

*SICYOPTERUS RAPA*, NEW SPECIES OF SICYDIINE  
GOBY (TELEOSTEI: GOBIIDAE), FROM  
RAPA, FRENCH POLYNESIA

Lynne R. Parenti and John A. Maciolek

ABSTRACT

*Sicyopterus rapa*, apparently endemic to one of the two southernmost islands of French Polynesia in the south central Pacific Ocean, is distinguished from congeners by a low number of premaxillary teeth and an unscaled ventral surface of the body in largest adults. Its putative closest living relatives are in the Marquesas and Indonesia.

Sicydiine gobies comprise a group of tropical and subtropical stream fishes that exhibit a relatively high degree of island-group endemism, particularly in the Pacific (Ryan, 1991; Marquet and Galzin, 1992). We described recently five new sicydiine species in three genera from the islands of Ponape and Palau, Micronesia, in the western Pacific, bringing the total number of nominal sicydiine species to about 100 (Parenti and Maciolek, 1993). Our objectives herein are to describe *Sicyopterus rapa*, a new species from Rapa, one of the two southernmost islands of French Polynesia, and to comment on Indo-Pacific sicydiine biogeography.

Rapa is a subcircular, volcanic island at approximately 27°36'S, 144°20'W in the south central Pacific Ocean (Fig. 1). The atoll is relatively small, 20 km in circumference, and high, maximum altitude approximately 656 m. Two hundred and sixty-eight fish species were reported from Rapa by Randall et al. (1990), including the new sicydiine described herein which they referred to as *Sicyopterus* sp. The fish fauna of Rapa, like that of other volcanic Pacific islands, such as the Hawaiian Islands, comprises principally marine, estuarine, and diadromous species, the last including gobioids and anguillid eels. Some fishes, including those in the gobiid subfamily Sicydiinae, are more properly called amphidromous: adults live and breed in freshwater; larvae are carried passively to the sea where they undergo transformation prior to ascending a stream (McDowall, 1992; Parenti and Maciolek, 1993). Populations live on islands high enough to maintain perennial freshwater stream systems, and in high-gradient, coastal streams.

The subfamily Sicydiinae Gill, 1860, as understood herein, comprises five genera: *Sicyopus* Gill, 1863, *Lentipes* Günther, 1861, *Sicydium* Valenciennes, in Cuvier and Valenciennes, 1837, *Sicyopterus* Gill, 1860, and *Stiphodon* Weber, 1895 (Hoese, 1984; Parenti and Maciolek, 1993; although, see Harrison, 1993, who recognizes a sixth genus, *Parasicydium* Risch 1980, which Parenti and Maciolek, 1993, consider tentatively to be a synonym of *Sicydium*). Parenti and Maciolek (1993) erroneously attributed first use of a family-group name for these genera to Bleeker (1874).

Sicydiine monophyly is well-supported (Parenti and Maciolek, 1993: 950-954). Hypothesized sister genera *Sicyopterus* and *Sicydium* share putative synapomorphies of a short, blunt ascending/articular process of the premaxilla (Parenti and Maciolek, 1993), and an oculoscapular-canal pore pattern characterized by fusion of pores H and K to form one pore, HK (Pezold, 1993), following canal pore terminology of Akihito et al. (1984).

Characters to distinguish between *Sicydium* and *Sicyopterus* were discussed by Akihito and Meguro (1979: table 3). Parenti and Maciolek (1993: table 2) eval-

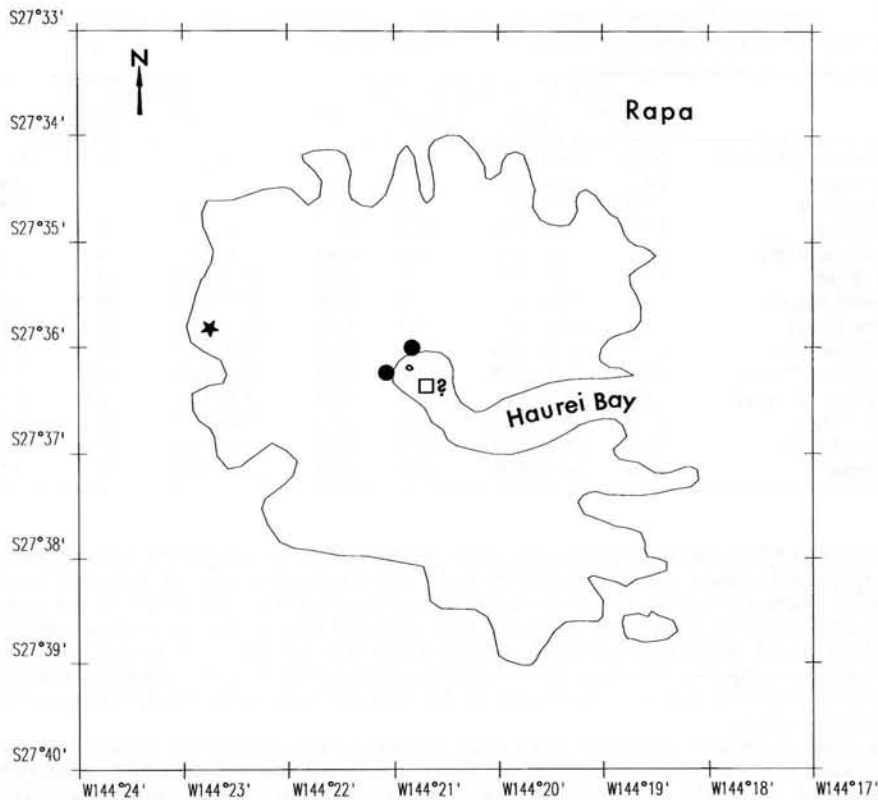


Figure 1. Outline map of Rapa, French Polynesia. Each circle represents one collection of *Sicyopterus rapa*, new species. The square represents one collection of *S. rapa* of indeterminate locality. The star approximates the summit of Mt. Perahu, Rapa's highest peak (2132 ft = 656 m).

uated polarity of those characters and diagnosed *Sicydium* as monophyletic based on a single specialization: a large, fleshy, swelling between posterior extent of labial (horizontal) and unicuspid dentary teeth. *Sicyopterus* is diagnosed as monophyletic by a distinct, medial gap between left and right premaxillary tooth rows.

*Sicydium* lives in insular and coastal streams of the tropical eastern Pacific and Atlantic oceans, including the Caribbean Sea. *Sicyopterus* is widespread throughout the tropical Indo-Pacific, including Madagascar, but absent from the eastern Pacific. Maugé et al. (1992) recognized three species of *Sicyopterus* from French Polynesia: *S. pugnans* (Ogilvie-Grant, 1884); *S. taeniurus* (Günther, 1877) under which they considered *S. marquesensis* Fowler, 1932, a probable synonym; and *S. caudimaculatus*, which they described as new from the Marquesas. Description of *Sicyopterus rapa* from the south central Pacific Ocean brings the number of recognized *Sicyopterus* species from French Polynesia to four.

#### MATERIALS AND METHODS

Representative specimens were cleared and either counterstained with alcian blue and alizarin red (Dingerkus and Uhler, 1977), or stained solely with alizarin. The species diagnosis includes those characters unique or otherwise hypothesized to be autapomorphic (sensu Hennig, 1966). Additional characters useful for identification are given in the description and comparisons.

Preserved color is that after fixation in formalin and storage in ethanol or isopropanol. Counts and

Table 1. Summary of standard length and proportional measurements of type specimens of *Sicyopterus rapa*. (Proportions expressed as percent of standard length)

	Males (N = 9, including holotype)				Females (N = 9)		
	Holotype	Range	Mean	SD	Range	Mean	SD
Standard length (mm)	62.5	40.0–64.8	53.4	9.60	44.5–74.7	57.0	10.70
Head length	24.2	21.5–25.3	23.5	1.47	20.2–25.9	23.1	1.60
Eye diameter	3.9	2.3–4.2	3.5	0.65	2.2–4.1	3.2	0.64
Snout length	11.4	8.8–11.4	10.3	0.70	7.8–13.0	11.0	1.62
Interorbital width	10.2	9.4–11.0	9.9	0.47	7.8–10.7	9.3	0.80
Body depth	17.3	15.1–19.8	17.2	1.59	15.3–26.8	18.3	3.50
Predorsal length	35.4	33.0–38.1	35.5	1.68	32.3–38.9	35.7	1.97
Precanal length	54.4	53.9–57.6	55.7	1.46	55.3–62.2	58.7	2.15
First dorsal base	13.3	11.8–19.4	14.0	2.49	11.9–16.7	13.5	1.87
Second dorsal base	30.1	28.3–33.3	30.8	1.74	25.1–33.5	29.0	2.58
Interdorsal fin space	3.2	2.3–5.6	3.5	1.08	2.9–5.8	4.6	0.97
Caudal length	25.9	21.7–25.9	22.9	1.25	17.6–21.2	20.2	1.08
Pectoral length	23.2	20.0–23.2	21.5	1.03	18.0–21.4	19.9	1.15
Anal base	25.6	24.1–30.0	26.4	1.91	20.5–25.9	23.2	1.79

measurements follow Parenti and Maciolek (1993). Measurements are straight-line distances recorded with metric dial calipers and are reported for males and females as a range of percent of standard length (SL; Table 1). Transverse scale rows are those along the mid-side of the body from just posterior to the dorsal extent of the gill opening to the point of caudal flexure. Anterior scales are small and irregularly placed. Scale counts are highly variable within sicydiine species because of this irregular scale placement; reported values are approximate. Counts were made from radiographs and cleared and stained or alcohol specimens. Values for the holotype are given in brackets following counts or measurement ranges.

Specimens of the new species are listed in the species account. Institutional abbreviations follow the Standard Symbolic Codes for Institutional Research Collections in Herpetology and Ichthyology (Leviton et al., 1985). The generic citation follows Eschmeyer (1990). Comparative material examined includes that listed in Parenti and Maciolek (1993), and the following:

*Sicyopterus brevis*, Seram, Indonesia, ZMA 110.981, syntypes, 2 spec.

*Sicyopterus caudimaculatus*, Marquesas, French Polynesia, MNHN 1989-1777, holotype, male, 88.0 mm SL, MNHN 1992-121, 31 paratypes, 25.0–95.0 mm SL.

*Sicyopterus micrurus*, Tutuila, American Samoa, CAS 67540, 3 spec.

*Sicyopterus taeniurus*, Guam, Marianas Is., CAS 67532, 3 spec.

*Sicydium plumieri*, Puerto Rico, USNM 313664, 4 spec.

### *Sicyopterus* Gill, 1860

*Sicyopterus* Gill, 1860: 101, as a subgenus of *Sicydium* Valenciennes, in Cuvier and Valenciennes, 1837 [type species *Sicydium (Sicyopterus) stimpsoni* Gill 1860: 101 by original designation].

### *Sicyopterus rapa*, new species

Figures 1–3, Table 1

*Sicyopterus* sp.—Randall, Smith, and Feinberg, 1990: 35, figure 46, Rapa, French Polynesia.

**Diagnosis.**—Distinguished from congeners by a low number (approximately 45 as opposed to 60 or more) of teeth on each premaxilla, and ventral body surface unscaled in largest adults.

**Description.**—First dorsal fin VI, depressed third spine longest, extending posteriorly well beyond second dorsal-fin insertion in males; second dorsal fin I,11; dorsal pterygiophore formula 3-12210; anal fin I,10; pectoral fin 17–19 [18]; pelvic fin I,5, interspinal membrane or frenum thick; branched caudal-fin rays 13–15 [15]; vertebrae 10 + 16 = 26; no rakers on first gill arch; branchiostegal rays 5.

Transverse scales in 44–62 [44] rows. Dorsal surface of head unscaled; oper-

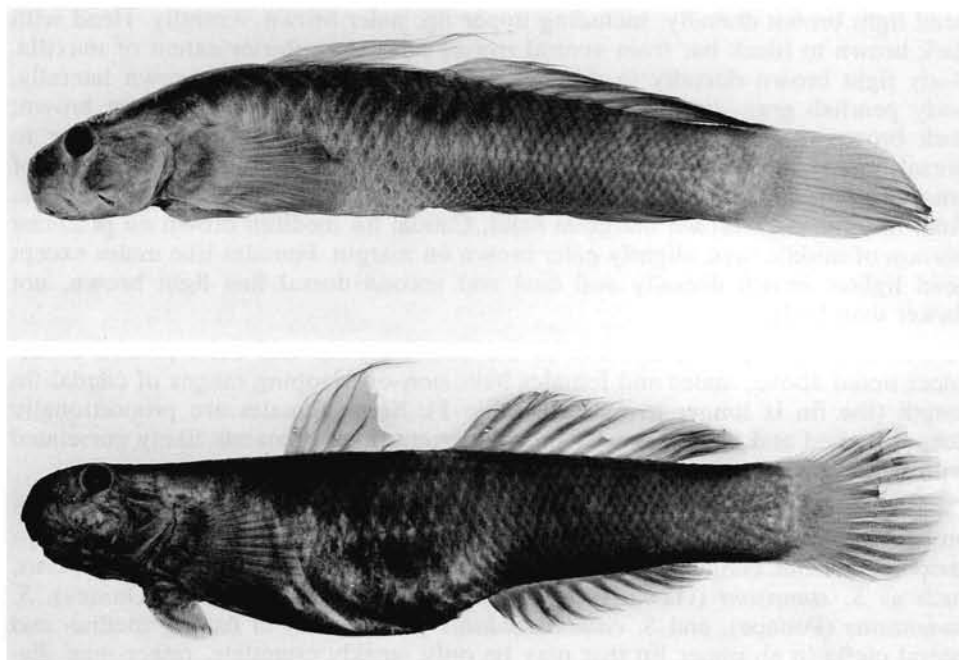


Figure 2 (upper). *Sicyopterus rapa*, new species. Holotype, BPBM 12923, male, 62.5 mm SL, Rapa, French Polynesia.

Figure 3 (lower). *Sicyopterus rapa*, new species. Paratype (allotype), USNM 330077, female, 66.7 mm SL, Rapa, French Polynesia.

culum, cheeks and lateral portion of body to first dorsal fin irregularly scaled with small cycloid scales; ventral surface of body unscaled in largest adults, otherwise incompletely covered with small cycloid scales; remainder of body to caudal peduncle covered with imbricate ctenoid scales; anterior portion of caudal-fin rays with smaller ctenoid or cycloid scales in one or two discrete rows dorsal and ventral to each ray. Three preopercular canal pores (M', N, and O'); anterior and posterior oculoscapular canals united, pore pattern A', B, C, D (single), F, HK and L'. Urogenital papilla blunt in males, slightly bilobed in females.

Mouth subterminal, small, maxilla ends at or just anterior to anterior edge of eye; upper lip with small median and large lateral clefts, approximately 8 to 11 weak crenulations on lip margins between medial and lateral cleft; small papilla posterior to medial cleft, row of papillae laterally on underside of lip; simple anterior naris about halfway between anterior margin of eye and posterior extent of upper lip; simple posterior naris anterior to eye. Premaxillary teeth tricuspid; approximately 45 teeth on each premaxilla. Dentary with 2–11 caniniform teeth, anterior two largest.

Head blunt and rounded in profile, head length 20.2–25.9 [24.2]; eye diameter 2.2–4.2 [3.9]; snout length 7.8–13.0 [11.4]; interorbital width 7.8–11.0 [10.2]; body depth 15.1–26.8 [17.3]; predorsal length 32.3–38.9 [35.4]; preanal length 53.9–62.2 [54.4]; first dorsal-fin base 11.8–19.4 [13.3]; second dorsal-fin base 25.1–33.5 [30.1]; interdorsal fin space 2.3–5.8 [3.2]; caudal-fin length 17.6–25.9 [25.9]; pectoral-fin length 18.0–23.2 [23.2]; anal-fin base 20.5–30.0 [25.6].

PRESERVED COLOR. Most specimens bleached somewhat in alcohol. Males with

head light brown dorsally, including upper lip, paler brown ventrally. Head with dark brown to black bar from ventral rim of orbit to posterior extent of maxilla. Body light brown dorsally to middle of caudal peduncle, light brown laterally, body pearlish gray, translucent ventrally. Pectoral and dorsal fins light brown; dark brown membrane between first-dorsal-fin rays 3 and 4, and posterior to dorsal-fin ray 5. Membrane of second dorsal fin dark brown on dorsal half of anterior portion of fin, darker brown on posterior portion. Pelvic disc pale brown. Anal fin with dark-brown marginal band. Caudal fin medium brown on posterior portion of middle rays, slightly paler brown on margin. Females like males except head lighter brown dorsally and anal and second dorsal fins light brown, not darker than body.

*Sexual Dimorphism.*—In addition to the dorsal-fin ray and color-pattern differences noted above, males and females have non-overlapping ranges of caudal-fin length (the fin is longer in males) (Table 1). Some females are proportionally deeper bodied and have a greater preanal length, measurements likely correlated with being gravid (compare Figs. 2, 3).

*Comparisons and Relationships.*—The low number (approximately 45) of teeth on each premaxilla and unscaled ventral adult-body surface distinguishes *Sicyopterus rapa* from congeners. *Sicyopterus rapa* is like certain other *Sicyopterus*, such as *S. stimpsoni* (Hawaii), *S. cynocephalus* (Philippines, New Guinea), *S. eudentatus* (Ponape), and *S. caudimaculatus* (Marquesas) in having median and lateral clefts in an upper lip that may be only weakly crenulate, rather than distinctly crenulate, nearly "fringed," as in *S. lividus* (Ponape), *S. pugnans* (Samoa, Moorea, Tahiti, and Fiji), and *S. panayensis* (Philippines). *Sicyopterus rapa* also shares with *S. caudimaculatus* tricuspid premaxillary teeth and a dark-brown to black bar from the ventral rim of the orbit to the posterior extent of the maxilla.

*Sicyopterus rapa* differs further from *S. caudimaculatus* in having a relatively low number (44–62 versus 66–70) of transverse scale rows, and in lacking the latter species' diagnostic markings: black, oval blotch on dorsal portion of base of caudal-fin rays and caudal peduncle, and blackish, subtriangular, midlateral band from base of pectoral fin to about middle of second dorsal fin in males. In both species, a dark bar extends vertically from the eye, as in certain other *Sicyopterus*, notably seven species from Papua New Guinea which have a variety of upper lip morphologies (Allen, 1991: 193–196, fig. 39), as well as in other gobioids, notably the Indo-Pacific freshwater and marine genus, *Stenogobius* (see Watson, 1991).

Phylogenetic relationships of sicydiine species have not been hypothesized rigorously, yet *S. rapa* may be considered a member of a monophyletic group of *Sicyopterus* that also includes *S. caudimaculatus* (Marquesas), and *S. brevis* (Seram, Indonesia). The group is diagnosed by three putative synapomorphies: upper lip weakly crenulate; premaxillary teeth tricuspid; and adult body and fin coloration generally drab. A weakly crenulate upper lip may be intermediate between a smooth lip or a lip with just median and lateral clefts and a deeply crenulate upper lip; polarity of this character is unclear. Distinct saddle bars or reticulations on the body that often extend onto the caudal fin characterize most sicydiines and putative close relatives, such as *Awaous*. We view absence of these color patterns, or presence of only an isolated caudal or subpectoral blotch (as in *S. caudimaculatus*), as derived.

*Distribution.*—Known only from tributaries of Haurei Bay, Rapa, French Polynesia, and an unspecified locality in Rapa collected by the 1934 T. Crocker Eastern Pacific "Zaca" Expedition.



*Etymology*.—The species epithet *rapa*, to connote occurrence of this species on Rapa, French Polynesia, used as a noun in apposition.

*Material Examined*.—28 specimens, 37.4–74.7 mm SL.

**HOLOTYPE**. BPBM 12923, male, 62.5 mm SL, coll. A. Sinoto and D. Bryant, 5 Feb 1971, shallow water in Pania River at head of Haurei Bay, Rapa, French Polynesia.

**PARATYPES**, SAME DATA AS HOLOTYPE. USNM 330077 (ex. BPBM 12923), female (allotype), 66.7 mm SL; BPBM 35782 (ex. BPBM 12923), 6: 3 males, 40.0–64.8 mm SL, 3 females, 44.5–64.1 mm SL; MNHN 1994-501 (ex. BPBM 12923), male, 45.5 mm SL, MNHN 1994-502 (ex. BPBM 12923) female 47.1 mm SL; CAS 81599 (ex. BPBM 12923), male, 64.2 mm SL, female, 74.7 mm SL. Unspecified locality, Rapa, coll. 8 Dec 1934, T. Crocker Eastern Pacific “Zaca” Expedition (sta. 047): AMNH 19941, 6: 47.9–65.9 mm SL.

*Nontype Material*.—Same locality as holotype: BPBM 35783 (ex. BPBM 12923), 3 females, 44–55 mm SL; BPBM 35784 (ex. BPBM 12923), male, 37.4 mm SL, female, 47.9 mm SL, both cleared and stained solely with alizarin. Rapa, 200 yards from mouth of stream into Haurei Bay, about 0.5 mi. S of Tapui I., 27°36'S, 144°18'W [approximate coordinates], AMNH 72762, 4, 43.4–67.4 mm SL, coll. 16 Apr 1970. R. Mathews, P. Goodrich, and C. L. Smith (field no. CLS 70-039). Unspecified locality, Rapa, coll. 8 Dec 1934, T. Crocker Eastern Pacific “Zaca” Expedition (sta. 047): AMNH 97491 (ex. AMNH 19941), 1 cleared and stained solely with alizarin.

*Remarks*.—Randall et al. (1990: fig. 46) published a photograph of the female allotype of *S. rapa*, USNM 330077 (ex. BPBM 12923).

*Biogeography*.—All but one (*Sicydium*) of the currently recognized sicydiine genera live in the central Pacific: *Sicyopus*, *Lentipes*, *Stiphodon*, and *Sicyopterus*, plus *Parasicydium* if one follows Harrison (1993) who places *Lentipes rubrofasciatus* Maugé et al., 1992 in that genus. *Sicyopus*, the most plesiomorphic sicydiine, and *Sicyopterus*, one of the two most derived genera, also live in the Indian Ocean (Parenti, 1991). Within sicydiines and other central Pacific fish taxa, generic sympatry is common. For example, five sicydiine species in three genera are known from Ponape, a volcanic island in the Eastern Caroline Islands, Micronesia: *Sicyopus nigriradiatus* Parenti and Maciolek, 1993, *Sicyopterus lividus* Parenti and Maciolek, 1993, *Sicyopterus eudentatus* Parenti and Maciolek, 1993, *Stiphodon caeruleus* Parenti and Maciolek, 1993, and *Stiphodon* cf. *elegans*. The first four of these species are endemic to Ponape, as far as known, the last was compared with a widespread western Pacific species, *Stiphodon elegans* (Steindachner, 1879). Similarly, Maugé et al. (1992) recognized seven sicydiine species in four genera from French Polynesia: *Sicyopterus pugnans*, *Sicyopterus taeniurus*, *Stiphodon elegans*, *Stiphodon stevensoni* (Jordan and Seale, 1906), *Sicyopterus caudimaculatus* (Ua Huka, Ua Poa, Nuku Hiva and Hiva Oa, Marquesas), *Sicyopus bitaeniatus* Maugé et al., 1992 (Ua Pou and Hiva Oa, Marquesas), and *Lentipes rubrofasciatus* (Ua Huka, Marquesas). The last three species are endemic to the Marquesas, as far as known, the other four widespread throughout the western Pacific.

Clearly, island-group endemism is relatively high in the Pacific. Yet, islands, or island groups, do not necessarily have monophyletic groups of sicydiine species, let alone genera. The Marquesas *Sicyopterus*, *S. caudimaculatus*, has putative close relatives in Rapa (*S. rapa*) and Indonesia (*S. brevis*). In addition, if Harrison's (1993) reclassification is corroborated, then the Marquesas *Lentipes*, referred

to by him as *Parasicydium rubrofasciatum*, has its closest relatives in the Ryukyus (*P. armatum*) and off the coast of West Africa (*P. bandama*). Springer (1982) viewed vicariance of widespread ancestral taxa to explain Marquesas endemism as preferable to postulating independent colonizations, and we agree. Furthermore, the ancestral taxa were widespread prior not only to specific, but to generic differentiation, reinforcing complexity of relationships of Pacific Plate endemics and the great age of their lineages.

#### ACKNOWLEDGMENTS

This research was supported initially by NSF grant BSR 89-06649 to the senior author while at CAS and completed in the Division of Fishes, USNM. T. Britt Griswold photographed the holotype and paratype (allotype). J. Clayton (USNM) and D. Catania (CAS) provided technical assistance. J. E. Randall and A. Suzumoto (BPBM), M. L. J. Stiassny and M. N. Feinberg (AMNH), and G. Duhamel (MNH) provided loans of, and other information on, specimens in their care. A. C. Gill (BMNH) and I. J. Harrison (MRAC) kindly read and commented on a draft of the manuscript. Two reviewers provided additional suggestions for revision. R. E. Watson kindly pointed out to us our previous error in family-group name authorship, and provided other information on sicydiines; we thank him for his time and interest.

#### LITERATURE CITED

- Akihito, (Prince) and K. Meguro. 1979. On the differences between the genera *Sicydium* and *Sicyopterus* (Gobiidae). Japan. J. Ichthyol. 26: 192–202.
- , M. Hayashi and T. Yoshino. 1984. Suborder Gobioidae. Pages 236–289 [English text], plates 235–355. in H. Masuda, K. Amaoka, C. Araga, T. Uyeno, and T. Yoshino, eds. The fishes of the Japanese Archipelago. Tokai University Press, Japan. 401 p.
- Allen, G. R. 1991. Field guide to the freshwater fishes of New Guinea. Christensen Research Institute, Papua New Guinea. publ. 9. 268 p.
- Bleeker, P. 1874. Esquisse d'un système naturel des Gobioides. Arch. Néerl. Sci. Nat. IX (1874): 289–331.
- Dingerkus, G. and L. D. Uhler. 1977. Enzyme clearing of alcian blue stained whole small vertebrates for demonstration of cartilage. Stain Tech. 52: 229–232.
- Eschmeyer, W. N. 1990. Catalog of the genera of Recent fishes. California Academy of Sciences, San Francisco. 697 p.
- Gill, T. N. 1860. Conspectus piscium in expeditione ad oceanum Pacificum septentrionalem, C. Ringold et J. Rodgers ducibus, a Gulielmo Stimpson collectorum. Sicydianae. Proc. Acad. Nat. Sci. Phila. 1860 (vol. 12): 100–102.
- Harrison, I. J. 1993. The West African sicydiine fishes, with notes on the genus *Lentipes* (Teleostei: Gobiidae). Ichthyol. Explor. Freshw. 4: 201–232.
- Hennig, W. 1966. Phylogenetic systematics. Univ. Illinois Press, Urbana. 263 p.
- Hoese, D. F. 1984. Gobioidae: relationships. Pages 588–591. in H. G. Moser, W. J. Richards, D. M. Cohen, M. P. Fahay, A. W. Kendall, Jr., and S. L. Richardson, eds. Ontogeny and systematics of fishes. Special Publication No. 1, Supplement to Copeia, American Society of Ichthyologists and Herpetologists. 760 p.
- 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 resources collections in herpetology and ichthyology. Copeia 1985: 802–832.
- McDowall, R. M. 1992. Diadromy: origins and definitions of terminology. Copeia 1992: 248–251.
- Marquet, G. and R. Galzin. 1992. Systématique, répartition et biomasse des poissons d'eau douce de Polynésie Française. Cybium 1992 16: 245–259.
- Maugé, A., G. Marquet, and P. Laboute. 1992. Les Sicydiinae (Gobiidae) des eaux douces de la Polynésie Française. Description de trois espèces nouvelles. Cybium 1992 16: 213–231.
- Parenti, L. R. 1991. Ocean basins and the biogeography of freshwater fishes. Aust. Syst. Bot. 4: 137–149.
- and J. A. Maciolek. 1993. New sicydiine gobies from Ponape and Palau, Micronesia, with comments on systematics of the subfamily Sicydiinae (Teleostei: Gobiidae). Bull. Mar. Sci. 53: 945–972.
- Pezold, F. 1993. Evidence for a monophyletic Gobiinae. Copeia 1993: 634–643.
- Randall, J. E., C. L. Smith and M. N. Feinberg. 1990. Report on fish collections from Rapa, French Polynesia. Amer. Mus. Novitates No. 2966. 44 p.

- Ryan, P. A. 1991. The success of the Gobiidae in tropical Pacific insular streams. *New Zealand J. Zool.* 18: 25-30.
- Springer, V. G. 1982. Pacific plate biogeography, with special reference to shorefishes. *Smiths. Contrib. Zool.* 367: 1-182.
- Watson, R. E. 1991. A provisional review of the genus *Stenogobius* with descriptions of a new subgenus and thirteen new species. (Pisces: Teleostei: Gobiidae). *Rec. West. Aust. Mus.* 15: 627-710.

DATE ACCEPTED: December 8, 1994.

ADDRESSES: (L.R.P.) *Division of Fishes, Department of Vertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560;* (J.A.M.) *P.O. Box 7117, Mammoth Lakes, California 93546.*