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Paraxenisthmus springeri, New Genus and Species of Gobioid Fish from the West Pacific, and Its Phylogenetic Position within the Xenisthmidae

ANTHONY C. GILL AND DOUGLASS F. HOESE

Paraxenisthmus springeri is described from two specimens from the Solomon Islands. It is unique among xenisthmids in having: vomer with two separate patches of teeth; palatine with elongate patch of teeth; coronomeckelian bone present; dorsal postcleithrum present; ceratobranchial 5 broad; infrapharyngobranchial 2 broad, with two anterior cartilage heads and well-developed tooth patch; infrapharyngobranchial 4 present; infrapharyngobranchial 4 toothplate large; and basibranchial 3 present. Based on a cladistic analysis of osteological and external characters, Paraxenisthmus is the sister group of a monophyletic group that includes all other xenisthmid genera (Allomicrodesmus, Rotuma, Tyson and Xenisthmus). Further evidence is presented that Allomicrodesmus, Rotuma, and Tyson form the sister group of Xenisthmus.


MATERIALS AND METHODS

Patterns of insertion of the first dorsal-fin pterygiophores between neural spines are given as a formula following Birdsong et al. (1988). The longitudinal scale count was taken from the upper margin of the pectoral-fin base obliquely to the midline, then to the end of the caudal peduncle; the count is expressed as anterior cycloid + posterior ctenoid scales. The transverse scale count was taken from the second dorsal-fin origin ventroposteriorly to the anal-fin base. The predorsal scale count was taken on the midline-forward from the first dorsal-fin origin. The postdorsal scale count is the number of rows crossing the dorsal midline of the caudal peduncle. Head length was taken from the tip of the upper jaw to the upper attachment of the opercular membrane. Head width was taken between the posterior margins of the preopercles; head depth was taken at the vertical through the posterior margin of the preopercle. Predorsal length is the distance from the anterior tip of the upper jaw to the first dorsal-fin origin; preanal length is the distance from the anterior tip of the upper jaw to the anal-fin origin. The least suborbital width is the narrowest distance from the eye to the posterior margin of the upper lip. Osteological information is based on the paratype, which was cleared and counterstained for cartilage and bone (Taylor and Van Dyke, 1985). Information on other xenisthmids largely follows that of Springer (1983; 1988, particularly table 1), verified by reexamination of his cited specimens. Our observations on the external morphology of Xenisthmus are from specimens that we are studying for a revision of that genus. Character polarization was performed by outgroup comparison with a range of eleotridids, odontobutids, Rhyacichthys, and several relatively plesiomorphic gobiids; a complete listing of comparative osteological material examined is given elsewhere (Hoese and Gill, 1993). Institutional acronyms follow Leviton et al. (1985). Meristic and morphometric values are given first for holotype, followed, where different, by the value for the paratype in parentheses.

Paraxenisthmus n. gen.

Type species.—Paraxenisthmus springeri n. sp.

Diagnosis.—The following specializations place Paraxenisthmus in the Xenisthmidae: lower lip with an uninterrupted, free ventral margin; premaxillary ascending process greatly reduced; rostral cartilage ossified; basibranchial 2 absent; and hypobranchial 3 reduced to small cartilage nubbin. It is unique among xenisthm-
mids in possessing the following characters: vomer with two widely separated patches of teeth; vomer indented anteriorly; palatine with a patch of teeth; coronomeckelian bone present; dorsal postcleithrum present; ceratobranchial 5 broad; infrapharyngobranchial 2 relatively broad, with two anterior cartilage heads and well-developed tooth patch; infrapharyngobranchial 4 present; infrapharyngobranchial 4 toothplate well developed; and basibranchial 3 present.

Etymology.—The generic name is from the Greek para, meaning beside or near, and alludes to the similarity to species of Xenisthmus. The gender is masculine.

Paraxenisthmus springeri n. sp.

Figures 1–10

Holotype.—BPBM 34995, 27.4 mm female, Solomon Islands, Florida Island, south side of Tanavulu Point, steep-sided gully with caves, 18–37 m, rotenone, J. E. Randall and G. R. Allen, 30 July 1973.

Paratype.—AMS I.32484-001, 30.5 mm female, collected with holotype.

Diagnosis.—See generic diagnosis.

Description.—First dorsal-fin rays VI; first dorsal-fin pterygiophore formula 3-22110; second dorsal-fin rays 1,11; anal-fin rays 1,10; pectoral-fin rays 18; pelvic-fin rays 1,5; segmented caudal-fin rays 9+8; branched caudal-fin rays 7+6 (7+5); upper unsegmented caudal-fin rays 8; lower unsegmented caudal-fin rays 8 (9, the lowermost a rudiment); longitudinal scales 15+53 (15+50); transverse scales 23 (24); predorsal scales 18; postdorsal scales 10; pseudobranch lobes 4; vertebrae 10+16.

As percentage of standard length: body depth at anal-fin origin 16.4 (17.7); body depth at pelvic-fin origin 17.9 (17.4); head length 29.6 (28.2); head width 20.4 (21.3); head depth 16.8 (17.4); snout length 6.6 (6.9); upper jaw length 15.3 (15.1); eye length 6.6 (6.9); bony interorbital width 1.5 (1.3); least suborbital depth 1.1 (1.0); caudal peduncle depth 11.3 (12.1); caudal peduncle length 19.7; base of last ray in second dorsal fin to hypural edge 16.4 (17.3); predorsal length 38.0 (40.0); first dorsal-fin spine length 11.3 (11.5); second dorsal-fin spine length 10.9 (13.4); fourth dorsal-fin spine length 10.2 (12.1); fifth dorsal-fin spine length 9.9 (11.1); sixth dorsal-fin spine length 5.1 (6.9); second dorsal-fin base length 27.4 (28.9); preanal length 65.1 (62.3); anal-fin base length 23.0 (22.3); pectoral fin length 23.7 (22.0); pelvic fin length 28.1 (28.1); pelvic-fin ray length 26.3 (28.2); fifth segmented pelvic-fin ray length 6.6 (9.8); central caudal-fin ray length 19.3 (20.0); longest caudal-fin ray length 23.7 (23.9).

Head slightly depressed with prominent cheeks; mouth oblique, forming an angle of about 40°–45° with body axis; anterior margin of jaws in line with upper quarter of eye; jaws reach posteriorly almost to vertical through posterior edge of eye; anterior nostril a short tube just behind upper lip, the tube when depressed reaching two-thirds of distance to anterior margin of upper lip; posterior rim of anterior nostril distinctly elevated and in contact with anterodorsal margin of eye; snout rounded in dorsal view; tongue free anteriorly, the tip emarginate with shallow indentation; interor-
bital narrow, the bony interorbital width about one-half pupil diameter.

Three rows of slightly curved, conical teeth at anterior of upper jaw, two rows on sides of jaw; three rows of slightly curved, conical teeth at anterior of lower jaw, two rows on sides of jaw; vomer with two widely separated oval patches of slightly recurved, conical teeth arranged in 3–4 rows; each palatine with an elongate patch of large, conical teeth arranged in 3–4 rows.

Predorsal area partly covered with cycloid scales, these extending forward to about a vertical through posterior edge of preopercle, with a narrow median triangular patch of scales reaching further forward to a vertical about midway between posterior margin of eye and posterior edge of preopercle; operculum with 3–4 small cycloid scales at anterodorsal corner; about 20–30 small cycloid scales arranged in an irregular arc extending around ventral part of cheek from posteroventral edge of eye to lower part of preopercle; pectoral-fin base covered with small cycloid scales; prepelvic area covered with small cycloid scales forward to edge of branchiostegal membranes; two rows of scales anteriorly and one row posteriorly between pelvic-fin bases; body scales ctenoid from below middle of first dorsal fin posteriorly to caudal peduncle; a narrow wedge of cycloid scales above ctenoid scales extending back to second dorsal origin; belly scales cycloid.

Gill opening extends forward to a vertical midway between eye and posterior margin of preopercle (Fig. 2); gill filaments short; gill rakers absent; positions of sensory pores and free neuromasts (free neuromasts) on head as shown in Figure 2.

First dorsal fin low, the origin well behind pelvic-fin insertion, above middle of second segmented pelvic-fin ray; second dorsal fin immediately behind, but separate from, first dorsal fin; segmented dorsal-fin rays bifid; anal-fin origin below first segmented ray of second dorsal fin; first segmented anal-fin ray unbranched, other segmented rays bifid; pectoral fin with broadly rounded distal margin, the central rays longest, the fin tip reaching to vertical through posterior tip of pelvic fin; uppermost ray and lowermost ray of pectoral fin unbranched, other rays bifid; pelvic-fin origin below lower part of pectoral-fin insertion and posterior margin of opercle; pelvic fin reaches just short of anus; segmented pelvic-fin rays unbranched; basal one-fifth to one-fourth of each ray connected by membrane (membrane possibly torn distally); caudal fin with concave posterior margin and convex upper and lower margins; central three caudal-fin rays distinctly shorter than three rays above and three rays below; most rays multiply branched, with three or four terminal tips.

Coloration of paratype in alcohol. — Head and body light brown; top of head with scattered melanophores; thin line of enlarged melanophores extending from ventral margin of eye to just behind posterior end of jaws; two broader lines of enlarged melanophores along posteroventral margin of eye over upper quarter of cheek; nape and dorsal margin of opercle with scattered mottling; body with extensive mottling forming about 12 short, more-or-less vertical bars; bars shorter, more rounded posteriorly, becoming oval spots on caudal peduncle; slightly curved vertical mottling below and between midside bars; dorsal with wavy mottling sometimes forming a V, with apex between midside bars; short vertical bar on midside at caudal-fin base; belly pale, largely free of melanophores; pectoral-fin base with small brown spot dorsally and small brown spot ventrally; first dorsal fin with few melanophores along distal margin and oblique band of melanophores from middle of first dorsal spine to base of fin between fifth and sixth spines; other fins whitish hyaline to hyaline.

Holotype is paler, with the dorsal and ventral mottling on the body weakly developed. Field notes from J. E. Randall indicate the freshly dead paratype was pale with yellow markings.

Osteology. — The following description of the osteology of *P. springeri* refers only to features that differ from those given by Springer (1983) for *Xenisthmus clarus*.

Cranium (Figs. 3–4): *Paraxenisthmus springeri* differs notably from *X. clarus* (see Springer, 1983, fig. 3) in the following: the skull is generally more rugose, with well-developed su-
Fig. 3. Skull of Paraxenisthmus springeri in (A) dorsal view; (B) right lateral view (reversed); and (C) ventral view. Abbreviations: BL—Baudelot’s ligament (left ligament not shown); BO—basioccipital; EPO—epioccipital; EXO—exoccipital; F—frontal; IC—intercalar; ICPTL—intercalar/posttemporal ligament (right ligament not shown); IHPSL—interhyal/parasphenoid ligament (right ligament not shown); LE—lateral ethmoid; ME—median ethmoid; PO—prootic; PS—parasphenoid; PTO—pterotic; S—sphenotic; SO—supraoccipital; V—vomer.

The praecipital crest and epioccipital spines; the vomer possesses two widely separated oval patches of conical teeth, each patch on anterolateral wing of vomer; the vomer is indented anteriorly (vs truncated); and the cordlike ligaments from each interhyal attach more medially and posteriorly on the parasphenoid (postero mediad vs anterolaterad of internal carotid foramina).

Jaws, suspensorium and superficial bones of the head (Figs. 4–5): Paraxenisthmus springeri differs from X. clarus (see Springer, 1983, fig. 5) in the following: the nasal bones are smaller; each palatine possesses an elongate patch of depressible, conical teeth (vs edentate in X. clarus); the posterior (opercular) process of the hyomandibula is shorter; the quadrate is narrower and the metapterygoid is expanded anteriorly to contact the ectopterygoid (vs metapterygoid and ectopterygoid separated from each other by a cartilage rim along the dorsal surface of the relatively broad quadrate); tiny coronomeckelian bones are present (vs absent); the rostral lacks a cartilaginous dorsal tip; the angulararcicular is shorter; the interopercle is less elongate and lacks a ventral notch; and the subopercle is deeper.

Hyoid and branchial arches (Figs. 6–7): The hyoid and branchial arches of P. springeri differ from those of X. clarus (see Springer, 1983, figs. 9, 11) in the following details: the urohyal lacks a deep notch in its posterior margin; anteromedial process on interhyal for attachment of interhyal/parasphenoid ligament is smaller and positioned nearer to medial tip of interhyal;
branchiostegal 3 lacks expanded proximal head; dorsal and ventral hypohyals are autogenous instead of fused; basibranhials 1 is larger with a prominent, rodlike posterior process (vs process absent); basibranhials 3 and 4 are present as small cartilage nubbins (vs absent); ceratobranhials 1–3 each have flattened posterior expansions (vs only ceratobranhial 3); ceratobranhial 5 relatively broad (vs narrow and rodlike); epibranchial 3 lacks well-developed cartilage-tipped uncinate process; gill rakers or ossified gill raker rudiments absent (vs present on epibranchials 1, on inner and outer surfaces of ceratobranhials 1–4, and variably on hypobranhial 1); infrapharyngobranchial 1 present as short cartilage rod (vs present as small nubbin of cartilage); infrapharyngobranchial 2 broad, with well-developed tooth plate and two anterior cartilage heads (vs edentate and rodlike with a single anterior cartilage head); infrapharyngobranchial 4 present as a cartilage nubbin (vs absent); and infrapharyngobranchial 4 tooth plate larger.

Paired fins and girdles (Figs. 8–9): The pectoral and pelvic fins and girdles of P. springeri closely resemble those of X. clarus (see Springer, 1983, figs. 5, 14–15) except in the following details: there are 18 (vs 17) pectoral-fin rays; a small rodlike dorsal postcleithrum is present (vs absent); there are no lateral extrascapular bones (vs two or three in X. clarus); the supracleithrum is not closely associated with the dorsal notch in the lateral process of the cleithrum; the ventral (intercalar) arm of the posttemporal bone is longer; all segmented pelvic-fin rays are unbranched (vs outermost four branched in X. clarus); and the pelvis is less complex, lacking an anterodorsally projecting laminar process.

Vertebrae and unpaired fins (Fig. 10): In addition to minor differences in fin-ray numbers, the vertebrae and unpaired fins of P. springeri differ from those of X. clarus (see Springer, 1983, fig. 17) in the following details: the pterygiophore that supports the first segmented dorsal ray lacks an autogenous middle radial; there are 15 (vs 16) epipleural ribs; and there is no autogenous cartilage (unossified uroneural vestige?) ventral to the second epural.

Etymology.—The specific name is for Dr. V. G. Springer in recognition of his contributions to the systematics of xenisthmids and other fishes.
Fig. 7. Paraxenisthmus springeri: (A) lateral view (reversed) of right hyoid bar; and (B) right lateral view (reversed) of anterior median hyoid and branchial elements. Abbreviations: ACH—anteri or ceratohyal; BB1—basibranchial 1; BH—basihyal; BR1,6—bran chiostral rays 1 and 6; DHH—dorsal hypohyal; IH— interhyal; IHPSL—interhyal/parasphenoid liga ment; PCH—posterior ceratohyal; UH—urohyal; VHH—ventral hypohyal.

Remarks.—This species is apparently piscivo rous, feeding on relatively large fishes. The gut of the paratype contained a large (5 mm), undigested portion of a blennioid, consisting of the caudal skeleton and terminal six vertebrae.

Monophyly and phylogenetic position.—A cladistic analysis of the Xenisthmidae is currently being undertaken by ACG. The following discussion of xenisthmid relationships is provided largely as a justification for naming the new genus (i.e., establish that it cannot be assigned to any existing xenisthmid genus without rendering that genus poly- or paraphyletic).

Springer (1983) placed Allomicrodesmus, Par axenisthmus (then undescribed), Tyson, and Xen isthmus in the gobiid subfamily Xenisthminae (elevated to familial status by Hoese, 1984) on the basis of the following three synapomorphies: lower lip with an uninterrupted, free ven tral margin; premaxillary ascending process greatly reduced or absent; and rostral cartilage ossified. He predicted several additional synapomorphies but lacked information for Allomicrodesmus and Paraxenisthmus: loss of basibranchial 4 and pterosphenoid, and added an additional synapomorphy (ceratobranchial 5 rodlike). He also listed a large number of potentially informative characters for Rotuma, Tyson, and Xen isthmus and discussed character states of some of these for Allomicrodesmus and Paraxenisthmus; he did not, however, discuss phylogenetic relationships of xenisthmid genera.

Paraxenisthmus and the gobiid Stonogobiops Polunin and Lubbock are the only gobiod fishes that are known to possess palatine teeth (Hoese and Randall, 1982). Although palatine teeth are primitively present in perciform fishes, we argue that their presence in Paraxenisthmus and Stonogobiops has resulted from apomorphic reversal. Because available evidence suggests that these genera are not closely related, we further argue that these reversals have occurred independently (i.e., autapomorphically) in each genus. Paraxenisthmus possesses an additional, striking autapomorphy: quadrate relatively narrow and metapterygoid expanded anteriorly to discovery of Rotuma, Springer (1988) rejected two of these synapomorphies (loss of basibranchial 4 and pterosphenoid) and added an additional synapomorphy (ceratobranchial 5 rodlike). He also listed a large number of potentially informative characters for Rotuma, Tyson, and Xen isthmus and discussed character states of some of these for Allomicrodesmus and Paraxenisthmus; he did not, however, discuss phylogenetic relationships of xenisthmid genera.
contact ectopterygoid. In other gobioids, the metapterygoid and ectopterygoid bones are separated from each other by a dorsal cartilage rim on the quadrate.

Paraxenisthmus lacks three of Springer’s (1988) xenisthmid synapomorphies: basibranchial 3 present instead of absent; tiny coronomeckelian bone present instead of absent; and ceratobranchial 5 broad instead of rodlike. In addition, it is relatively plesiomorphic in possessing dorsal postcleithrum; relatively broad infrapharyngobranchial 2, with well-developed tooth plate and two anterior cartilage heads (vs rodlike and edentate with single anterior cartilage head, or absent); cartilaginous infrapharyngobranchial 4 tooth plate (vs reduced or absent); and anteriorly notched vomer (vs truncate or pointed). Information on these characters is lacking for Allomicrodesmus.

Paraxenisthmus shares a single synapomorphy with Tyson (ceratobranchial 1–4 without gill rakers or teeth). It also resembles Tyson in possessing vomerine teeth. Vomerine teeth are known from only a few gobioid genera, including some species of the microdesmid Ptereleotris Gill, the gobids Vomerogobius Gilbert, Palatogobius Gilbert, Stonogobiops, and one species of Cryptocentrus (Ehrenberg) Cuvier and Valenciennes, the eleotrids Kimberleyeleotris Hoese and Allen, Bostrychus Lacepède, Gobiomorus Lacepède, and the odontobutid Percottus Dybowski (Hoese and Randall, 1982; Akihito, 1986; Hoese and Allen, 1987). Without knowledge of the relationships of the Xenisthmidae to other gobioids, it is not possible to determine whether the presence of vomerine teeth in Paraxenisthmus and Tyson is apomorphic within the Xenisthmidae.

Allomicrodesmus, Rotuma, and Tyson share a single synapomorphy with Paraxenisthmus (all pelvic soft rays simple). Paraxenisthmus also shares a synapomorphy with Rotuma and Tyson (epibranchial 1 without gill rakers or teeth), but information on this character is lacking for Allomicrodesmus. Some species of Xenisthmus also lack rakers or teeth on epibranchial 1.

Springer (1983, 1988) did not present any autapomorphies for Xenisthmus; we hypothesize that the genus is monophyletic on the basis of a single specialization (branchiostegal 3 with an expanded proximal head; see Springer, 1983, fig. 9). Xenisthmus and Paraxenisthmus are more plesiomorphic than other xenisthmids in lacking at least the following eight specializations: (1) scales absent; (2) first dorsal fin with fewer
Fig. 11. Hypothesized relationships of xenisthmid genera. Numbers refer to apomorphies that support the relationships shown; those enclosed by parentheses require verification in Allomicrodesmus. (1) Lower lip with uninterrupted, free ventral margin; (2) premaxillary ascending process greatly reduced; (3) rostral cartilage ossified; (4) basibranchial 2 absent; (5) hypobranchial 3 reduced or absent; (6) palatine teeth present; (7) quadrate narrow and metapterygoid expanded to contact ectopterygoid; (8) basibranchial 3 absent; (9) coronomeckelian bone absent; (10) ceratothranclal 5 rodlike; (11) dorsal postcleithrum absent; (12) infrapharyngobranchial 2 reduced and edentate; 12', infrapharyngobranchial 2 absent; (13) infrapharyngobranchial 4 absent; (14) infrapharyngobranchial 4 toothplate reduced; 14', infrapharyngobranchial 4 toothplate absent; (15) vomer truncate or pointed; (16) proximal tip of branchiostegal ray 3 expanded; (17) scales absent; (18) sensory pores absent; (19) fewer than six first dorsal-fin spines; (20) all segmented dorsal-fin rays simple; (21) all segmented anal-fin rays simple; (22) pectoral-fin rays simple; (23) fifth segmented pelvic-fin ray vestigial or absent; (24) pelvic-fin spine vestigial or absent.

Paraxenisthmus
Xenisthmus
Allomicrodesmus
Rotuma
Tyson

16
(12,14'), 17-24
6,(7)
(8-15)
1-3,(4,5)

than six spines; (3–5) all segmented dorsal-, anal- and pectoral-fin rays simple; (6) fifth segmented pelvic-fin ray vestigial or absent; (7) pelvic-fin spine vestigial or absent; and (8) sensory canal pores on head absent. They are also more pleiomorphic than at least Rotuma and Tyson in possessing infrapharyngobranchial 2 and an infrapharyngobranchial 4 toothplate. Xenisthmus and Paraxenisthmus share a condition that is apparently unique among gobioids: metapterygoid expanded dorsally to articulate with anterolateral edge of sphenotic. However, the metapterygoid is highly modified in Rotuma, in which it is reduced and fused to the symplectic (Springer, 1988), and Tyson, in which it is absent. Information on the structure of the metapterygoid of Allomicrodesmus is lacking. It is, therefore, not possible to evaluate whether the metapterygoid expansion is a valid synapomorphy of Xenisthmus and Paraxenisthmus or whether it was present in the common ancestor of the Xenisthmidae.

The most parsimonious interpretation of the distribution of the above characters is that Paraxenisthmus is the sister group of a monophyletic group that includes all other xenisthids and that Xenisthmus is the sister group of a clade that includes Allomicrodesmus, Rotuma, and Tyson (Fig. 11). In accepting these relationships, we argue that Paraxenisthmus and Tyson have independently lost teeth and rakers from ceratobranchials 1–4 (and gained vomerine teeth?). Interpretation of the remaining apomorphic characters shared by Paraxenisthmus and certain xenisthmid genera is equivocal. For example, the absence of the branched pelvic-fin rays may have evolved independently in Paraxenisthmus and the common ancestor of the Allomicrodesmus-Rotuma-Tyson clade, or it may have evolved in the common ancestor of the Xenisthmidae, then reversed in Xenisthmus. Both hypotheses require two evolutionary steps and are, therefore, equally parsimonious.

Acknowledgments

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New Species of Tree Frog of the Genus *Hyla* (Anura: Hylidae) from Northern Honduras

**JAMES R. McCranie, LARRY DAVID WILSON, AND KENNETH L. WILLIAMS**

*A new species of *Hyla* is described from the western portion of the Cordillera Nombre de Dios of northern Honduras. The new species is unusual in having both a tuberculate dorsum and a bold ventral pattern. Based on adult morphology and osteological characteristics, the new species appears to be most closely related to *H. lancasteri* of Costa Rica and western Panamá.*

**Hyla insolita** sp. nov.

*Holotype.—University of Kansas, Museum of Natural History (KU) 219984, an adult male, from 2.5 km (airline) NNE La Fortuna (15°26′N, 87°18′W), 1550 m elevation, Cordillera Nombre de Dios, Departamento de Yoro, Honduras, collected 14 Aug. 1991 by J. R. McCranie, K. L. Williams, and L. D. Wilson. Original number LDW 9587.*


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