelson (1983) divided them into two genera: *Encrasicholina* Fowler (1938) (*E. devisi*, *E. heterolobus*, *E. oligobranchus*, *E. purpurea*, and *E. punctifer*) and *Stolephorus* Lacépède (1803) (*S. andhraensis*, *S. apiensis*, *S. baganensis*, *E. brachycephalus*, *S. carpentariae*, *S. chinensis*, *S. commersonii*, *S. dubiosus*, *S. holodon*, *S. indicus*, *S. insularis*, *S. pacificus*, *S. ronquilloi*, *S. tri*, and *S. waitei*). However, Baldwin (1984) and Wongratana (1985) more recently retained them all in the widely used *Stolephorus*. Reexamination of my data (Wongratana, 1980) and the newly accumulated data incorporated with Nelson's (1983) work confirms the similarity of these two genera but I now tend to agree that *Encrasicholina* should be separated from *Stolephorus*.

After my manuscript on new Australian species was submitted for publication (Wongratana, 1987), I was fortunate to receive from Dr. G. Nelson two specimens (formerly AMNH 31433) of an undescribed species of

Stolephorus collected from a point about three miles north of Wallal, Eighty Mile Beach, Western Australia. At the same time, specimens of the same genus were received from the British Museum (Natural History), London. Among the BMNH material were specimens with relatively high gill-raker counts; they were considered as representing a clinal increase in eastward populations of *S. commersonii* by Wongratana (1980, 1985). With the recent work of Baldwin (1983, 1984) I recognize two specimens (BMNH 1971.8.25.110–111), 59.0–60.0 mm SL, with gill-raker counts 22–23 + 30–31 from Fiji as *S. apiensis*. Nine other specimens (BMNH 1974.9.25.1–9, 53.0–59.5 mm SL, with higher gill-raker counts 25–27 + 32–35) proved to be another new species described herein. The loss of all scales and the limited available specimens of both new species have prevented the comparative study of striation patterns on the scales, and the digestive tract in connection with the gas bladder, which may show differences from closely related species.

In order to make the names available to others, and to prevent the use of nomina nuda, diagnoses of the new species are presented here. More information about these new taxa will be given in a monograph on the Indo-West Pacific clupeoid fishes now in preparation.

Type specimens have been deposited in the American Museum of Natural History, New York (AMNH), the British Museum (Natural History), London (BMNH), Royal Ontario Museum, Canada (ROM), and the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM). Length of maxilla is the measurement between the tip of the mouth and posterior end of the bone. A small gap just before origin of the dorsal fin is not included in the count of the number of predorsal scales. Fin-ray counts refer to total number unless indicated otherwise.

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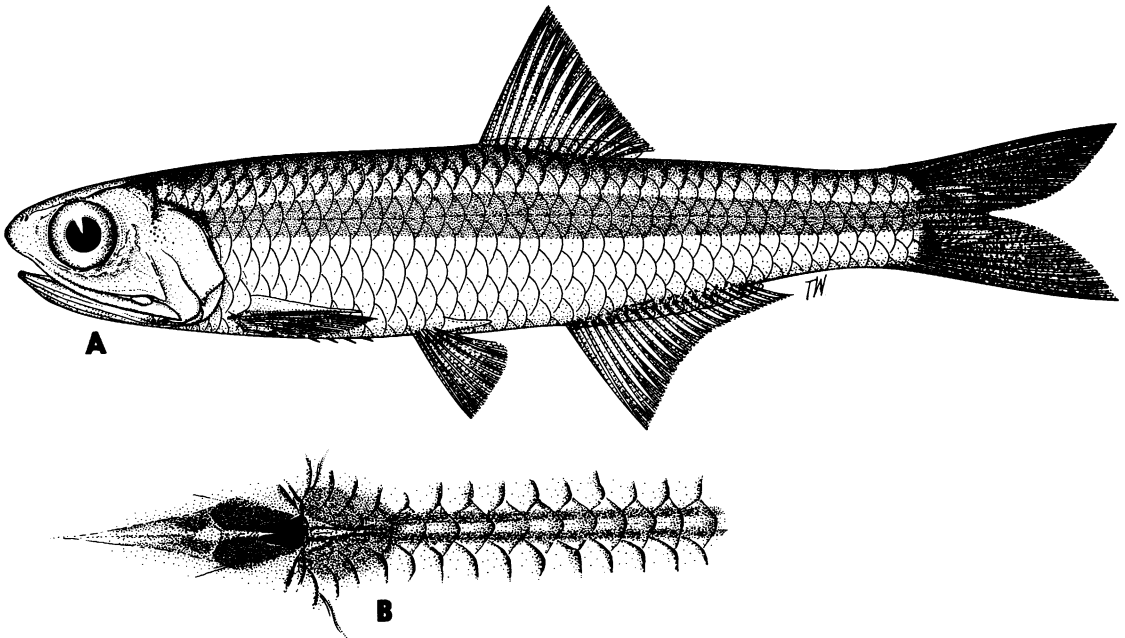


Fig. 1. *Stolephorus multibranchus*, new species, A. holotype, BMNH 1974.9.25.7, 59.5 mm SL, Metalanim Harbour, Ponape, Caroline Islands. B. Inset showing anterior part of the double dusky band on midline of back; the darkest area is position of the posterior frontal fontanelles.

ments and suggestions of Dr. Robert H. Gibbs, Jr. (USNM). Thanks are also due to Mr. Alwyne Wheeler (BMNH), Dr. E. J. Crossman (ROM), Dr. P. J. P. Whitehead, and Dr. G. Nelson for the loan of specimens. This work was conducted during the course of my Smithsonian Postdoctoral Fellowship. The National Marine Fisheries Service Systematics Laboratory helped in many ways. Drafts of the manuscript were typed by Virginia Thomas. Ruth Gibbons was very helpful in preparing photographs of my drawings and in providing other technical assistance.

SYSTEMATICS

Stolephorus multibranchus, new species

Figure 1A, B

MATERIAL: The holotype: BMNH 1974.9.25.7, 59.5 mm in standard length (SL), from Metalanim Harbour, Ponape, Caroline Islands, Townsend Cromwell Cruise, Baiting Operation, Station 102, November 19, 1971, T. S. Hida. Paratypes: AMNH 57158, a specimen, 59.0 mm SL; BMNH 1974.9.25.1–6, mixed lot of 6 specimens, 54.0–57.0 mm SL;

and USNM 280364, a specimen, 54.0 mm SL; all were taken with the holotype.

DIAGNOSIS: A *Stolephorus* species with evenly rounded posteroventral edge of preoperculum, no predorsal spine or interpelvic scute; similar to sympatric *S. pacificus* (of Guam and Kosia) in its high count of gill rakers (25–27 + 32–35 vs. 21–27 + 33–38), but differing chiefly in having longer maxilla (18.0–20.2 vs. 15.8–16.7% SL) reaching posterior border of preoperculum (vs. only to anterior margin of preoperculum), as well as greater width of head at operculum (10.7–11.4 vs. 10.0–10.5% SL), and presence of double dusky band on midline of back from head to origin of dorsal fin. A pair of dusky bands on midline of back and tip of depressed pelvic fins reaching to below bases of front dorsal-fin rays, evidently make it most similar to *S. commersonii*, but that species has gill rakers only 17–21 + 23–28, deeper body depth (19.2–22.6 vs. 18.6–19.6% SL in *S. multibranchus*), and usually more predorsal scales (18–19 vs. 15–17 in *S. multibranchus*). Other useful taxonomic characters of the new species are the absence of toothed knobs at

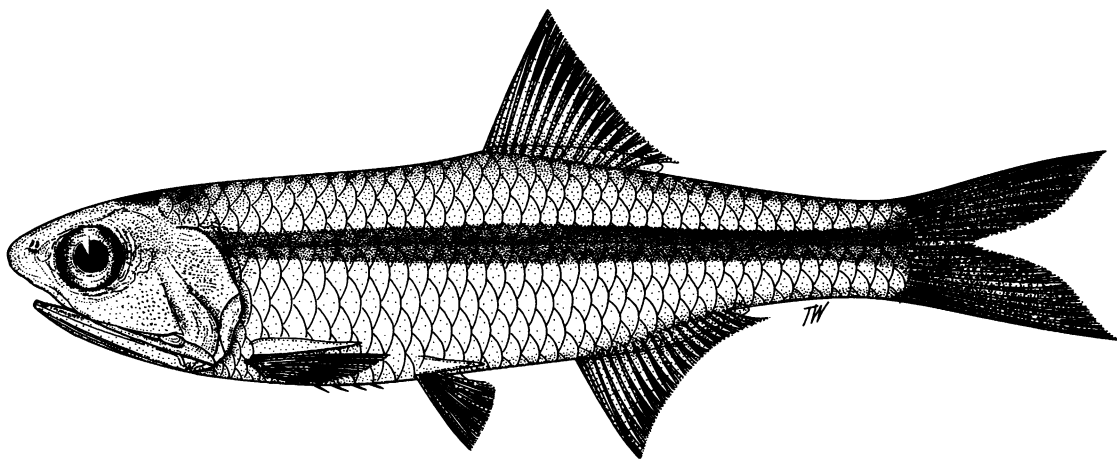


Fig. 2. *Stolephorus nelsoni*, new species, holotype, AMNH 57157, 74.0 mm SL, 3 mi north of Wallal, Eighty Mile Beach, Western Australia.

base of anterior gill rakers on epibranchial one; gill rakers on posterior face of third epibranchial 6–7; branchiostegal rays 12–13; dorsal-fin rays iii 12–13; anal-fin rays iii 18–20, originating below base of third or fourth dorsal-fin ray; pectoral-fin rays i 12–14; lateral scales 35–36; and needlelike prepelvic scutes 2–4; pyloric caeca 12.

ETYMOLOGY: The specific epithet *multi-branchus* (Greek *multi* for “many” and *branchus* for “gill”) refers to its possession of many gill rakers.

DISTRIBUTION: Known only from the type locality, Ponape, Caroline Islands.

RELATIONSHIPS: The misidentification of this new species as *S. commersonii* in Wongratana (1980, 1985) suggests a relationship to that species, especially in its similar double band on the midline of the back from the head to the dorsal fin. However, the high count of gill rakers (19–23 + 29–31) in *S. apiensis* is fewer than in this new species but very slightly more than *S. commersonii*, and they share couplet 14 in the following key.

***Stolephorus nelsoni*, new species**

Figure 2

MATERIAL: The holotype: AMNH 57157, 74.0 mm SL, from 3 mi north of Wallal, Eighty Mile Beach, Western Australia, April 15, 1969, G. Nelson, W. H. Butler, and D. E. Rosen. Paratypes: ROM 39271, two specimens, 66.0–72.0 mm SL, from Townsville

in Cleaveland Bay, Queensland, October 5, 1981; and USNM 280176, a specimen, 72.5 mm SL, taken with the holotype.

DIAGNOSIS: *Stolephorus nelsoni* shares with *S. carpentariae*, *S. chinensis*, *S. tri*, and *S. waitei* the presence of toothed knobs at base of anterior gill rakers on epibranchial one and its maxilla tip reaching about to hind edge of interoperculum. It has 4–5 needlelike prepelvic scutes, and 35–36 scales on lateral series. From *S. carpentariae* (from the Gulf of Papua and northern coasts of Australia), it differs in having rounded posteroventral edge of preoperculum (vs. concave edge), anal fin originating below eleventh to twelfth (vs. fourth to sixth) dorsal-fin ray, fewer predorsal scales (15 vs. 16–20), and teeth on upper edge of ceratohyal (vs. absent). From *S. chinensis* (from Thailand, Malay Peninsula, and South China Sea), it is easily separable by having fewer gill rakers on ceratobranchial (23–24 vs. 25–28), fewer predorsal scales (15 vs. 18–21), pelvic-fin tips reaching to below third or fourth dorsal-fin ray (vs. usually well before dorsal-fin origin), anal fin originating below eleventh or twelfth dorsal-fin ray (vs. sixth to eighth dorsal-fin ray), and first and third infraorbital bones with slightly produced posterior tips (vs. bluntly short). It is distinguished from *S. tri* (from Thailand, Malay Peninsula, and Indonesia) chiefly by having no predorsal spine or interpelvic scute and higher gill-raker count (18–19 + 23–24 vs. 15–18 + 18–22). From *S. waitei* (from west

coast of India to South China Sea and northern coast of Australia), it differs in having a more compressed and deeper body (22.7–23.5 vs. 18.0–21.7% SL), fewer anal-fin rays (20–21 vs. 21–23), anal fin originating vertically below eleventh or twelfth (vs. eighth or ninth) dorsal-fin ray, tip of depressed pelvic fins reaching below third or fourth dorsal-fin ray (vs. usually before dorsal-fin origin), more gill rakers on epibranchial (18–19 vs. usually 14–17) and fewer predorsal scales (15 vs. 18–20). These four species also have more or less distinct dark spots at base of dorsal- and anal-fin rays or a dusky band on the back, but these markings are usually absent in the new species.

ETYMOLOGY: It is a pleasure to name this species for Dr. Gareth Nelson of the American Museum of Natural History in appreciation and recognition of his knowledge and classic works on the comparative anatomy and cladistic relationships among clupeoid fishes. He kindly provided the specimens of this species in his care and suggested that it might be undescribed.

DISTRIBUTION: Known from Wallal, Eighty Mile Beach, Western Australia and Townsville in Cleaveland Bay, Queensland.

RELATIONSHIPS: Within the 18 species of *Stolephorus*, *S. pacificus*, *S. indicus*, and *S. advenus* form a group closer to *Encrasicholina* chiefly because of their relatively short maxilla. Interestingly, *S. indicus* is the species which has fewer striations on scales and a

hollow gas bladder, which relate it more closely to species of *Encrasicholina*. The three species share the character of an evenly rounded preoperculum with *S. brachycephalus*, *S. multibranchus*, n. sp., *S. nelsoni*, n. sp., *S. apiensis*, *S. commersonii*, *S. chinensis*, and *S. waitei*, which have a long maxilla as found also in the third group which includes *S. carpentariae*, *S. holodon*, *S. andhraensis*, *S. ronquilloi*, and *S. insularis* but all the species of this latter group have a concave preoperculum (some specimens of *S. waitei* from western Pacific may also have a slightly concave preoperculum). It is noteworthy that development of a weak predorsal spine in some specimens or populations of *S. insularis* may indicate that it is related both to the previous species and the remaining species of *Stolephorus* which include *S. dubiosus*, *S. baganensis*, and *S. tri*. These three species are more closely related to *Thryssa* (including *Thrissina*, treated as a separate genus by Nelson, 1982) chiefly by the presence of a fully developed predorsal scute and more or less reticulated striations on scales.

It is likely that the presence of toothed knobs at the bases of the anterior gill-rakers on epibranchial one, which is found in *S. nelsoni*, n. sp. and *S. chinensis* and *S. waitei* of the second group of species, *S. carpentariae* of the third group of species, and *S. tri* of the fourth group, were independently developed in connection with their feeding habits.

KEY TO INDO-PACIFIC SPECIES OF *ENGRAULIS*, *ENCRASICHOLINA*, AND *STOLEPHORUS*

Small and young adult specimens of *Thryssa* may look like *Stolephorus*, however, they have more anal-fin rays (27–49 vs. 17–25), and have pre- and postpelvic scutes (14–20 + 6–13).

- 1a. No prepelvic scutes; anal fin originating vertically well behind base of last dorsal-fin ray; gas bladder sacklike throughout its course; intestine forming twisted coils; pyloric caeca 20–31 (east coast of Africa to Japan, Australia and New Zealand) *Engraulis japonicus*
- 1b. Prepelvic scutes present, needlelike (but usually absent in *Encrasicholina purpurea*); anal fin usually originating vertically before or slightly behind base of last dorsal-fin ray; gas bladder constricted at middle and forming a smaller or threadlike tube anteriorly; intestine more or less straight; pyloric caeca 7–20 2
- 2a. Anal fin usually originating vertically behind base of 11th dorsal-fin ray; muscular portion of isthmus terminating a short distance behind hind border of branchiostegal membrane, leaving portion of urohyal exposed and forming a fleshy knob or bony platelike structure; preopercular canal present only on preoperculum; lateral scales 39–43; fundus of stomach elongate; pigmented stripe along flanks, pyloric caeca usually darkish (*Encrasicholina*) 3
- 2b. Anal fin usually originating before base of 12th dorsal-fin ray; isthmus entirely formed by muscle, none of urohyal exposed; branches of preopercular canal extending onto operculum; lateral scales

- 34–39 (to 42 in *S. indicus*); fundus of stomach short (but long in *S. indicus*); band along flanks more or less silvery, pyloric caeca pale (*Stolephorus*) 7
- 3a. Maxilla bluntly rounded posteriorly and scarcely projecting beyond 2nd supramaxilla, but not to anterior border of preoperculum; urohyal with fleshy knob; anal-fin rays ii 12–15, with origin clearly behind dorsal-fin base; pectoral-fin rays 13–17; posterior frontal fontanelles more or less oval in shape 4
- 3b. Maxilla pointed posteriorly and clearly projecting beyond 2nd supramaxilla to anterior part of preoperculum; urohyal plate bony; anal-fin rays ii–iii 14–17, with origin commencing below base of 12th dorsal-fin ray to slightly behind base of that fin; pectoral-fin rays 12–14; posterior frontal fontanelles more or less sigmoid or triangular in shape 5
- 4a. Gill rakers usually 19–22 + 26–29, 6 on posterior face of 3rd epibranchial; prepelvic scutes usually absent, some specimens with 1–5 thin scutes; pyloric caeca 12–15 (Hawaiian Islands) *E. purpurea*
- 4b. Gill rakers usually 15–20 + 23–26, 4 on posterior face of 3rd epibranchial; 2–6 moderately developed needlelike prepelvic scutes; pyloric caeca 14–18 (widespread in Indo-Pacific) *E. punctifer*
- 5a. Portion of maxilla behind 2nd supramaxilla slightly shorter than broad, its teeth small and even; gill rakers 13–14 + 17–18; unbranched dorsal-fin rays iii; anal-fin origin $\frac{1}{4}$ – $\frac{1}{3}$ eye diameter vertically behind base of last dorsal-fin ray; tip of depressed pelvic fins reaching to below base of 7th dorsal-fin ray (Philippines, Indonesia, New Guinea, and Fiji) *E. oligobranchus*
- 5b. Portion of maxilla behind 2nd supramaxilla about as long as or longer than broad, some teeth on its posterior half enlarged; gill rakers 19–25 + 21–29; unbranched dorsal-fin rays ii–iii; anal-fin origin below base of 12th dorsal-fin ray to vertically behind base of that fin; tip of depressed pelvic fins reaching to below base of 1st to 5th dorsal-fin ray (widespread in Indo-West Pacific) 6
- 6a. Unbranched dorsal- and anal-fin rays ii; portion of maxilla behind 2nd supramaxilla longer than broad; gill rakers 20–25 + 23–29, 7–9 on posterior face of 3rd epibranchial; anal-fin origin below base of 12th dorsal-fin ray to just behind base of that fin; tip of depressed pelvic fins just reaching below dorsal-fin origin or very slightly behind it (east coast of Africa, Red Sea to southeast Asia, Japan, Papua New Guinea, and northwest coast of Australia) *E. heterolobus*
- 6b. Unbranched dorsal- and anal-fin rays iii; portion of maxilla behind 2nd supramaxilla as long as broad; gill rakers 19–21 + 21–26, 6–7 on posterior face of 3rd epibranchial; anal-fin origin below base of 14th dorsal-fin ray to clearly behind base of that fin; tip of depressed pelvic fins reaching below base of 2nd to 5th dorsal-fin ray (northeast coasts of Indian Ocean to China Sea, Papua New Guinea, and northern coasts of Australia) *E. devisi*
- 7a. No predorsal spine (except in some populations of *S. insularis*); no interpelvic scute; body depth 14.0–23.3% SL; total dorsal-fin rays usually 15–17; striae on scales not reticulated; distal end of 1st infraorbital bone terminating a short distance before hind border of 3rd infraorbital (except in *S. insularis*); no double pigment line along midline of back from behind dorsal fin (except in *S. ronquilloi* and *S. insularis*) 8
- 7b. Predorsal spine and interpelvic scute present; body depth 21.0–26.0% SL; total dorsal-fin rays usually 14–15; striae on scales reticulated; distal end of 1st infraorbital bone terminating at hind border of 3rd infraorbital; a double pigment line along midline of back from behind dorsal fin 22
- 8a. Posteroventral edge of preoperculum evenly rounded; 3 branchiostegal rays on posterior ceratohyal; roof of mouth undotted (except in *S. waitiei*); a large patch of dense dark spots at just behind occiput 9
- 8b. Posteroventral edge of preoperculum concave; 2 branchiostegal rays on posterior ceratohyal (except 3 in *S. carpentariae*); roof of mouth dotted with dark or darkish; a small patch of few dark spots at just behind occiput 18
- 9a. Maxilla tip reaching to a short distance before or to very slightly behind anterior border of preoperculum; lateral scales usually 37–42 10
- 9b. Maxilla tip reaching well beyond anterior border of preoperculum; lateral scales usually 34–39 12
- 10a. Pelvic-fin tip terminating well before dorsal origin; gill rakers 16–19 + 21–25; lateral scales usually 38–42; pyloric caeca 15–18 (but unknown in *S. advenus*); bases of dorsal and anal-fins with faint dark dots or absent (Indo-West Pacific) 11
- 10b. Pelvic-fin tip terminating below base of 1st or to 4th dorsal-fin ray; gill rakers 21–27 + 33–38;

- lateral scales usually 37–38; pyloric caeca 13; bases of dorsal and anal fins with prominent dark dots (Guam, Kosiae) *S. pacificus*
- 11a. Body depth 16.6–19.3% SL; length of maxilla 15.5–17.5% SL; length of head 23.5–26.1% SL; branchiostegal rays 12–14; pyloric caeca 15–18; posterior frontal fontanelles plain darkish; posttemporal region and bases of dorsal and anal fins with faint dark dots (east coast of Africa, Mauritius to Southeast Asia, Hong Kong, Papua New Guinea, Australia, Samoa, and Tahiti) *S. indicus*
- 11b. Body depth 19.4% SL; length of maxilla 15.3% SL; length of head 22.6% SL; branchiostegal rays 11; number of pyloric caeca unknown; posterior frontal fontanelles dotted with dark; no markings on posttemporal region or bases of dorsal and anal fins (Cobourg Peninsula of Northern Territory, Australia) *S. advenus*
- 12a. Pelvic-fin tip terminating below bases of 1st or to 4th dorsal-fin ray; teeth on palatine and pterygoids weakly developed; no toothed knob at base of anterior gill rakers on epibranchial one (except in *S. nelsoni*) 13
- 12b. Pelvic-fin tip terminating about a quarter of eye diameter vertically before dorsal-fin origin (very rarely to below anterior dorsal-fin rays); teeth on palatine and pterygoids fairly well developed; toothed knobs present at bases of anterior gill rakers on epibranchial one 17
- 13a. Branchiostegal rays usually 12–13; anal-fin rays usually 20–23; pectoral-fin rays 13–15 (Indo-West Pacific) 14
- 13b. Branchiostegal rays 10–11; anal-fin rays usually 22–24, pectoral-fin rays usually 12–13 (Gulf of Papua, Northern Territory, and Queensland) *S. brachycephalus*
- 14a. Gill rakers 25–27 + 32–35 (Ponape, Caroline Islands) *S. multibranchus*, n. sp.
- 14b. Gill rakers 17–23 + 23–31 (Indo-West Pacific) 15
- 15a. Body depth 17.0–22.6% SL; head length 19.8–26.4% SL; 1st and 3rd infraorbital bones with blunt posterior tips; no toothed knob at base of anterior gill rakers on epibranchial one; predorsal scales 17–19; posterior frontal fontanelles sigmoid in shape; posttemporal region, bases of dorsal, and anal fin with dark spots (Indo-West Pacific) 16
- 15b. Body depth 22.7–23.5% SL; head length 26.2–27.3% SL; 1st and 3rd infraorbital bones with pointed posterior tips; toothed knobs at bases of anterior gill rakers on epibranchial one; predorsal scales 15; posterior frontal fontanelles triangular; no prominent markings on posttemporal region, or on back; spots at bases of dorsal and anal fins usually absent (Wallal of Eighty Mile Beach, Western Australia and Townsville in Cleaveland Bay, Queensland) *S. nelsoni*, n. sp.
- 16a. Gill rakers 19–23 + 29–31; needlelike prepelvic scutes 3–5; no markings on back (Fiji, Samoa) *S. apiensis*
- 16b. Gill rakers 17–21 + 23–28; needlelike prepelvic scutes usually 2–3, rarely 0–1 or 4–5; a double dusky band along midline of back from occiput to dorsal fin (Mauritius, Zanzibar, India, South China Sea, New Guinea, Northern Territory, Queensland, and Samoa) *S. commersonii*
- 17a. Gill rakers 18–19 + 26–27; anal-fin origin usually below bases of 6th to 7th dorsal-fin rays; dorsal-fin rays usually 16–17; pectoral-fin rays usually 12–13; branchiostegal rays 11–12; posterior frontal fontanelles relatively large, broadly pointed anteriorly; 1st and 3rd infraorbital bones with blunt, short posterior extension; snout with indistinct dark spots, lower jaw and roof of mouth unspotted (Gulf of Thailand, South China Sea to Hong Kong) *S. chinensis*
- 17b. Gill rakers 14–17 + 19–24; anal-fin origin usually below bases of 8th to 9th dorsal-fin rays; dorsal-fin rays usually 16; pectoral-fin rays usually 13–14; branchiostegal rays 12–13; posterior frontal fontanelles small, especially in larger fish, greatly tapering and pointed anteriorly; 1st and 3rd infraorbital bones with produced posterior extension; snout and usually anterior half of lower jaw and roof of mouth spotted with dusky black (southwest coast of India to Southeast Asia, Northern Territory, and Queensland) *S. waitei*
- 18a. No double pigmented line along midline of back; prepelvic needlelike scutes usually 6–7; 4–5 gill rakers on posterior face of 3rd epibranchial 19
- 18b. Double pigmented line along midline of back behind dorsal fin; prepelvic needlelike scutes usually 5–7; 5–6 gill rakers on posterior face of 3rd epibranchial 21
- 19a. Anal-fin rays 20–22, originating below base of 7th to 9th dorsal-fin ray; tip of depressed pelvic fins reaching to below dorsal-fin origin or about half eye diameter before it; pseudobranchial filaments usually 14–19; teeth on palatine and pterygoids forming a narrow granular patch; no teeth on ceratohyal or dorsal hypohyal; 1st and 3rd infraorbital bones with blunt short posterior extension; gill rakers 14–15 + 20–21 or 17–22 + 24–29 (southeast coast of Africa or Indo-Australian region) 20

- 19b. Anal-fin rays 21–23, originating below base of 2nd to 7th dorsal-fin ray; tip of depressed pelvic fins falls about three-fourths to one eye diameter vertically before dorsal origin; pseudobranchial filaments 11–14; teeth on palatine and pterygoids forming a large granular patch; teeth present on upper edge of anterior ceratohyal and dorsal hypohyal; 3rd and 4th infraorbital bones with produced posterior extension; gill rakers 15–18 + 21–25 (Gulf of Papua, Northern Territory, and Queensland) *S. carpentariae*
- 20a. Gill rakers 17–22 + 24–29; head length 23–26, mean 24.7% SL; posterior frontal fontanelles blackish (southeast coast of Africa) *S. holodon*
- 20b. Gill rakers 14–15 + 20–21; head length 22–25, mean 23.5% SL; posterior frontal fontanelles spotted (Bay of Bengal, Singapore, Gulf of Papua, Northern Territory, and Queensland) *S. andhraensis*
- 21a. Gill rakers usually 19–21 + 27–30; tip of depressed pelvic fins vertically below origin of dorsal fin to about half an eye diameter before it; no predorsal spine; posterior end of 1st infraorbital bone terminating well before hind border of 3rd infraorbital; isthmus with a few or many dark dots (Philippines) *S. ronquilloi*
- 21b. Gill rakers usually 16–20 + 22–28; tip of depressed pelvic fins about a quarter of eye diameter vertically before dorsal-fin origin; predorsal spine small or absent; posterior end of 1st infraorbital bone opposite hind border of 3d infraorbital; isthmus without dark markings (Gulf of Oman to Java Sea, South China Sea, and China) *S. insularis*
- 22a. Gill rakers 19–24 + 25–31, 5–7 on posterior face of 3rd epibranchial; pyloric caeca 7–12 (Bay of Bengal, Java Sea, and Gulf of Thailand) *S. dubiosus*
- 22b. Gill rakers 14–19 + 18–24, 3–6 on posterior face of 3rd epibranchial; pyloric caeca 11–16 .. 23
- 23a. Gill rakers usually 16–19 + 20–24, 3–6 on posterior face of 3rd epibranchial; scales distinctly reticulated; pyloric caeca 11–13; granular teeth on palatine and pterygoids forming a narrow patch; no double pigment line along midline of back between occiput and dorsal fin (Malay Peninsula, Gulf of Thailand, and Sarawak) *S. baganensis*
- 23b. Gill rakers usually 15–17 + 19–22, 5–6 on posterior face of 3rd epibranchial; scales slightly reticulated; pyloric caeca 15–16; granular teeth on palatine and pterygoids forming a large patch; a double dusky band along midline of back from occiput to dorsal fin (Java Sea, Gulf of Thailand, and Sarawak) *S. tri*

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